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Alexey V. Filippov[1], Boris I. Gurevich[1], Boris E. Kozlovsky[1], Maria A. Kuznetsova[1], Alexandr N. Rogozhin[1], Svetlana Y. Spiglazova[1], Tatiana I. Smetanina[1], Alexey N. Smirnov[2]

[1]All Russian Research Institute of Phytopathology (VNIIF), Moscow region, Odintsovo district, Bolshiye Vyazemy, Russia;
[2]Moscow Agricultural Academy (MAA), Moscow, Russia.
Adres for correspondence: A. V. Filippov, e–mail: alexey@vniif.rosmail.com

A RAPID METHOD FOR EVALUATION OF PARTIAL POTATO RESISTANCE TO LATE BLIGHT AND OF AGGRESSIVENESS OF *PHYTOPHTHORA INFESTANS* ISOLATES ORIGINATING FROM DIFFERENT REGIONS

ABSTRACT

The procedure of evaluation is based on mathematical simulation model of the late blight (LB) development in combination with laboratory testing of detached leaflets artificially inoculated with *Phytophthora infestans*. An incubation period, amount and sizes of lesions and sporulation capacity are estimated. Each couple "tested *Phytophthora* isolate and tested potato cultivar" is compared with a standard couple "*Phytophthora* isolate N161 and standard cultivar". A simulator on the base of these data calculates area under the curve for LB development and yield loss due to LB for a situation when a yield loss of a standard cultivar infected with a standard isolate is equal 35%. Comparison of a new rapid laboratory method and field methods showed satisfactory correlation. Resistance to late blight was evaluated for 47 potato cultivars with the new method. It was also shown that some variations in foliar aggressiveness existed among *P. infestans* populations from different regions.

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Key words: aggressiveness, late blight, mathematical model, potato cultivars, resistance, yield losses

INTRODUCTION

Late blight caused by oomycete *Phytophthora infestans* (Mont.) de Bary is the most destructive potato disease. The pathogen affects leaves and stems, causing their untimely dying, which results in the decrease of tuber yield. Moreover, the causal agent infects the tubers produced by affected plants. During storage the tubers rot and the total losses largely increase.

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A striking increase of *P. infestans* pathogenicity was observed at the beginning of 1980s. Then, the widespread clone of the pathogen with mating type A1, designated as US–1, was displaced by new, more variable populations in almost all potato growing regions (Spielman *et al.* 1991). In many regions the A2 mating type was detected (Vorobyeva and Gridnev 1983, Hohl and Iselin 1984, Shaw *et al.* 1985, Bagirova and Dyakov 1998, Elansky *et al.* 2001). The isolates representing "new" populations were found to be more aggressive than those from the "old" populations (Day and Shattock 1997, Flier *et al.* 1998). A risk of tuber blight infection has also essentially increased. More powerful epidemiological potential of *P. infestans* caused a strong decrease of the efficiency of formerly used protective measures on potato. According to the data by Schepers (2000), in the recent years a number of fungicide applications to protect potatoes against late blight in the countries of European Community has fluctuated between 7 and 20 sprays in the season, which is higher by 40% as compared with the 1970s. The changes of pathogenicity within populations of *P. infestans* did not allow to perform the resolution for the countries of European Community to reduce by 2000 the application of fungicides on potato by 50%, as related to the doses applied in the years 1986–1988.

In Russia, fungicides are only applied in big potato growing enterprises (formerly the collective or state farms). In potato production, their rate is below 10%. Mainly potato is grown in small private farms and gardens (dachas) of city dwellers. The cultivars planted in private gardens are susceptible to late blight, but fungicides are hardly ever applied. The conditions in these gardens for late blight development are more favourable than those in big potato growing farms. Taking into consideration such a structure of potato growing in Russia, we believe that to reduce losses of potato yield caused by late blight it is necessary both to grow resistant cultivars and develop strategies involving only a supporting role of fungicides.

It is well known that growing of potato cultivars with partial resistance to late blight is one of the most important components of the integrated pest management in this crop (Colon *et al.* 1995, Peters *et al.* 1999). Terms and a frequency of sprays with fungicides are determined by a level of cultivar resistance (Fry 1978, Cooke *et al.* 2001, Nielsen and Bødker 2001). However, correct evaluation of the resistance is only possible under certain conditions. In a field, the preconditions are (i) the presence of appropriate potential of inoculum in the first phases of potato growth and (ii) meteorological conditions favourable for the pathogen development. If development of late blight is weak and retarded, it is a great risk to obtain misleading information on the resistance level.

Most of the known laboratory methods to estimate potato resistance to late blight are based on measurement of quantitative characteristics of certain stages of infection cycle, such as infection, incubation, rate of tissue necrotization and sporulation capacity (Popkova and Stroikov

1977, Nielsen and Bødker 2001). They enable to determine the parameters characterizing the infection cycle in a variety of pathogen–host pairs, whereas they do not provide any information on the quantitative influence of the disease on potato yield.

Our current investigations were aimed at:

1. elaboration of laboratory methods to estimate aggressiveness of *P. infestans* and partial resistance of potato to the pathogen,
2. comparison of aggressiveness of populations currently occurring on the Russian territory and evaluation of levels of partial resistance to them of potato cultivars.

MATERIALS AND METHODS

The method used was based on our previously elaborated model "Epiphthora" of late blight development on potato leaves (Gurevich *et al.* 1977, 1979, Bobkova *et al.* 1982). This model allows to demonstrate a disease progress curve on the leaves during a vegetation period. It also makes possible to calculate yield losses caused by untimely dying of leaves on moderately susceptible potato plants after inoculation with a moderately aggressive *P. infestans* isolate. The main parameters of the model are: amount of necrotic lesions (per unit of leaf area), lesion size, incubation period and sporulation capacity.

To use the model for reproducing a disease progress curve and yield losses for other potato cultivar and/or other isolate of *P. infestans*, it is necessary to perform a laboratory trial to calculate and introduce the parameters of blocks for investigated "pathogen–host" pair, related to the pair that was used to construct the model. The standard pair includes potato cv. Sante and *P. infestans* isolate 161.

In practice, the information on interaction within "pathogen–cultivar" pairs is reliable provided that meteorological conditions are favourable for disease development. Therefore, in the model there have been introduced meteorological data for the vegetation season (Moscow region, 1993) during which epiphytotic development of late blight on cv. Sante following artificial inoculation with a standard *P. infestans* isolate was evaluated. The infestation rate of plants of standard cultivar at the flower–bud formation stage was 0.1, and the yield losses about 35%. These meteorological conditions and the "strain 161 – cv. Sante" pair were used as a standard (i.e. parameters at each stage of the infection cycle correspond to 1.).

The following procedures to estimate partial resistance of cultivars to late blight and aggressiveness of the causal agent have been established:

<u>First step.</u> In the early spring potato plants are planted and maintained in a climatic chamber until the stage of 5–6 leaves. Detached leaves are inoculated with a mixture of ten *P. infestans* isolates collected in each of the studied regions. After appearance on the leaves

of late blight spots and sporulation, the sporangia are transferred upon oatmeal agar for accumulation to be used in the second step (see below). In this phase, *P. infestans* isolates that are not able to affect plants of a certain cultivar are eliminated.

Second step. Both, tested and standard cultivars are planted in the field (30 plants/cultivar). At the plant stage of 7–9 leaves, one leaf from the middle part of the stem is detached. Afterwards the leaves of each cultivar are inoculated with the pathogen re–isolate (secondary isolate) picked out (at the first step) from this cultivar. It is necessary to compare each tested "pathogen – cultivar" pair with the standard one.

Test description

For measurement of inoculation efficiency ten leaves of each cultivar are sprayed with suspension of sporangia at concentration 7.2×10^3 sporangia per ml. After inoculation, the leaves are incubated in a moist chamber at 18°C. After 3 days a number of necroses per 1 cm^2 of leaf is determined.

Incubation period is measured as a number of days from inoculation to appearance of the first symptoms.

To compare the diameters of necroses, the leaves are inoculated with individual drops of zoospore suspension (1–2 drops per leaflet). The concentration of zoospores is the same as that described above. After inoculation, the leaves are incubated for 18 h in darkness in a moist chamber at 18°C. Afterwards, the residuals of suspension are removed from the leaves with a filter paper and the leaves are incubated at 20°C. After 4 days the diameters of necroses are measured.

For measurement of sporulation capacity the leaves from the test described above are used. Ten leaflets with necroses are put in 15 ml of distilled water and shaken. The leaflets are removed, a volume of the suspension is measured and a number of sporangia per one spot is counted by means of Goryaev chamber (hemocytometer).

Determination of resistance of potato plants to late blight. The calculations are performed by means of specialized software or nomogram. The nomogram (Fig. 1) includes the following scales:

A – index of infection in % (number of necroses [N] × size of necroses [D], as the parts of the standard);

B – calculated yield loss in % (for late [L], mediate [M] and early [E] cultivars);

C – incubation period, as the parts of the standard;

D – sporulation capacity, as the parts of the standard.

Scale B represents calculated yield losses as the result of pre–mature dying of leaves from late blight under the standard meteorological conditions (moderately favourable for disease development) and at the appearance of disease symptoms during the flower–bud formation stage.

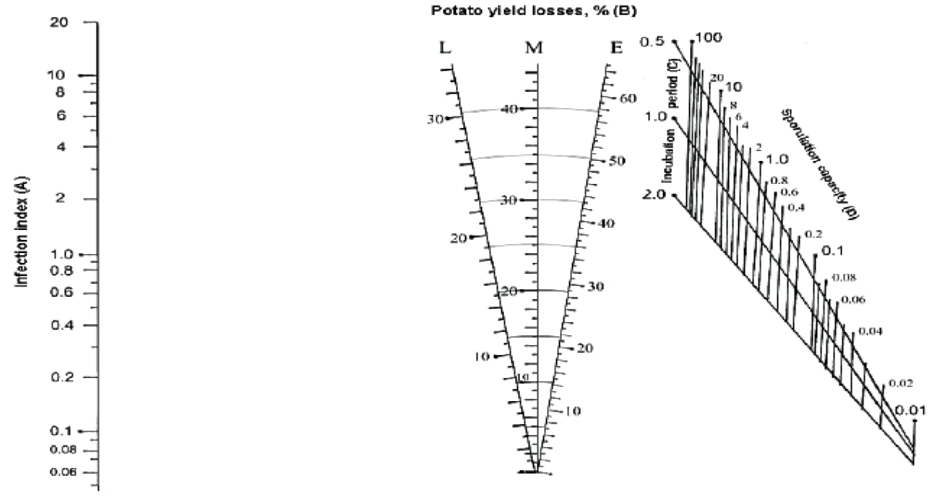

Fig. 1. Nomogram for determination of potato yield losses from late blight

Classification of potato specimens in relation to the level of resistance to late blight and calculated yield losses are shown in Table 1.

Table 1

Classification of potato specimens in relation to resistance to LB (scored in 1–9, where 9 = resistant) and calculated yield losses

Cultivars	Resistance to LB	Calculated yield losses [%]
Resistant (R)	9–8	< 5
Moderately resistant (MR)	7–6	5–15
Moderately susceptible (MS)	5–4	16–35
Susceptible (S)	3–1	> 35

A level of aggressiveness of *P. infestans* isolates based on the potential yield losses can be expressed as follows:

HA – highly aggressive (yield losses > 35%);
MA – moderately aggressive (16–35%);
WA – weakly aggressive (5–15%);
NA – not aggressive (< 5%).

The proposed method of estimation of "*P. infestans* – potato cultivar" interaction was used in the following investigations:

1. A comparison of laboratory and field methods of estimation of partial potato resistance to late blight.

The experiment was conducted under the field and laboratory conditions in 2000. In the tests 31 potato cultivars were evaluated.

Healthy tubers of each cultivar (30 per plot) were planted. Tubers of cv. Sante were planted on two margins of each plot (10 rows per margin).

They had been produced by the plants grown in 1999 in a nearby plot. In the autumn, *P. infestans* isolates were collected from the leaves for laboratory testing in 2000. In this way both the field and laboratory trials were performed using the same *P. infestans* isolates. At the time of planting in 2000, 2% of seed tubers of cv. Sante showed the symptoms of natural late blight infection. Thus, development of late blight from natural sources of infection (blighted tubers of cv. Sante) on tested cultivars was evaluated. Meteorological conditions during the summer season were favourable for late blight development. The first foci of infection in the field were found in early cultivars at the flower–bud formation stage. The leaves of many cultivars became blighted as early as the middle of August. The infestation rates were estimated according to the scale of British Mycological Society (Anonymous 1947). The observations were conducted every day beginning from the first detection of late blight symptoms. Based on the results obtained, the area under the disease progress curve was determined and corresponding yield losses were estimated (Gurevich *et al.* 1977).

The isolates collected in 1999 from cv. Sante were used in 2000 for testing the cultivars under laboratory conditions. Detached leaves of plants were artificially inoculated. The tests were done using the technique described above.

2. Comparative analysis of the level of partial resistance of different potato cultivars to late blight and of aggressiveness of P. infestans isolates collected in different geographic regions.

Experiment 1. In 1997, *P. infestans* isolates originated from potato fields located in three different regions: Moscow, Sakhalin and Toluca Valley in Mexico. Respectively, 62, 50, and 32 isolates were collected. Ten isolates were selected from each regional population. They were reproduced on tuber slices of cv. Sante. Sporangia were rinsed with water. Sporangial suspensions were mixed in equal proportions and concentrations. Three mixed inocula (Moscow, Sakhalin, and Mexican populations) of equal final volume and concentration of sporangia 7.2×10^3 per ml were thus prepared. Detached leaves of 31 potato cultivars were inoculated. To estimate a level of partial resistance of potato leaves, all the aforementioned procedures were used.

Experiment 2. The experiment was conducted in 2002. Plants of potato cultivars: Bryanskaya Novinka, Lina, Lorkh, Lugovskoy, Nevsky, New York 121, Sante and Velor were tested. As above, detached leaves of field–grown plants were inoculated with re–isolates from four geographic *P. infestans* populations (collected in 2001): Moscow, Tula and Leningrad regions and the Stavropol territory.

Statistical analysis was done by means of software Microsoft Excel 2000.

RESULTS

A comparison of laboratory and field methods of estimation of partial potato resistance to late blight

The yield losses estimated using a laboratory method were satisfactorily correlated with those assessed under field conditions (r=0.78 at P=0.05) (Table 2). The laboratory method slightly overestimated the

Table 2

Resistance of potato cultivars to late blight estimated under laboratory conditions and in the field in meteorological conditions moderately favourable for the disease development (Moscow region, 2000)

Cultivar	I (laboratory estimation)		II (field estimation)	
	Yield loss [%]	Level of resistance[1]	Yield loss [%]	Level of resistance[1]
Vineta	56	S	47	S
Roko	39	S	39	S
Rusalka	38	S	36	S
Samarsky	39	S	43	S
Goryanka	57	S	55	S
Xantia	42	S	38	S
Colette	53	S	32	MS
Legend	39	S	19	MS
Success	39	S	16	MS
Caty	50	S	16	MS
Alvara	19	MS	19	MS
Maidas	24	MS	19	MS
Snegyr	32	MS	19	MS
Argos	24	MS	17	MS
Panda	33	MS	16	MS
Scarlet	30	MS	33	MS
Genovator	29	MS	27	MS
Rosamunda	28	MS	29	MS
Tristar	26	MS	25	MS
Phasan	25	MS	19	MS
Nivan	26	MS	24	MS
Sierra	24	MS	16	MS
Adler	21	MS	20	MS
Sante	30	MS	21	MS
Nakra	23	MS	7	MR
Velor	11	MR	9	MR
Red rose	15	MR	8	MR
Lena	12	MR	12	MR
Mars	14	MR	8	MR
Olympus	11	MR	3	R
Victory	12	MR	4	R

[1] S – susceptible, MS – moderately susceptible, MR – moderately resistant, R – resistant

level of susceptibility of potato cultivars to late blight. However, it was typical and did not exceed the limits of two closed gradations.

The difference in estimated yield losses between field and laboratory assessment could result from the fact that meteorological and phytosanitary conditions in 2000 did not fully correspond to the conditions introduced into the model. However, the obtained results indicate that the proposed laboratory method allows to differentiate and classify potato cultivars and *P. infestans* isolates in respect of their partial resistance and aggressiveness, respectively, with the exactness satisfactory enough for practical purposes.

Comparative analysis of the level of partial resistance of different potato cultivars to late blight and of aggressiveness of P. infestans isolates collected in different geographic regions

Experiment 1

The level of aggressiveness of *P. infestans* isolates collected in Sakhalin in 1997 was higher than the respective levels for isolates representing Moscow and Mexican populations (Table 3).

It is noteworthy that only one cultivar (Belosnezhka) of 41 tested ones was resistant to isolates from all the three *P. infestans* populations, only one (Velor) exhibited stable moderate resistance and none of the cultivars exhibited stable susceptibility. Almost 22% of cultivars expressed stable moderate susceptibility.

Experiment 2

The isolates of *P. infestans* collected in different regions of European part of Russia showed different levels of aggressiveness to the tested potato cultivars (Fig. 2). The isolates from Tula and Leningrad popula–

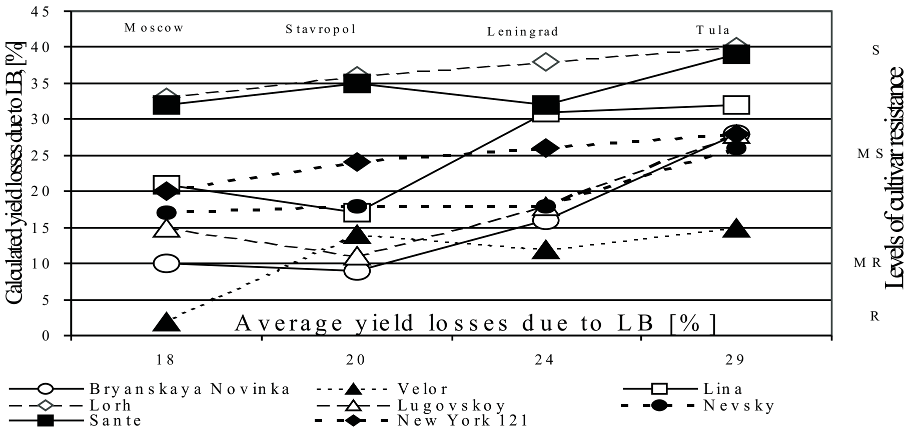

Fig. 2. Variations of levels of partial resistance of 8 potato cultivars to *P. infestans* isolates from four regions of European part of Russia in 2001

tions expressed the highest aggressiveness. The average indexes for yield losses in 8 tested cultivars were 29% and 24%, respectively.

Table 3

Mutual influence "*P. infestans* – potato cultivar" at inoculation of leaves with isolates of three pathogen populations

Potato cultivar	Origin of isolates								
	Moscow region			Mexico[1]			Sakhalin		
	I[2]	II[3]	III[4]	I	II	III	I	II	III
Belosnezhka	1	NA	R	1	NA	R	2	NA	R
Lugovskoy	2	NA	R	2	NA	R	28	MA	MS
Lina	2	NA	R	3	NA	R	34	MA	MS
Fable	2	NA	R	9	WA	MR	41	HA	S
Red rose	2	NA	R	35	MA	MS	43	HA	S
Bryanskaya Nov.	3	NA	R	3	NA	R	34	MA	MS
Velor	11	WA	MR	8	WA	MR	12	WA	MR
Olympus	11	WA	MR	17	MA	MS	31	MA	MS
Lena	12	WA	MR	13	WA	MR	29	MA	MS
Mars	14	WA	MR	27	MA	MS	37	HA	S
Alvara	19	MA	MS	18	MA	MS	19	MA	MS
Adler	21	MA	MS	11	WA	MR	42	HA	S
Nakra	23	MA	MS	28	MA	MS	31	MA	MS
Maidas	24	MA	MS	9	WA	MR	24	MA	MS
Sierra	24	MA	MS	12	WA	MR	43	HA	S
Argos	24	MA	MS	24	MA	MS	28	MA	MS
Phasan	25	MA	MS	23	MA	MS	29	MA	MS
Nivan	26	MA	MS	14	WA	MR	26	MA	MS
Tristar	26	MA	MS	18	MA	MS	20	MA	MS
Victory	27	MA	MS	10	WA	MR	26	MA	MS
Rosamunda	28	MA	MS	21	MA	MS	25	MA	MS
Genovator	29	MA	MS	18	MA	MS	19	MA	MS
Scarlet	30	MA	MS	18	MA	MS	35	MA	MS
Sante	30	MA	MS	29	MA	MS	37	HA	S

Table 3

Continued

Potato cultivar	Origin of isolates								
	Moscow region			Mexico[1]			Sakhalin		
	I[2]	II[3]	III[4]	I	II	III	I	II	III
Snegyr	32	MA	MS	36	HA	S	45	HA	S
Mavka	32	MA	MS	18	MA	MS	40	HA	S
Panda	33	MA	MS	23	MA	MS	35	HA	MS
Bryansk del.	39	HA	S	35	MA	MS	44	HA	S
Roko	39	HA	S	37	HA	S	34	MA	MS
Rusalka	38	HA	S	32	MA	MS	35	MA	MS
Samarsky	39	HA	S	35	MA	MS	49	HA	S
Success	39	HA	S	16	MA	MS	37	HA	S
Platina	41	HA	S	31	MA	MS	53	HA	S
Xantia	42	HA	S	25	MA	MS	36	HA	S
Ditta	43	HA	S	27	MA	MS	39	HA	S
Romina	44	HA	S	33	MA	MS	33	MA	MS
Rocket	46	HA	S	35	MA	MS	45	HA	S
Karlita	47	HA	S	30	MA	MS	48	HA	S
Karlina	48	HA	S	31	MA	MS	42	HA	S
Caty	50	HA	S	23	MA	MS	40	HA	S
Colette	53	HA	S	35	MA	MS	52	HA	S
Average $LSD_{0.95}$ =5.3		27.3			21.2			34.1	

[1] These isolates were collected by Dr. W. Flier
[2] I – level of pathogenicity (%)
[3] II – level of aggressiveness of isolates (NA – not aggressive, WA – weakly aggressive, MA – moderately aggressive, HA – highly aggressive)
[4] III – level of cultivar resistance (S – susceptible, MS – moderately susceptible, MR – moderately resistant, R – resistant

DISCUSSION

It has been demonstrated in this work that *P. infestans* populations developing in different geographic regions can essentially differ in their aggressiveness to potato plants. In many cases the levels of potato resis– tance to Sakhalin, Tula, and Leningrad populations w/ere lower than those to Moscow, Mexican, and Stavropol populations. Our results do not support the conclusions derived elsewhere (Forbes and Tolstrup 1999) that partial resistance of potato to late blight is stable, irrespec– tive of the conditions of potato cultivation and of the features of local pathogen populations. Although in our experiments, like in those of Forbes and Tolstrup (1999), the resistance ratings for cultivars after plant inoculation with isolates of different origin did not differ essentially, there were marked differences in the quantitative expression of resistance.

The revealed variations in aggressiveness of late blight indicate that a particular potato cultivar can exhibit different levels of partial resistance when planted in different regions. Interregional spread of the disease may result in the situation that cultivars known to be resistant to local *P. infestans* populations can elsewhere be assessed as much less resistant. It cannot be excluded that the variability of *P. infestans* aggressiveness corresponds to the historically limited period during which "old" genotypes of pathogen are displaced by "new" genotypes. Perhaps, in the future, the differences between strains and populations will not be so significant due to the stabilizing selection (although a general level of aggressiveness of "new" populations is expected to be higher than that of the "old" ones). Our data support the opinion expressed by Niederhauser (1962) assuming the "erosion of field resistance" of potato cultivars to late blight. Recently, similar results were obtained in the Netherlands (Flier *et al.* 2002). The authors suggest that the specificity characterizing interactions between *P. infestans* strains and partial resistance of potato cultivars can greatly influence both the stability and durability of the resistance. Significant variations in aggressiveness within *P. infestans* population in Northern Ireland should be taken into account at selection of strains for testing breeding material (Cook *et al.* 2002). In the studies of Earnshaw and Shattock (2002), an offspring strain obtained after *P. infestans* mating, compared with parental strains, expressed a higher level of aggressiveness. Certainly, the polygenic background of resistance ensures more prolonged protection of potato against late blight, as compared with race-specific resistance. However, both partial and race-specific resistance can collapse following the appearance and spread of more aggressive pathogen strains. Our data indicate that potato cultivars exhibiting a certain level of partial resistance to highly aggressive strains of *P. infestans* (like those from Bryansk or Tula) generally express comparatively high, or even higher level of resistance to less aggressive isolates. From the standpoint of practice, it is more useful to assess potato resistance to late blight using isolates from the most aggressive populations.

The most appropriate region for field trials on the Russian territory is Sakhalin, as the local population of *P. infestans* is highly aggressive, and meteorological conditions during the vegetation season are almost always favourable for late blight development. If the field conditions like those in the Sakhalin region are not available, the laboratory method described in the paper can be recommended.

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