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A comparison of tuber slice and whole tuber tests for the assessment of potato resistance to tuber blight (*Phytophthora infestans* (Mont.) de Bary)

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Abstract

The resistance of potato tuber tissues to colonization by *Phytophthora infestans* was compared in 10 selected cultivars in two trials: on tuber slices and whole tubers with cut rose ends. When resistance to sporulation was used as the discriminating criterion, the selected cultivars segregated in a distinctly different order than when arranged according to other resistance components. Both the tuber slice test and the whole tuber test allowed resistance to sporulation to be assessed in the tested group of cultivars. The results obtained in both trials were reproducible and both criteria, i.e. the percentage of mycelium-covered area as well as sporulation intensity were equally useful for the assessment. No significant influence of the fungal growth though the tuber slice tissue was observed on the assessment of sporulation in comparison to the whole tuber test where the fungus grew directly on the wounded tissue after inoculation. Assessment of the percentage of the area of the tuber slice exhibiting visible necrosis was found to be useless due to the lack of correlation with two criteria of resistance to colonization used in the whole tuber test, i.e. the rate and depth of penetration. The most useful parameter of the whole tuber test appeared to be assessment of the depth of penetration of the tuber tissues. This parameter showed the least variability and good correlation with other criteria used to evaluate resistance to colonization.

INTRODUCTION

An important goal of resistance breeding is producing verieties of potato tubers resistant to blight. Tubers can have various degrees of resistance to infection by the fungus, *Phytophthora infestans*, and to penetration of internal tissues by its mycelium as well as being able to affect the reproduction ability of the

fungus in various ways. The correct choice of the proper testing methods is of great importance for the evaluation and selection of breeding materials.

Plant resistance is a complex feature and only after various criteria are applied can its particular elements be discerned. Various methods of inoculation reveal various types of resistance. The inoculation of whole, undamaged tubers, used by Stewart et al. (1983) and Wastie et al. (1987) allows the resistance to infection of tissues surrounding the tuber and of lenticels and eyes to be evaluated. This method of inoculation is most reminiscent of natural conditions where whole tubers are infected in the soil during vegetation. The inoculation of injured tubers or tuber slices immediately after removal allows, depending on the criterion used, the resistance of the internal tissues to colonization and sporulation of the pathogen to be evaluated. Various inoculation techniques are used here. Tubers injured by passing a roller with metal spikes over their surface (Bjor, 1987), by using a corkbore (Lapwood, 1965; Durska, 1976), tuber halves (Lapwood, 1965; Pietkiewicz, 1976; Durska, 1976; Schober and Hoppner, 1972) or bits of tissues cut from a tuber (Langton, 1972; Deal et al., 1974; Durska, 1976) have been used for experimental infection.

The slice test was worked out by Lapwood (1965): 11 mm thick tuber slices were inoculated using discs of filter paper submerged in inoculum. Piotrowski et al. (1973) modified this test by introducing a drop of inoculum between two 5 mm thick slices. The slice test was also used by Pietkiewicz (1976), Durska (1976) and Darsow (1978) to evaluate the resistance of tubers.

When injured tubers, tuber halves or bits of tissue taken from tubers were evaluated, the resistance of tuber flesh to colonization was also assessed (Lapwood, 1965; Schober and Hoppner, 1972; Durska, 1976; Bjor, 1987) as well as its resistance to sporulation (Schober and Hoppner, 1972; Pietkiewicz, 1976). In the case of the slice test, mainly resistance to sporulation was evaluated (Lapwood, 1965; Schober and Hoppner, 1972; Piotrowski et al., 1973; Pietkiewicz, 1976; Darsow, 1987). Only Darsow (1987) graded the browning of the flesh on the surface of the tuber, which can be considered to be an evaluation of the resistance of the flesh to colonization.

The tuber slice test is one of the most commonly used laboratory methods of assessing the resistance of potato tubers to late blight. Lapwood (1965) and Piotrowski et al. (1976) considered it the most convenient method. It is often used in studies on the resistance of cultivars and in mass tests in the evaluation of potato breeding material (Pietkiewicz, 1977; Bhatia and Young, 1985;

Darsow, 1987; Zarzycka, 1987).

In the evaluation of the resistance of breeding materials it is very important to pick an evaluation method which tests the most significant resistance trait and is, at the same time, simple to use and gives reproducible results. In the search for more precise methods of assessing and segregating the studied material in respect to the resistance of tubers to late blight, a comparative evaluation of the suitability of 2 laboratory methods of inoculation of tubers, that is, the tuber slice and tuber test along with several criteria of tuber flesh resistance to colonization and sporulation, was undertaken. The study was aimed at finding an answer to the question if using these two tests, a similar segregation of the material in respect to tuber resistance can be obtained, do they give reproducible results and which of these methods is best suited for the evaluating of the resistance of potato breeding material.

MATERIAL AND METHODS

The studies were carried out in 1985-1987 on 10 cultivars used as standards of resistance or susceptibility representing groups of varieties of various degrees of earliness: Irys, Cynia, Jaśmin, Dalia, Pola, Sokół, Sowa, Bronka, Bzura, Tarpan. Two methods of tuber inoculation were used:

I. Tuber test: the tuber was inoculated by placing a disc of filter paper saturated with a suspension of spores on the cut rose-end of the tuber. The following three criteria were used to assess the resistance of tubers to colonization of its tissues (Zarzycka, 1988):

1) the area of the browned (necrotic) tissue on the tuber longitudinal section - - estimated as a percentage,
2) the depth of penetration of the tuber by the pathogen (depth of the brown, necrotic tissue), in mm,
3) the rate of penetration of the tuber tissues by pathogen according to the formula: $r = \frac{1}{2}\left(\lg \frac{1}{1-x_1} - \lg \frac{1}{1-x_2}\right)$ where: x_1 and x_2 denote the percentage of browned area on the tuber longitudinal section 4 and 6 days after inoculation, expressed as decimals (Piotrowski et al., 1973), as well as the following criteria for evaluation of tuber resisatance to sporulation (Zarzycka, 1988),
4) the development of mycelium on the injured, inoculated tuber surface, assessed as the percentage of mycelium-covered surface,

5) sporulation intensity (development of conidiophores) on the injured surface of the tuber. The following scale was used:

0 – lack of conidiophores

1 – few conidiophores (average of 25/mm²), short, poorly branched

2 – numerous conidiophores (average 100/mm²), long, branched

3 – very numerous conidiophores, long, highly branched, forming a nap-like fur.

II. The slice test: two 10 mm thick slices were cut from the middle part of a tuber and inoculated by placing a drop of inoculum between them. Due to the limited thickness of the slice it was not possible to apply the same criteria in the evaluation of flesh resistance as in the tuber test. The browning (necrosis) of the tissue on the upper external surface of the slice was therefore evaluated. The area of necrosis was expressed as a percentage of the total area. In addition, the following criteria were used to evaluate sporulation:

1) the development of the mycelium on the upper external surface of the tuber slice, expressed at the percentage of the area covered by it,
2) sporulation intensity (development of conidiophores) using the 0-3 scale described in p. I.

The inoculum was an aqueous suspension of conidiophores of 3 races of *P. infestans* of a combined virulence of 1, 2, 3, 4, 5, 7, 10, 11, that is, pathogenic for forms of potatoes characterized by specific resistance determined by complementary resistance genes R_1 , R_2, R_3 , R_4 , R_5 , R_7, R_{10} , R_{11} . Using an inoculum with such a composition enabled the disclosure of unspecific resistance which is masked by R genes (B l a c k et al., 1953). The inoculum had an initial concentration of 50 sporangia in 1 mm² . The conidiophore suspension was incubated at 10°C in order for zoospores to be formed and freed. The tubers and slices were incubated at a temperature of 16°C after inoculation and evaluated 6 days later according to the criteria listed above (in pt. I. 3 also after 4 days).

In all, 4 experiments were conducted in 1985-1987 in which both tests were used to compare the reaction of tubers to infection by *P. infestans*. In each, 10 cultivars in 3 repetitions were studied, 10 objects (tubers and slices) in each repetition.

The results were analysed using variance analysis, using in the case of the percentage data the Bliss transformation to degrees. The resistances of the studies varieties as assessed by the particular criteria were compared using the Duncan test.

The relationships among the criteria for evaluating resistance were determined using linear correlation coefficients calculated on the basis of mean values of the combinations in the individual experiments.

In order for it to be possible to determine the resistance of varieties using single values characterizing a given resistance trait, the primary data (obtained from observations of both tests) were transformed using the formula:

$$y_{ij} = \frac{\bar{x}_i}{100 \cdot x_{ij}} \qquad \text{where:}$$

y_{ij} – is the transformed value, x_{ij} – the primary data, $\bar{x}$ – the primary mean value, j – the number of varieties, i – the number of evaluation criteria.

This made it possible to normalize the mean values of the particular parameters of resistance assessment. In this way, units for resistance of flesh to colonization and units for resistance to sporulation were obtained. Each variety was characterized by a single value which was the average of the criteria evaluating the given resistance trait. The transformation of the LSD values according to the same principles gave as a result an abstract mean LSD value which enabled the division of the material into groups of cultivars that are similar in respect to resistance.

RESULTS

Assessment of colonization of tuber tissue

Significant differentiation of the studied cultivars in the resistance of their tuber flesh to colonization by *P. infestans* was found (Table 1) regardless of the evaluation criterion. The ranking of the studied cultivars on the basis of their resistance depended on the test and evaluation criterion used. The cultivar Sokół, followed by Cynia and Sowa, were found to be the most resistant when the depth and rate of colonization were assessed in the tuber test and browning in the slice test. However, when browning was evaluated on the tuber longitudinal section cultivar Sowa was least infected, followed by Irys and Tarpan. The most susceptible according to the tuber test (all parameters) was cultivar Bzura, then Jaśmin, whereas according to the slice test, the most susceptible was Dalia and then Bzura. These results on colonization of tuber tissue were burdened with a high degree of error (from 25,2 to 52,5 %). Significant correlation among the parameters of the tuber test was found (Table 3), but only the correlation coefficients between the penetration rate and browning of tissues on the longitudinal section (0,729) and between the rate and depth of penetration (0,639) were relatively high. When similar criteria used in both tests, e.g, tissue browning on the tuber longitudinal section in the tuber test and on the surface of the slice in the slice test were

compared, significant correlation was found, albeit the value of the correlation coefficient was relatively low (0,402) (Table 3). No correlation between this parameter of the slice test and the remaining parameters of the tuber test was found. The ordering of the cultivars in respect to the results of the browning criterion in both tests was not the same (Table 1). The browning intensity was significantly higher on the longitudinal section of the tuber than on the surface of the slice (Table 2).

Table 1

Infection of tubers of some potato cultivars by *Phytophthora infestans* in the whole tuber and the tuber slice tests

Cultivar	Evaluation of tuber flesh colonization				Evaluation of sporulation			
	penetration depth (MM)	penetration rate (r)	browned tissue (%)		area covered by mycelium (%)		sporulation score 0-3	
	A	A	A[1)]	B[2)]	A	B	A	B
Irys	6,7 bc	0,757 abc	16 ab	16 b	92 ef	94 e	2,6 e	2,2 e
Cynia	4,3 ab	0,699 abc	22 bc	5 a	98 f	93 e	2,7 e	2,0 d
Jaśmin	7,4 c	0,998 c	31 cd	14 b	87 de	78 de	2,1 d	1,9 d
Dalia	7,2 bc	0,913 bc	22 bc	56 d	90 ef	92 e	2,5 e	2,4 e
Pola	6,9 bc	0,738 abc	30 cd	15 b	40 b	33 b	0,7 b	1,8 b
Sokół	3,8 a	0,420 a	24 bc	4 a	9 a	7 a	0,3 a	0,2 a
Sowa	4,4 ab	0,482 ab	10 a	23 b	75 cd	52 bc	1,9 d	1,2 b
Bronka	7,0 bc	0,987 c	32 cd	19 b	66 cd	45 bc	1,3 c	1,0 b
Bzura	10,3 d	1,571 d	38 d	41 c	54 bc	56 bcd	1,3 c	1,4 bc
Tarpan	5,5 b	0,625 abc	15 ab	16 b	57 bc	63 cd	1,5 c	1,5 c
Error (%)	25,2	51,1	52,5	31,5	13,1	13,4	9,3	8,9

A – tuber test, B – tuber slice test, 1) – on tuber longitudinal section, 2) – on slice surface

Table 2

Comparison of the assessment of tuber infection by the tuber and slice tests [1)]

Criterion / Method	Assessment of colonization	Assessment of sporulation	
	tissue browing (%)	area covered by mycelium (%)	sporulation (score 0-3)
tuber test	24,5 b	69,2 a	2,7 a
slice test	19,2 a	64,9 a	2,5 a

1) – mean values from the cultivars

Table 3

Correlation coefficients between evaluation criteria for resistance to *Phytophthora infestans* in the tuber and slice tests

Criteria			Evaluation of tuber flesh colonization			Evaluation of sporulation			
			penetration depth (mm)	penetration rate (r)	browned tissue (%)	area covered by mycelium (%)		sporulation (score 0-3)	
			A		B	A	B	A	B
Evaluation of tuber flesh colonization	browned tissue (%)	A	0,428**	0,729**	0,402**	0,053	0,112	0,031	0,120
	penetration depth (mm)			0,639**	0,285	0,036	0,057	0,334	0,036
	penetration rate (r)				0,217	0,270	0,240	0,268	0,252
	browned tissue (%)	B				-0,487**	-0,570**	-0,492**	-0,579**
Evaluation of sporulation	area covered by mycelium (%)	A					0,780**	0,794	0,773**
	sporulation (score 0-3)							0,800**	0,730**
	area covered by mycelium (%)	B							0,743**

A – tuber test, B – slice test, Limit value at p = 0,01: 0,393 (**)

It can therefore be stated that the evaluation of tissue browning in the studied cultivars by the slice test can not replace the assessment by the criteria used in the tuber test. From among the criteria used in the latter, the most worthy of attention is the depth of penetration. This parameter was burdened by the relatively lowest error (25,2 %) and the ranking of the cultivars according to it was similar to that achieved using the remaining criteria of the tuber test.

Evaluation of sporulation

Significant differentiation among the studies cultivars was found in respect to mycelium development and sporulation intensity of *P. infestans* irrespective of the test used and evaluation criterion applied (Table 1). The results obtained in both the tuber and slice tests based on both assessment criteria allowed a similar ranking of the tested cultivars. Sokół was the most resistant cultivar, followed by Pola, while the most susceptible cultivars were Irys, Dalia and Cynia. Significant correlation was found among all of the criteria used for assessing resistance to sporulation in both tests and the value of these correlation coefficients was high (from 0,730 to 0,800) – (Table 3). The results of the resistance evaluation were

burdened with a low error (from 8,9 to 13,4 %) – (Table 1). The mycelium development intensities and sporulation intensities did not differ significantly from each other in both tests (Table 2).

It may thus be stated that both inoculation methods and both evaluation criteria are equally suitable for assessing the resistance of the studied group to sporulation. The use of only one of these criterions would be sufficient to evaluate the discussed trait.

Comparison of the assessment of colonization of tuber flesh and sporulation

After jointly analyzing all of the evaluation results it was found that the criteria for evaluation of resistance to sporulation gave a different ordering of the studied cultivars than do the criteria for colonization of the flesh (Fig. 1). In spite of the fact that the cultivar Sokół exhibited a high resistance in respect to both components, the sporulation-susceptible varieties Sowa, Tarpan and Cynia were relatively resistant to colonization of the flesh, while Bzura, which had flesh susceptible to penetration, was fairly resistant to sporulation.

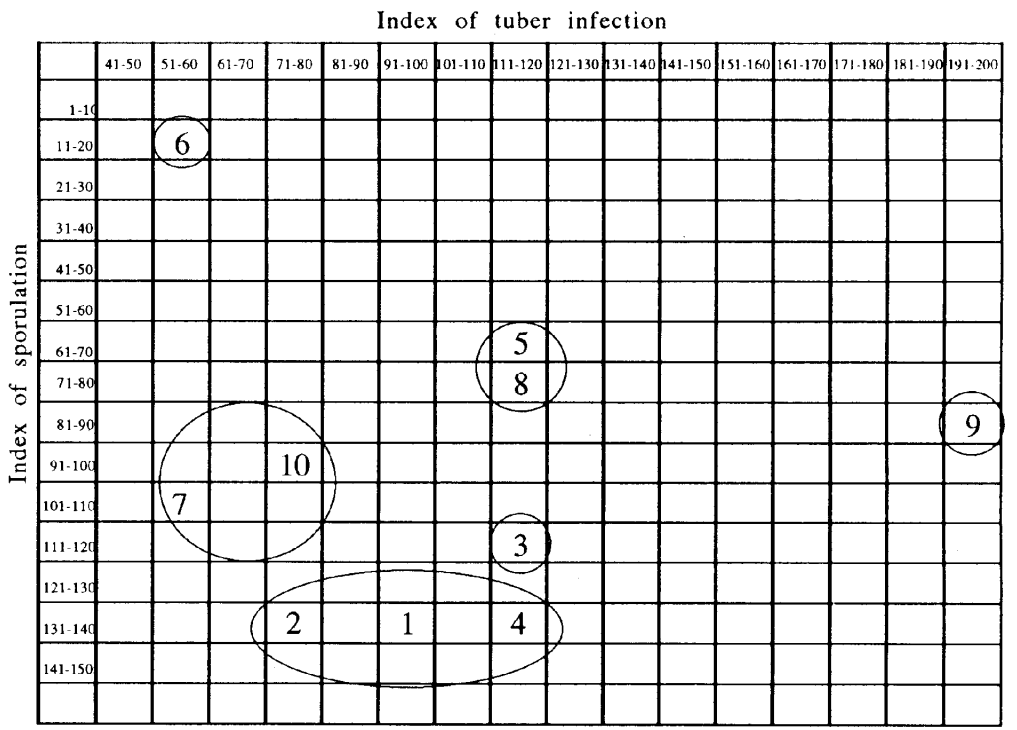

Fig. 1. Comparision of different cultivars of potato in resistance of tubers on colonization and sperulation

(X) Group of cultivars similar in resistance

Cultivars number: 1 – Irys, 2 – Cynia, 3 – Jaśmin, 4 – Dalia, 5 – Pola, 6 – Sokół, 7 – Sowa, 8 – Bronka, 9 – Bzura, 10 – Tarpan

Generally speaking, it was possible to divide the studied material into the following groups on the basis of similar resistance:

1. Only one cultivar, Sokół, could be assigned to the group in which weak infection of the flesh by the fungus was accompanied by poor development of the mycelium and poor sporulation.

2. The cultivars Tarpan and Sowa represented a group characterized by weak infection of the flesh and moderately intense development of mycelium and sporulation.

3. Bronka and Pola represented cultivars in which the flesh was moderately infected and the development of the mycelium and sporulation was moderately intense.

4. A group in which the moderately intense infection of the flesh was accompanied by strong development of mycelium and sporulation encompassed the cultivars Cynia, Irys and Dalia. The variety Jaśmin may also be included here, although it was characterized by slightly weaker sporulation.

5. The group in which a high degree of infection of the flesh was accompanied by intense development of the mycelium and sporulation contained only the cultivar Bzura.

No correlation was found between the assessment criteria of the colonization of the flesh in the tuber test and the parameters of sporulation evaluation in both tests (Table 3). However, a strong negative correlation existed between the criteria used to assess resistance to sporulation in both tests and the evaluation of browning in the slice test (the value of the correlation coefficient ranged from 0,492 to 0,579) – when there was intense browning of the tissue the development of the mycelium and sporulation were usually weak, and when sporulation was intense, browning was weak.

DISCUSSION AND CONCLUSIONS

The experiments conducted in this study have made it possible to compare the results obtained by two different laboratory tests, each evaluating the tubers of a selected group of cultivars in respect to their resistance to colonization and sporulation. The first question which emerges poses the problem if it is necessary to use 2 resistance components, or if only one is sufficient. Literature data show that although many researchers working on methods of evaluating tuber resistance took into consideration both the intensity of penetration of the flesh by the fungus and the density of conidiophores (L a p w o o d, 1 9 6 5; S c h o b e r and

Hoppner, 1972; Durska, 1976), the most usefull evaluation criteria in laboratory tests on tubers and slices were found to be the assessment of the intensity of mycelium development and sporulation, mainly because of the low variability of these traits (Lapwood, 1965; Piotrowski et al., 1973; Durska, 1976; Pietkiewicz, 1977). The results presented herein also confirm this opinion, however, they also show that the criteria evaluating sporulation may lead to a different ordering of cultivars than the criteria evaluating the colonization of tuber flesh by the fungus. This phenomenon was indicated only by Lapwood (1965) who found intense mycelium development accompanied by weak penetration of tuber flesh in some cultivars. He expressed the suspicion that some field-susceptible cultivars may be evaluated as resistant in laboratory tests. On the other hand, Pietkiewicz (1976) came to the conclusion that the resistance of tubers to sporulation was clearly related to their reaction to colonization of their flesh and that the correct evaluation of flesh resistance may be made on the basis of evaluation of sporulation.

The studies carried out so far by this author (Zarzycka, 1988), confirmed by the results presented herein, show that the resistance of tubers to colonization of their tissues and to sporulation my be traits occurring independently of each other. Resistance to colonization in the studied cultivars was often accompanied by susceptibility to sporulation, although no cultivars were found in which susceptibility to penetration was related to resistance to sporulation. The occurrence of both discussed resistance components was found only in the cultivar Sokół.

The problem should now be raised which of the discussed components of tuber resistance plays a greater role in the process of disease development. The tubers become infected during vegetation, therefore a crucial role will be played here by the resistance of the covering tissues, lenticels and eyes to infection (Lacey, 1967). During storage of the tubers, the disease usually develops within them – the important role here will be the resistance of the tuber flesh to colonization. However, sporulation of the pathogen on the tubers plays a minimal role in the development of an epidemic, both in the field and in storage. It may only play a part in the development of primary infection in plants from diseased tubers. Therefore, laboratory tests should evaluate not only the resistance of tubers to sporulation but also their resistance to colonization of their flesh by the fungus. Such a double assessment of both discussed resistance components was carried out by Darsow (1987) in the slice test, in which he evaluated the intensity of mycelium development and the surface of browned tissue. Schober

(1974) and Schober and Hoppner (1972) assessed the development of aerial hyphae and colonization of tissues by the fungus on tuber halves.

The next question to be answered is which of the applied criteria is/are most usefull in evaluating the resistance components. When the resistance to sporulation was evaluated, the same criteria were used in both tests even though the conditions under which the fungus developed were different. In the tuber tests the fungus grew and formed conidiophores directly on the injured surface of the tuber. In the slice test, the pathogen had first to penetrate the slice and then grow on the injured surface, on which in the meantime, peridermal tissue had formed. It should seem that the factor differentiating the resistance of the studied cultivars in the slice test would be the rate of penetration of the mycelium from the internal surface of the slice to its external surface along with the effect of the forming peridermal tissue. According to Clarke and Kassim (1977) the presence of peridermis around the injured tissues may affect the rate of growth of the fungus in the tuber tissues. However, the results of the study presented in this report do not confirm such a hypothesis. The intensity of mycelium and conidiophore development as well as sporulation did not differ significantly between that on the surface of the tuber inoculated immediately after injury and that on the surface of the slice which the fungus reached only after some time. Thus the conclusion is that the condition of fungus growth do not have a distinct influence on the intensity of sporulation. Therefore, both tests and both criteria turned out to assess equally well the resistance of the selected group of cultivars to sporulation.

A full assessment of the resistance of tuber flesh to colonization could only be carried out using the tuber test. The limited thickness of the slice made it impossible to use such criteria as depth of penetration, surface of the infected tissue on a longitudinal section of the tuber or rare of spreading of the infection. Only two criteria could be compared in both tests: browning of the tissue on the external surface of the slice with the browning of the tissue on the cut surface of the tuber in the tuber test. A significant difference was found in this study between the evaluation of the browning of the tissues in both tests in the selected cultivars. Therefore, an assessment of the penetration of the tissue by the fungus on the surface of the slice could not replace the assessment of the penetration of the tissues inside the tuber, all the more since in some cultivars it was difficult to assess the surface browning because the growing mycelium sometimes masked it. Each of the criteria of tuber resistance assessed a somewhat different aspect of this resistance. It was found in some cases that only a small surface area of the tissue had been infected while the fungus had penetrated deeply into the tuber (but along a narrow strip of tissue). In other cases, a large area of the surface was

found to be infected accompanied by only slight penetration. All of the criteria of evaluation of the resistance of tuber flesh to colonization were subject to high variability, much higher than that of the criteria of resistance to sporulation.

The results of this study support those of L a p w o o d (1965). From among all of the criteria assessing the resistance of tuber flesh to colonization, the most suitable seems to be the evaluation of the depth of penetration into the tuber. This due to the low variability of this criterion and the similar ordering of cultivars according to it as according to, on one hand, evaluation based the colonization rate and, on the other, on the browing of the tissue on the tuber half. The most work-consuming and most variable is assessment of the penetration rate of the flesh by the fungus. At this point, the usefulness of both tests for assessing the resistance of tubers to late blight may be brought up. The slice test primarily allows resistance to sporulation to be assessed, the tuber test – both resistance to sporulation and colonization of tuber flesh.

The author of this report feels that there is a lack of a convincing reference point for the results obtained in this study. The method used in Poland of evaluating the infection of tubers under natural conditions by calculating the percentage of infected tubers presents serious reservations.

According to the studies by L a p w o o d (1977), natural infection of tubers depends not only on the rainfall intensity which washes spores off from leaves onto the soil, but most of all on the degree of infection of and sporulation intensity on the above-ground plant parts.

The particular potato cultivars show various resistance of these parts to blight (this trait is not correlated with the resistance of tubers) and are infected to different degrees. Due to this, the developing tubers of the various cultivars are subject to various degrees of infection pressure and the obtained results are actually incomparable.

In addition, the date on which the observations conducted also has an effect on the results, as do the conditions under which the tubers are stored, since they affect the rate at which the disease develops. It should also be added that those cultivars or lines in which the fungus develops in the external part of the tuber and is visible through the covering layers will always be more harshly evaluated than those cultivars whose tubers have susceptible internal tissues (Z a r z y c k a, 1988). But it should be emphasized here that although the method of evaluating the infection of tubers under natural conditions has its faults, it is used to assess browining, that is, resistance to colonization and not to sporulation.

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