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Resistance to *Phytophthora infestans* in diploid and tetraploid potato families. 1. Resistance in detached leaflets

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Abstract. Potato families, segregating for resistance to *Phytophthora infestans*, were tested repeatedly to evaluate the distribution of resistance to *P. infestans*, the repeatability of testing results and correlation between resistance and some other characters. Four diploid and four tetraploid families were evaluated together with their parents and with potato cultivars used as standard. For all inoculations a virulent fungus isolate MP 245 was used. Leaflets were collected from plants growing in the field (summer tests) or in a glasshouse (autumn and spring tests). Segregation of major genes determining resistance was detectable in most families. In families originating from mating a resistant parent with a susceptible partner some progeny genotypes with resistance level of the resistant parent could be identified. In families originating from two parents showing only some resistance, a transgression of resistance could be found in the progeny. The expression of resistance depended on testing conditions. Some genotypes were consistently superior or inferior in resistance under all testing conditions, but often repeated evaluations of genotypes did not provide consistent results and significant interactions genotypes × tests were detectable.

Key words: detached leaflets, *Phytophthora infestans*, potato, resistance evaluation.

Introduction

Although *Phytophthora infestans* is the most important potato pathogen (ANONYMOUS 1992) and there are many available sources of resistance to it, the progress in the development of resistant potato cultivars is disappointing

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(ROSS 1986). Our understanding of genetic variation in resistance or its evaluation methods may not be satisfactory.

Development of potatoes resistant to *P. infestans* is an important element in the breeding program at the Młochów Research Center. To get more information on the inheritance of resistance to *P. infestans* and on the methods of its evaluation, selected diploid and tetraploid genotypes, obtained in this program, were utilized as parents to develop progeny genotypes evaluated repeatedly under various testing conditions. In this paper the results of testing detached leaflets are reported.

Material and methods

Evaluated potato genotypes

Genotypes of diploid (D) and tetraploid (T) families were evaluated together with their parents and standard cultivars (Bzura, Sokół and Irys) at the Młochów Research Center. They were sown in 1991 or in 1992. The reaction to *P. infestans* was evaluated in first year seedlings grown in the field (spaced 62 × 62 cm) and in their tuber progeny grown either in the field (spaced 40 × 60 cm) or in a glasshouse in autumn or spring (usually in 8-cm pots).

Two diploid (D4 and D5) and three tetraploid families (T5, T6 and T7) were sown in 1991 (Table 1). All genotypes of each family were evaluated both in 1991 and 1992. Those superior in resistance of leaflets or tubers, were propagated and evaluated also in 1993 and 1994, if virus infection did not interfere with their further propagation.

Two diploid (D7 and D8) and one tetraploid family (T9) were sown in 1992 (Table 1). Many seedlings from each family were grown to assess, as far as possible, the whole range of reactions to *P. infestans*. In diploid families young seedlings were inoculated with PVY and PVM to eliminate all those susceptible to these viruses. In spring 1993 the resistance was evaluated only in T9. Genotypes of each family, which in 1992 were found to be extreme in leaflet or tuber reaction (resistant or susceptible) were propagated and evaluated in 1993 and 1994. In autumn 1993 the plants growing in the glasshouse received improved growth conditions (planting into 18 cm pots and additional illumination).

Parents and standard cultivars were propagated and evaluated in triplicate together with the genotypes of each family. The parents differed in their resistance level to *P. infestans*. In diploid families only one of the parents (D2-411, D2-429, D3-338 or DG 88-201) was resistant to *P. infestans*. Among

Table 1. The evaluated diploid (D) and tetraploid (T) potato families

Family symbol	Parents ♀	Parents ♂	resistance of parents[1]	No. of genotypes
Families sown in 1991				
D4	DW 84-1457	D2-429	S × R	52
D5	D3-338	DG 82-198	R × S	52
T5	T3-436	PS 1300	M × M	62
T6	T3-423	PS 137	M × M	43
T7	T3-423	PS 1300	M × M	28
Families sown in 1992				
D7	D2-411	DW 84-1457	R × S	617
D8	DG 88-201	DW 84-1457	R × S	359
T9	T3-243	PS 137	M × M	729

[1] R – resistant, M – moderately resistant, S – susceptible.

resistant ancestors of all these parents are both *Solanum verrucosum* PI 195170 and *S. microdontum* PI 265579. There were two parents susceptible to *P. infestans* in diploid families (DG 82-198 and DG 84-1457). DW 84-1457 was outstanding in resistance to viruses and DG 82-198 originated from *S. phureja*, which had some resistance to *P. infestans*. In all tetraploid families a late maturing parent (PS 137 or PS 1300) was crossed with an early maturing one (T3-243, T3-423 or T3-436). Both groups of tetraploid parents showed some resistance to *P. infestans*. The late maturing parents originated from the resistant clone I 1039, kindly provided by the International Potato Center in Peru; the early maturing ones were selected from the progeny of a resistant clone PS 646 originating from *S. demissum* hybrids.

The cvs. Bzura, Sokół and Irys were used as standard. According to cultivar assessment data (KAMASA 1995), expressed in 9-grade scale (9 = resistant), the cv. Bzura has the highest foliage resistance among Polish potato cultivars (8) and is late maturing, the cv. Sokół is susceptible (3) and mid-late while the cv. Irys is susceptible (3) and first early.

Evaluation of the resistance of detached leaflets

Lateral leaflets of the first terminal pair were collected from young, fully developed leaves. They were placed in plastic trays and inoculated on the abaxial side with one drop of inoculum per leaflet, placed near the midrib. Each drop contained ca 2000 sporangia in 0.04 ml. The inoculum was chilled before use to stimulate zoospore liberation. The trays, covered with glass (high

Table 2. Testing leaflets for their reaction to *P. infestans*

Test	Inoculation with *P. infestans*		
	replications (no.)	leaflets per repl. (no.)	date of inoculation
Families sown in 1991			
'91 summer 1	1	5	1991 Jul. 16
'91 summer 2	1	5	Aug. 7
'92 spring 1	1	3	1992 Mar. 3
'92 spring 2	1	3	Mar. 10
'92 summer 1	1	5	Jun. 23
'92 summer 2	1	5	Jun. 30
'92 autumn 1	2	3	Sep. 24
'92 autumn 2	2	3	Oct. 10
'93 summer 1	2	3	1993 Jun. 28
'93 summer 2	2	3	Jul. 7
'93 autumn 1	2	3	Oct. 7
'93 autumn 2	2	3	Oct. 14
'94 summer 1	2	3	1994 Jun. 23
'94 summer 2	2	3	Jun. 30
'94 summer 3	2	3	Jul. 8
Families sown in 1992			
'92 summer 1	1	3	1992 Jul. 2
'92 summer 2	1	3	Jul. 8
'93 spring	1	2	1993 Mar. 8
'93 summer	2	3	Jun. 29
'93 autumn 1	2	3	Sep. 29
'93 autumn 2	2	3	Oct. 8
'93 autumn 3	2	3	Oct. 15
'94 summer 1	2	3	1994 Jun. 23
'94 summer 2	2	3	Jun. 30
'94 summer 3	2	3	Jul. 8

humidity) were kept in a growth chamber at 16°C with constant illumination. After six days the leaflets were scored for lesion size and intensity of sporulation, using a 9-grade scale, from 1 (lesion covering the whole leaflet and extensive sporulation) to 9 (no lesion; possible necrotic spots, without sporulation). A highly virulent isolate of *P. infestans* MP 245 (ŚWIEŻYŃSKI et al. 1996) was used in all inoculations. Its original virulence was: 1, 2, 3, 4, 6, 7, 10, 11. Only in 1991 it was not used singly, but in a mixture with two other virulent isolates. The fungus isolate MP 245 was maintained on rye-agar. Before use, it was passed at least twice on tuber slices or leaves. The evaluated samples of each progeny genotype in each test consisted of 2-5 leaflets in 1-2 replications (Table 2).

Statistical analysis

Correlations were evaluated using the rank correlation coefficient of Spearman. The significance of differences between the genotypes was evaluated with the multiple range test of Duncan. Comparisons of groups of genotypes with their parents were based on the two sample t-test. Calculations were made with the package MSTAT-C.

Results

Reaction of parents and standard cultivars to *P. infestans* in individual tests

In individual tests the genotypes could be separated into several classes differing significantly in resistance level. The diploid resistant parents D2-411, D3-338 and DG 88-201 were resistant in most tests (mean reactions in individual tests ranged from 7.0 to 9.0); the diploid susceptible parents DG 82-198 and DW 84-1457 were susceptible in most tests (ranging from 1.0 to 6.9). The reactions of the diploid resistant parent D2-429 and that of the tetraploid parents were variable. The interaction genotypes × tests was evaluated in groups of tests performed in the same season. It was usually found to be statistically highly significant. The effects were sometimes considerable. E.g. in the test '92 summer 1 the diploid parent D2-429 had significantly less resistant leaflets (6.5) than T3-423 (9.0). On the other hand D2-429 in the two tests '92 autumn 1 and 2 had significantly more resistant leaflets (9.0) than T3-423 (5.5 and 4.8). In the reaction of standard cultivars, according to expectation, the cv. Bzura was usually resistant while the cv. Irys was usually susceptible. However, all the three cultivars were susceptible (ranging from 4.1 to 5.1) in the tests '92 autumn 2 and '93 spring, and moderately resistant in the tests '94 summer 1-3 (ranging from 5.1 to 6.9) (Table 3).

Correlation of results of resistance testing in individual genotypes within families

Rank correlation coefficients (r_s) were calculated for both tests performed in the testing season (upper part of Table 4 and first row of Table 5) and mean results of testing seasons (lower part of Table 4 and second row of Table 5).

In diploid families r_s was relatively high. It ranged from 0.638 to 0.918 for tests within season and from 0.528 to 0.825 for different testing seasons.

In tetraploid families r_s was variable. For tests within season r_s was usually as high, as in diploid families, but it was only 0.000 in family T6 for tests '91

Table 3. Reaction to *P. infestans* in detached leaflets of the parents of potato families sown in 1991 and 1992 and in standard cultivars

Test	Diploid parents						Tetraploid parents					Standard cultivars		
	D2 411	D2 429	D3 338	DG.82 -198	DG.88 -201	DW.84 -1457	PS 137	PS 1300	T3 243	T3 423	T3 436	Bzura	Sokół	Irys
Results of testing with families sown in 1991[1]														+
'91 summer 1							6.0 c	6.6 bc		8.0 a	6.3 c	7.2 b	2.7 d	1.1 e
'91 summer 2							9.0 a	8.8 a		7.0 a	7.1 a	8.1 a	3.1 b	1.1 b
'92 spring 1		6.2 b	9.0 a	2.0 c		1.0 d						2.5 c	1.5 cd	1.8 cd
'92 spring 2		9.0 a	9.0 a	5.9 b		5.8 b						3.0 c	2.7 c	2.0 c
'92 summer 1		6.5 c	8.1 ab	3.0 d		3.2 d	9.0 a	7.9 b		9.0 a	9.0 a	9.0 a	3.1 d	2.0 e
'92 summer 2		7.1 b	8.3 ab	2.7 c		3.0 c	9.0 a	7.3 b		9.0 a	9.0 a	9.0 a	2.8 c	1.3 d
'92 autumn 1		9.0 a	9.0 a	4.5 cd		3.4 d	5.4 bc	6.1 bc		5.5 bc	6.6 b	8.2 a	5.1 bc	3.4 d
'92 autumn 2		9.0 a	9.0 a	4.6 cd		3.3 d	4.3 cd	5.7 bc		4.8 cd	4.5 cd	4.3 cd	4.9 cd	5.1 bcd
'93 summer 1		7.2 b	9.0 a	5.1 c		3.2 d	4.7 c	4.3 c		4.9 c	5.2 c	4.9 c	5.0 c	4.2 c
'93 summer 2		6.0 bc	9.0 a	6.2 b		4.6 de	4.7 de	5.8 bcd		4.9 cde	5.0 cd	6.3 b	5.7 bcd	3.8 e
'93 autumn 1		4.7 bc	9.0 a	4.9 b		4.6 bcd	3.5 de	3.3 e		4.9 b	4.5 bcd	3.7 cde	3.7 cde	3.0 e
'93 autumn 2		1.4 e	9.0 a	2.7 de		2.2 de	5.7 b	5.3 b		4.6 bc	5.2 b	4.8 bc	2.4 de	3.4 cd
Results of testing with families sown in 1992[1]														
'92 summer 1	9.0 a				7.0 b	2.5 c	9.0 a		9.0 a			9.0 a	2.1 cd	1.0 d
'92 summer 2	9.0 a				7.0 b	3.5 c	9.0 a		9.0 a			9.0 a	2.8 cd	1.5 d
'93 spring							2.3 ab		1.3 b			5.0 a	4.1 ab	4.1 ab
'93 summer	7.4 ab				9.0 a	6.9 ab	6.4 ab		4.9 b			6.6 ab	6.2 ab	5.9 ab
'93 autumn 1	9.0 a				8.7 a	2.8 d	7.1 ab		4.5 cd			5.2 bc	2.7 d	3.1 cd
'93 autumn 2	9.0 a				7.7 ab	5.4 c	6.7 bc		6.1 bc			5.8 bc	2.8 d	2.1 d
'93 autumn 3	9.0 a				7.2 b	1.9 e	6.3 b		4.6 cd			5.8 bc	3.4 de	2.7 e
Results of testing with both groups of families[1]														+
'94 summer 1	8.8 a	7.2 b	9.0 a	6.7 b	9.0 a	4.8 d	6.4 b	6.4 b	6.1 bc	7.3 b	6.5 b	6.5 b	6.9 b	5.1 cd
'94 summer 2	8.8 a	8.0 a	8.6 a	6.7 b	9.0 a	3.6 d	6.4 bc	6.6 b	5.4 c	6.8 b	5.9 bc	6.0 bc	6.7 b	5.9 bc
'94 summer 3	8.8 a	7.5 b	7.4 b	5.3 de	8.8 a	6.3 cd	5.5 de	5.9 cde	4.9 e	5.1 e	5.7 cde	6.6 bc	5.9 cde	5.4 de

Results not differing significantly at the P=0.05 level are marked with the same letter in each test

[1] reaction is expressed in 9-grade scale (9 = resistant)

summer 1 and 2 and –0.022 in family T7 for tests '92 autumn 1 and 2. To explain this lack of correlation the respective correlation tables were evaluated (data not shown). It was found that in T6 most genotypes were resistant in both tests (they received grade 9.0); the few remaining ones reacted not consistently in both tests. In T7 the lack of correlation is due to the fact that in test '92 autumn 2 all genotypes of the family were susceptible (as shown in Table 3, leaflets of both parents and those of all standard cultivars were also susceptible in this test). The values of r_s for results obtained in different seasons depended on

Table 4. Rank correlation coefficients (r_s) between results of testing detached leaflets of individual genotypes in potato families sown in 1991; diploid (D4, D5) and tetraploid (T5, T6, T7) families

Correlated results	Family				
	D4	D5	T5	T6	T7
r_s for results of tests within season					
'91 summer tests 1 and 2	0.638**	0.680**	0.415**	0.000	0.717**
'92 spring tests 1 and 2	0.709**	0.694**	0.697**	0.737**	0.477**
'92 summer tests 1 and 2	0.752**	0.918**	0.979**	0.986**	0.944**
'92 autumn tests 1 and 2	0.744**	0.857**	0.409**	0.507**	–0.022
r_s for mean results of testing seasons					
'91 summer and '92 spring	0.647**	0.548**	0.507**	0.725**	0.443*
'91 summer and '92 summer	0.566**	0.825**	0.562**	0.714**	0.596**
'91 summer and '92 autumn	0.580**	0.792**	0.320*	0.128	–0.037
'92 spring and '92 summer	0.531**	0.568**	0.807**	0.857**	0.810**
'92 spring and '92 autumn	0.713**	0.544**	0.275	0.020	0.056
'92 summer and '92 autumn	0.528**	0.762**	0.189	0.020	–0.026

Significance of r_s at P = 0.05 (*) or P = 0.01 (**)

the season. In tetraploid families sown in 1991 mean results of the tests '91 summer, '92 summer and '92 spring were consistent in general, respective r_s values ranging from 0.443 to 0.857. On the other hand, tests '92 autumn were inconsistent with them, the respective r_s values ranging from 0.037 to 0.320 (Table 4). In the evaluation of the family T9 tests '92 summer and '93 spring were also inconsistent (r_s = 0.011).

Distribution of genotypes within families according to their reaction to *P. infestans*

The distribution of genotypes within families (Fig. 1) was based on mean results of the tests '92 summer (all families), '92 autumn (families sown in 1991) and '93 spring (family T9).

Table 5. Rank correlation coefficients (r_s) between results of testing detached leaflets of individual genotypes in families sown in 1992; diploid (D7, D8) and tetraploid (T9) families

Correlated results	Family		
	D7	D8	T9
r_s for results of tests within season			
'92 summer tests 1 and 2	0.690**	0.893**	0.976**
r_s for mean results of testing seasons			
'92 summer and '93 spring	–	–	0.011

Significance of r_s at P = 0.01 (**)

Table 6. Reaction of detached leaflets to *P. infestans* in summer and autumn of 1993 in genotypes selected in 1992 as extreme in reaction

Reaction[1]	No. of genotypes in family											
	D7				D8				T9			
	summer		autumn		summer		autumn		summer		autumn	
	R[2]	S[3]	R	S	R	S	R	S	R	S	R	S
9	10	5	1		43	7	6		6			
8-8.9	7	4	8	4	6	4	17		6	4		
7-7.9	9	4	10	3	5	7	10	2	17	2	1	
6-6.9		6	4	4	2	4	9	3	16	3	10	
5-5.9		3	3	2		1	5	1	12	6	16	1
4-4.9	3	1	1	2		1	4	4	3	3	28	4
3-3.9		1	1	1			5	5	2	3	8	7
2-2.9			1	5				8	2	1	1	9
1-1.9				3				1				1
Total	29	24	29	24	56	24	56	24	64	22	64	22
Mean[4]	7.9	7.2	7.0	5.1	8.7	7.7	7.0	4.0	6.6	5.8	4.9	3.2
Dif.[5]		0.7		1.9*		1.0**		3.0**		0.8*		1.7**

[1] in 9-grade scale (9 = resistant).

[2] R – genotypes with detached leaflets resistant in 1992 (grade 9).

[3] S – genotypes with detached leaflets susceptible in 1992 (grade < 4).

[4] mean reaction level in 1993.

[5] difference between the mean reaction level of R and S genotypes, significance at P = 0.05 (*) or P = 0.01 (**).

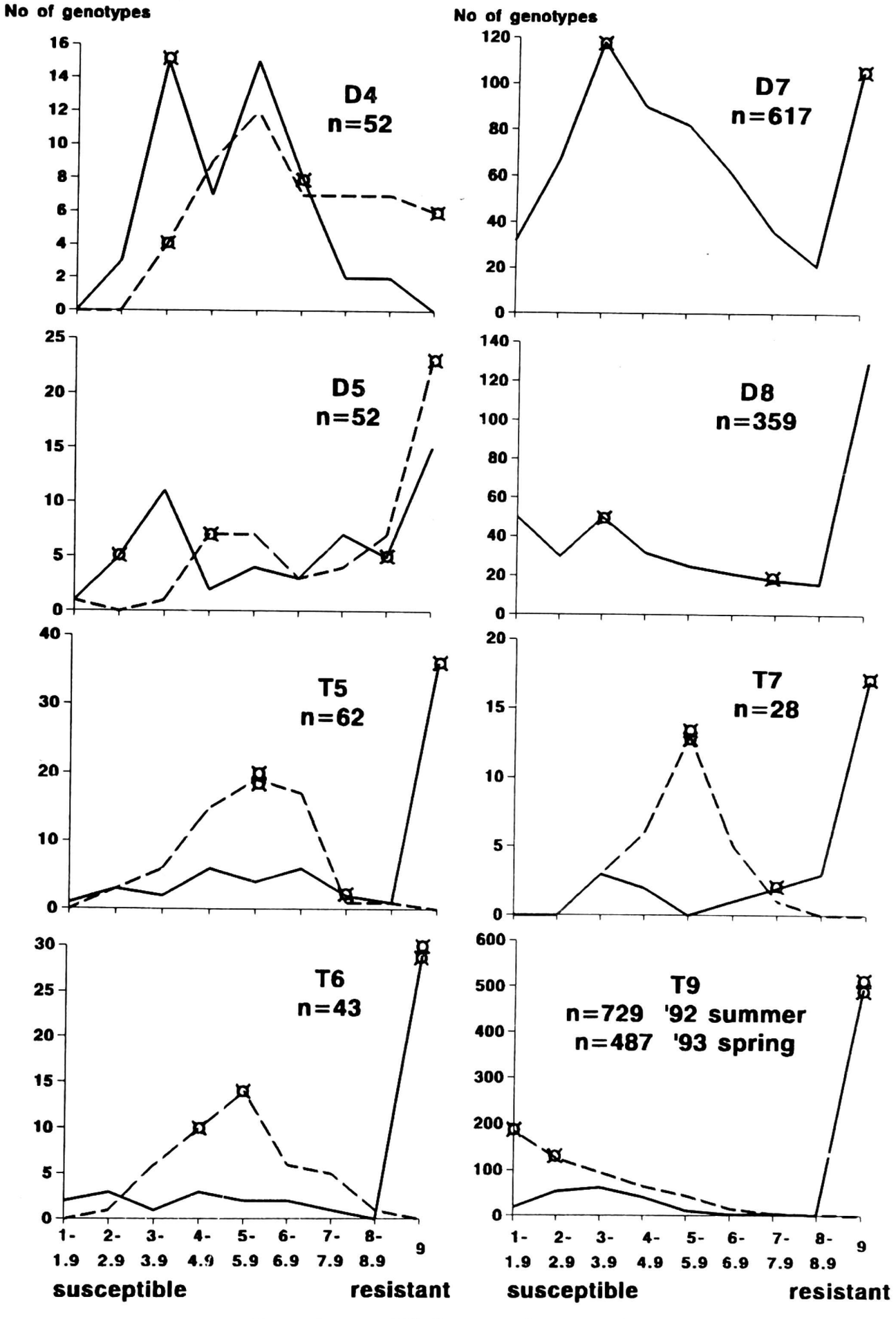

Fig. 1. Distribution of genotypes in individual potato families according to their reaction to *P. infestans* in detached leaflets

_____ '92 summer, - - - - '92 autumn (for T9 test '93 spring), ✧ – resistance level of the parents, n – no. of genotypes

In individual families the mean difference between both groups was usually small, ranging from 0.7 to 1.0 grades in summer and from 1.7 to 3.0 in autumn of 1993 (Table 6).

Further evaluation (in 1994) of progeny genotypes at least equal in their leaflet resistance to the more resistant parent in 1993

In 1994, those genotypes were evaluated, which were at least as resistant, as their more resistant parent in both summer and autumn evaluations in 1993. Only 1-6 such genotypes were found in individual families (Table 7). In families T5, T6 and T9 the selected genotypes were significantly superior to a more resistant parent in 1994. In the remaining families they were usually not significantly different from their more resistant parent.

Discussion

Foliage resistance to *P. infestans* evaluated by testing detached leaflets

Three factors determine the reaction of detached leaflets: the fungus pathogenicity, the resistance level of the potato and testing conditions.

Much attention was paid to using a pathogenic inoculum. MP 245 was the most virulent pathotype available. However, its pathogenicity was not quite stable (ŚWIEŻYŃSKI et al. 1996). The detectability of two peaks in some progeny distributions indicates that the resistance due to the presence of major genes was not always overcome by this isolate.

The resistance level of most diploid resistant parents was so high and that of diploid susceptible parents was so low that under various testing conditions they were consistenty found to be respectively resistant or susceptible (Table 3). Similar results could be obtained with other fungus isolates and other potato genotypes. STEWART (1990) tested leaflets collected from plants of various age. Over a broad age range leaflets of differentials R2 and R5 were consistenty resistant and those of R1 were consistenty susceptible to the fungus isolate 1.3.4.7.8.10.11; ŚWIEŻYŃSKI et al. (1991) tested two potato genotypes (DG 85-3437 and DG 84-325) during four years. In this period 74 tested leaflets of DG 85-3437 were never found to be susceptible, while all the 78 tested leaflets of DG 84-325 were susceptible.

Many evaluated genotypes did show a variable reaction, depending on the test. A significant interaction genotypes × tests was detectable in repeated testing of parents and standard cultivars. It was sometimes so high that the correlation coefficients between results of evaluation in different tests were

very low (Tables 4 and 5), the distribution of genotypes within families could differ considerably, depending on testing period (Fig. 1) and in successive years the genotypes could change their reaction from resistance to susceptibility and vice versa (Table 6).

Several factors could be responsible for this instability. The resistance of plants is changing with age (UMAERUS 1970) and evaluation in the period of rapid growth in '94 summer could be responsible for small differences in resistance between the standard cultivars (Bzura, Sokół and Irys). The resistance was reported to be weaker under short day conditions (UMAERUS 1970) or at low light intensity (VICTORIA, THURSTON 1974). These factors could be responsible for the weak expression of resistance in the tests '92 autumn, and '93 spring. The resistance of genotypes is known to depend on such factors, as temperature, photoperiod and light intensity (DARSOW et al. 1988, TURKENSTEEN 1989, NEWTON et al. 1993) and the relation between resistance and maturity was found to depend on the year of testing (DARSOW 1989). It is likely that differences in the reaction of individual genotypes to varying testing conditions could be responsible for the low repeatability of genotype evaluations in successive years (Table 6). If the resistance of the leaflets is not strongly expressed, even individual leaflets of an apparently homogeneous sample may differ considerably in reaction. This was found in the described experiments (data not presented) and was also reported by other authors (CARNEGIE, COLHOUN 1982, STEWART 1990).

Detached leaflets are used for evaluation of potato foliage resistance to *P. infestans* (ZARZYCKA, SUJKOWSKI 1988). The results obtained indicate that care must be taken to test detached leaflets which do not differ in reaction from leaflets of plants, subjected to the infection pressure of the fungus in nature. This is obtained easily if differences in resistance are great, as was found with some resistant and susceptible parents in this report. If differences in resistance are small and genotypes differ in maturity or their specific requirement for resistance expression, the results of leaflet testing may be of a limited value. Increasing the sample size is unlikely to be helpful (as shown in Tables 4 and 5, samples of 3 leaflets in 2 replications were sufficient to provide a reasonable repeatability of evaluations in successive tests). The problem is to obtain leaflets suitable for testing.

Segregation of potato genotypes for resistance of their detached leaflets to *P. infestans*

The distribution of genotypes within individual families was so variable, depending on the testing period, that few general conclusions may be drawn. The detectability of two peaks in the distribution of genotypes in most families

(Fig. 1) is an indication that major genes for resistance segregate in these families. This could be expected, as a similar segregation was found in families, from which some resistant parents were selected (ŚWIEŻYŃSKI et al. 1991).

In most diploid families obtained from mating a resistant parent with a susceptible partner genotypes could be identified with the resistance level of the more resistant parent; in tetraploid families, in which both parents had some resistance, genotypes more resistant than their parents could be found. The difference was often statistically significant (Table 7). A transgression in resistance was also obtained by JASHINA (1968) and BLACK (1970). Its nature could not be clarified by the reported experiments.

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