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FULL RESEARCH PAPER

Host–pathogen interaction between *Phytophthora infestans* and *Solanum nigrum*, *S. villosum*, and *S. scabrum*

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Abstract Potato and tomato are the two major hosts for *Phytophthora infestans* causing late blight. The susceptibility of leaves and whole plants of *Solanum nigrum*, *S. villosum*, and *S. scabrum* to infection by *P. infestans* was tested under laboratory conditions. Out of 39 plants representing 38 different *S. nigrum* accessions, 16 were highly resistant (seven accessions did not show any symptoms of infection, nine were highly resistant showing necrotic lesions in the place of infection), and 23 plants of *S. nigrum* were colonized by, at least, 1 of the 2 isolates of *P. infestans* (17 accessions were infected with two *P. infestans* isolates, and 6 accessions showed different reactions depending on the isolate used for inoculation). Three accessions of *S. villosum*, and one accession of *S. scabrum* were tested and did not show any symptoms of infection. The majority of *S. nigrum* accessions infected by *P. infestans* in a detached leaf assay were also infected in the whole plant assay. The reaction of field- and greenhouse-grown plants to inoculation with *P. infestans* in detached leaf assays was similar, but in some cases leaves from field-grown plants reacted as resistant in comparison with the leaves from greenhouse-grown plants, which were susceptible.

Keywords Late blight · Potato · Tomato

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Introduction

Late blight, one of the most important diseases of potato (*Solanum tuberosum*), is caused by the oomycete *Phytophthora infestans*. Unprotected crops in favourable weather conditions and in the presence of inoculum source can be destroyed within 10 to 14 days (Govers 2005). This pathogen has a wider range of hosts represented by other solanaceous species: *Lycopersicon esculentum*, *Solanum sarrachoides*, *S. triflorum*, *S. dulcamara*, *S. sisymbriifolium*, *Nicotiana benthamiana*, and plants of genus Calibrachoa (Bectell et al. 2006; Dandurand et al. 2006; Flier et al. 2003). *Solanum nigrum*, a weed growing predominantly in solanaceous crops, such as tomato and potato (Stankiewicz et al. 2001), has been regarded for years as a non-host for *P. infestans*, due to infrequent infection under natural conditions in England (Hirst and Steadman 1960), Wales (Deahl et al. 2004) and The Netherlands (Flier et al. 2003), and the lack of infection under laboratory conditions (Colon et al. 1993; Platt 1999). Non-host resistance is highly effective and durable, and hence, it

is often suggested that the mechanisms of non-host resistance can be exploited to generate resistant crop plants (Thordal-Christensen 2003). *S. nigrum* has been used as a source of resistance for potato breeding (Colon et al. 1993; Horsman et al. 1997; Zimnoch-Guzowska et al. 2003), though the mechanisms of resistance to *P. infestans* in this species are not well known. *Solanum villosum* and *S. scabrum* are closely related species to *S. nigrum* (Edmonds and Chweya 1997). These weed plants may be a source of resistance for breeding when resistant, but are also a source of infection in the field when they are susceptible or partially resistant.

The goals of the present studies were: (1) to assess susceptibility of different accessions of *S. nigrum*, *S. villosum*, and one accession of *S. scabrum* to *P. infestans* (2) to compare the results obtained after inoculation of detached leaves with the results obtained after inoculation of whole plants, (3) to determine the interaction between plant accessions with two different *P. infestans* isolates, and (4) to evaluate the influence of greenhouse- and field-growing conditions on *S. nigrum* plants on disease development in a detached leaf assay.

Materials and methods

Plant material

Plant material used in this study was represented by 38 different accessions of *S. nigrum*, collected in 8 European countries, in Africa, South America and North America; 3 accessions of *S. villosum*; one of *S. scabrum*; and 2 susceptible late blight potato cvs Bintje and Craigs Royal (Table 1). *S. nigrum*, *S. villosum* and *S. scabrum* are predominantly self-pollinating species and are often characterized by a high degree of homozygosity and concurrent genetic uniformity of plants both within a population and from generation to generation (Edmonds and Chweya 1997). In preliminary experiments (data not presented) five to seven plants per accession were tested for resistance to *P. infestans* in detached leaf assays, and because the results were uniform within each accession, one plant per accession was further tested, with the exception that two plants of *S. nigrum* accession 15 were tested, because within this accession both resistant and susceptible plants were found. The seeds from one plant of each accession were collected, with the exception of *S. nigrum* accession 15 when seeds were collected from two plants, and in the next season sibling plants were used in the further leaf tests and in whole plant assays. Plants were space-isolated from each other in the greenhouse to prevent cross-pollination. No bags were used on plants.

Phytophthora infestans isolates

For testing the resistance, two *P. infestans* isolates, MP 324 collected from potato cv Gloria and MP 637 collected from potato cv. Vineta, maintained in the pathogen collection at The Plant Breeding and Acclimatization Institute, Młochów Center, were used. These isolates differ from each other in the place and the year of collection, the resistance to metalaxyl and pathotype (Table 2.). The isolate MP 324 has been highly aggressive to potato since 1997 (frequently used in testing potato resistance to late blight), and the isolate MP 637 was chosen from the isolates collected in 2005. Both isolates were characterized by complex virulence. Inoculum consisted of a sporangial suspension that was prepared as described by Zarzycka (2001) from sporulating lesions of potato leaflets and adjusted using a haemocytometer to a concentration of 50,000 sporangia ml^{-1}.

Detached leaf assay

All accessions and the two potato cultivars from greenhouse-grown plants were tested for resistance to the two isolates of *P. infestans* in the detached leaf assay (with the exception of accession 9 of *S. nigrum* which was tested only with one *P. infestans* isolate MP 324) (Table 3). Five or ten leaves per accession were tested in three experiments with the *P. infestans* isolate MP 324, and in two experiments with the isolate MP 637.

Greenhouse- and field-grown plants of 11 accessions of *S. nigrum* (Table 4), differing in resistance to *P. infestans*, were compared with respect to their reaction to *P. infestans* inoculation in detached leaf assays. Ten leaves per accession from field- and greenhouse-grown plants were inoculated with the isolate MP 324 in two experiments.

In all experiments fully developed leaves were detached from the middle part of the 6- to 12-week-old greenhouse-grown plants (sodium light was applied

Table 1 Plant material used in this study: species, place of harvest, and origin

Accession nomenclature	Species and/or accession number	Location	Region	Origin
N2	*Solanum nigrum* (*ngr*) 944750125	Chile	Valdivia	1
N5	*ngr* 954750302	United Kingdom	Birmingham	1
N6	*ngr* 954750304	United Kingdom	Birmingham	1
N8	*ngr* 954750310	United Kingdom	Birmingham	1
N9	*ngr* 954750317	United Kingdom	Birmingham	1
N10	*ngr* 954750322	United Kingdom	Birmingham	1
N12	*ngr* 954750327	United Kingdom	Birmingham	1
N13	*ngr* 954750329	United Kingdom	Birmingham	1
N14	*ngr* 954750330	United Kingdom	Birmingham	1
N15	*ngr* 954750331	United Kingdom	Birmingham	1
N16	*ngr* 954750341	United Kingdom	Birmingham	1
N20	*ngr* 954750309	United Kingdom	Birmingham	1
3	*ngr*	France	Unknown	2
25	*ngr* SOL 20/02	France	Unknown	3
N3	*ngr* 954750156	France	Unknown	1
20	*ngr* SOL40/01	Germany	Unknown	3
28	*ngr* SOL 44/77	Germany	Lipsk	3
N19	*ngr* 984750019	Germany	Karlsruhe	1
19	*ngr* SOL23/02	The Netherlands	Wageningen (Arboretum)	3
22	*ngr* SOL42/01	The Netherlands	Utrecht	3
N18	*ngr* 974750120	The Netherlands	Wageningen (CPRO)	1
N1	*ngr* 944750095	Mexico	Cuernavaca	1
1	*ngr*	Poland	Belsk	2
2	*ngr*	Poland	Warszawa (Ulrychów)	2
6	*ngr*	Poland	Wrocław	2
8	*ngr*	Poland	Lublin	2
9	*ngr*	Poland	Warszawa	2
10	*ngr*	Poland	Bydgoszcz	2
13	*ngr*	Poland	Warszawa	2
14	*ngr*	Poland	Unknown	2
15	*ngr*	Poland	Kórnik	4
16	*ngr*	Poland	Poznań	4
30	*ngr*	Poland	Unknown	5
17	*ngr* SOL50/77	Romania	Unknown	3
18	*ngr* SOL169/0	Russia	Moscow	3
23	*ngr* SOL55/77	Russia	Moscow	3
24	*ngr* SOL 35/79	Sweden	Lund	3
21	*ngr* SOL33/78	Tunisia	Unknown	3
4	*Solanum villosum* (*vll*)	United Kingdom	Birmingham	5
26	*vll*	Hungary	Budapest	3
N4	*vll* 954750300	United Kingdom	Birmingham	1
29	*Solanum scabrum*	Poland	Unknown	6

Seeds of *S. nigrum* were kindly provided by: *1* Botanical Garden of Nijmegen, The Netherlands; *2* Agricultural University, Warsaw, Poland (PL); *3* Institute of Plant Genetics and Crop Plant Research, Gatersleben, Germany; *4* Institute of Plant Protection, Poznań, PL; *5* Botanical Garden, Warsaw, PL; *6* Plant Breeding and Acclimatization Institute, Młochów, PL.

– 14 h day) or field-grown plants. Leaves were placed on wet cellulose wadding in a plastic tray. Each leaf was inoculated by depositing one 30 µl drop of the inoculum on the abaxial side of the leaf. The trays with leaves were covered with glass. The inoculated leaves were incubated for 7 days at 16°C with a constant illumination of about 1,600 lx. After the first 24 h of incubation the leaves were turned abaxial side down. Each leaf was

Table 2 Characteristics of two Polish *P. infestans* isolates used in experiments

Isolate	Voivodeship and place of origin (latitude and longitude)	Sample date	Host (species and cultivar)	Mating type[a]	Resistance to metalaxyl[b]	Pathotype[c]
MP 324	West Pomeranian (N54°11′ E16°11′)	1997	*Solanum tuberosum* cv. Gloria	A2	Resistant	1.2.3.4.6.7.10.11
MP 637	Lower Silesian (N51°9′ E15°59′)	2005	*Solanum tuberosum* cv. Vineta	A2	Sensitive	1.2.3.4.7.8.10.11

[a] Determined by pairing a tested isolate with the A1 tester culture or the A2 tester on rye agar and observation of oospores on the plate with the opposite mating type standard.

[b] Evaluated according to Bakonyi et al. (2002), Perez et al. (2001) and Daggett et al. (1993).

[c] Evaluated in the detached leaflet assay on the set of 11 Black's differentials (Black et al. 1953; Malcolmson and Black 1966)

scored as either R – lacking the visible infection symptoms, R^N – possessing necroses of a size less or equal to the area of inoculation drop without sporulation, or S – with sporulating lesions. Intensity of sporulation was scored in three categories: weak (sporangia weakly visible or observed under microscope), medium, and intensive.

Whole plant assay

Greenhouse-grown 5-week-old plants, representing 19 *S. nigrum* accessions, 2 of *S. villosum*, 1 of *S. scabrum*, and 2 susceptible cultivars of potato, were inoculated with the MP 324 *P. infestans* isolate by spraying to run-off with a hand sprayer. Inoculated plants were covered with a plastic tunnel to increase humidity and kept at 16°C under constant illumination of about 1,600 lx for 7 days. Additionally, plants were sprayed with water once a day during the incubation. The results of the test were grouped into three categories: R – plants without any visible symptoms of infection, R^N – with small necroses, without sporulation, S – plants with severe lesions. The number of inoculated plants differed depending on the accession (Table 3). Two potato cultivars, Bintje and Craigs Royal, served as susceptible controls.

Results

Detached leaf assay

All three groups types of resistance reactions, R, R^N, and S were observed on the leaves of the *S. nigrum* plants. (Fig. 1a–d). Out of 39 plants representing 38 accessions of *S. nigrum*, 16 were highly resistant to the 2 *P. infestans* isolates: 7 did not show any symptoms of infection, 9 showed non-sporulating lesions (with some exceptions when single leaves were infected) (Table 3.). Five accessions (30, N14, N5, N12, N13) were highly resistant to the isolate MP 324, but not to isolate MP 637, and one accession (10) was not infected by the isolate MP 637, but by isolate MP 324. In the group of accessions infected by both *P. infestans* isolates, 17 accessions showed symptoms of infection in at least two separate tests. Some variation of results was observed among tests (Table 3), when the leaves were infected in one test but not in the other. The test marked III in Table 3, when MP 324 was used for inoculation, was the most variable. Four accessions infected in previously performed test(s) were not infected in test III. Sometimes, within 5 or 10 leaves tested per accession, single or few leaves were not infected. The sporulation observed on 23 of the *S. nigrum* accessions varied from weak to intensive. In general the sporulation was more intensive after inoculation of *S. nigrum* with the isolate MP 637 than with MP 324. Isolate MP 637 sporulated intensively on five accessions (N13, 28, N6, N8, 20) in both tests, and MP 324 on one accession (2) in three tests. Interactions between *S. nigrum* plants and the two isolates were observed, where five accessions were infected only with the MP 637 isolate and not with MP 324, and one accession was infected only with the MP 324 isolate, but not with MP 637. Three *S. villosum* accessions (N4, 4, 26), and one of *S. scabrum* (29) did not show any symptoms of infection with either of the two *P. infestans* isolates in all experiments conducted. The symptoms of infection with intensive sporulation were observed on the two susceptible potato cultivars. It was also observed that the development of symptoms was slower on *S. nigrum* leaves than on the potato leaves.

The leaves of five highly resistant accessions of *S. nigrum* did not show any symptoms of infection after

Table 3 Reaction of *S. nigrum*, *S. villosum, S. scabrum*, and *S. tuberosum* to infection with two isolates of *P. infestans* (MP 324 and MP 637) in the detached leaf assay, and with one isolate (MP 324) in the whole plant assay

Host	Detached leaf					Whole plant
Accession no.	*P. infestans* isolates					
	MP 324			MP 637		MP 324
	I	II	III	I	II	
S. nigrum						
21	R	R	R	R	R	$R+R^N$ (15)[1]
N1	–	R	R	R	R	–
N9	–	R	R	R	R	–
N10	–	R	R	R	R	–
N16	–	R	R	R	R	–
N20	–	R	R	R	R	–
N19	–	R	R	R	R	–
N2	–	R	R	R	R^N	–
6	–	R	R	R	R^N	–
15/5	R^N	R	R	R	R	R^N (1)
22	R^N	R^N	R	R	R	R^N (11)
16	R^N	R	R	R	R	R (2)
25	R^N	R^N	R	R	R	$R+R^N$ (15)
N18	–	R	R	R^N	R	–
24	R^N	R	R	R	R^N	R^N (14)
18	R^N	R^N	R^N	R	R^N	R (15)
10	S^a	S^b	S^a	R	R	R^N (12)
30	R^N	R	R	S^a	S^a	R (11)
N14	–	R^N	R^N	S^b	S^c	–
N5	–	R	R	S^c	S^b	–
N12	–	R^N	R	S^b	S^a	–
N13	–	R	R^N	S^c	S^c	–
3	S^a	S^a	S^b	S^a	S^c	–
17	R	S^c	S^b	S^b	R	S (12)
15/3	S^a	S^c	R	S^b	S^b	S (4)
28	R	S^a	S^c	S^c	S^c	S (14)
N3	–	S^a	S^b	S^b	S^c	–
19	S^a	S^a	S^a	S^b	S^c	S (2)
N6	–	S^c	R	S^c	S^c	–
8	S^a	S^a	S^a	S^c	R	S (2)
13	S^a	S^c	S^c	S^b	S^b	S (4)
N8	–	S^a	R	S^c	S^c	–
N15	–	S^a	S^a	S^b	S^c	–
1	S^a	S^a	S^b	S^a	S^c	–
23	S^a	S^a	R	S^b	S^a	R^N (7) S (3)
14	S^a	S^c	S^c	S^b	S^c	–
20	S^a	S^c	S^c	S^c	S^c	S (12)
9	S^b	S^c	–	–	–	S (3)
2	S^c	S^c	S^c	S^b	S^c	S (6)
S. villosum						
4	R	R	R	R	R	R (14)
26	R	R	R	R	R	R (8)
N4	–	R	R	R	R	–
S. scabrum						
29	R	R	R	R	R	R (14)
S. tuberosum						
Bintje	S^c	S^c	S^c	S^c	S^c	S (5)
Craigs Royal	S^c	S^c	–	S^c	–	S (5)

Number of tested plants per accession in parenthesis.

R: lacking visible infection symptoms, R^N: necroses of the size less or equal to the area of inoculation drop, without sporulation, *S*: sporulating lesions, –: not inoculated

[a] Very weak sporulation (sporangia observed under microscope) and weak sporulation.

[b] Medium sporulation.

[c] Intensive sporulation.

inoculation with *P. infestans* (Table 4) regardless of the field or the greenhouse growing conditions of tested plants. Also, no differences in reaction of two susceptible *S. nigrum* accessions to inoculation with *P. infestans* were observed. For another four accessions of *S. nigrum*, when the leaves originated from the greenhouse-grown plants, symptoms of infection were observed (with the exception of a single leaf of one accession, which was not infected in one out of two tests). However, when the leaves originated from field-grown plants some differences in reaction to inoculation with *P. infestans* occurred. One accession (N6) did not show any symptoms of infection, and the other accession (N15) was infected in the first but not in the second test. Accession 17 had mixed reactions within each test with the majority of the leaves resistant, and accession N8 had both sensitive and resistant reactions in one test but was resistant in the second test.

Whole plant assay

Highly resistant plants did not show any symptoms of infection or showed small necroses without sporulation, while susceptible plants showed severe lesions (Fig. 1e and f). From 19 accessions of *S. nigrum* tested, 10 were highly resistant and 9 were susceptible. Two accessions of *S. villosum*, and one of *S. scabrum*, were also highly resistant in the whole plant assay (Table 3).

Table 4 Reaction of *S. nigrum* leaves, collected from greenhouse- and field-grown plants, to inoculation with *P. infestans* isolate (MP 324)

Accession no.	Tested leaves collected from plants grown in the			
	Field		Greenhouse	
	I	II	I	II
16	R	R	R	R
21	R	R	R	R
24	R	R	R	R
N9	R	R	R	R
N19	R	R	R	R
N6	R	R	S	S
17	R (9) S (1)	R (7) S (3)	S	S
N8	S (6) R (4)	R	S	S
N15	S	R	S	S (4) R (1)
2	S	S	S	S
13	S	S	S	S

Number of leaves in parenthesis, out of ten tested, expressing different reactions within the same test.

S: sporulating lesions, *R*: lacking visible infection symptoms or necroses of the size less or equal to the area of inoculation drop, without sporulation.

Discussion

The susceptibility of a wide range of 38 different accessions of *S. nigrum*, 3 of *S. villosum* and 1 of *S. scabrum* to *P. infestans* were screened under laboratory conditions. Inoculation of *S. nigrum* with two different isolates of *P. infestans* revealed a range of reactions from no symptoms, non-sporulating lesions, to sporulating lesions. The mechanism of *S. nigrum* resistance to *P. infestans* is not well known. Resistant accessions in our study showed a lack of visible symptoms or had non-sporulating lesions. Our phenotypic observations showed similarities to an *R* gene-mediated type of resistance to *P. infestans* in potato. Colon et al. (1993) did not observe any sporulation on *S. nigrum*-SN18 after inoculation with *P. infestans*. On the same accession, Vleeshouwers et al. (2000) found rapid host cell necroses (HR), intercellular hyphae, and encasement of haustorial primordia 22 h after inoculation with *P. infestans*, indicating that the nature of resistance in *S. nigrum* may not be essentially different from that in *S. demissum* conditioned by *R* genes. Several acces-

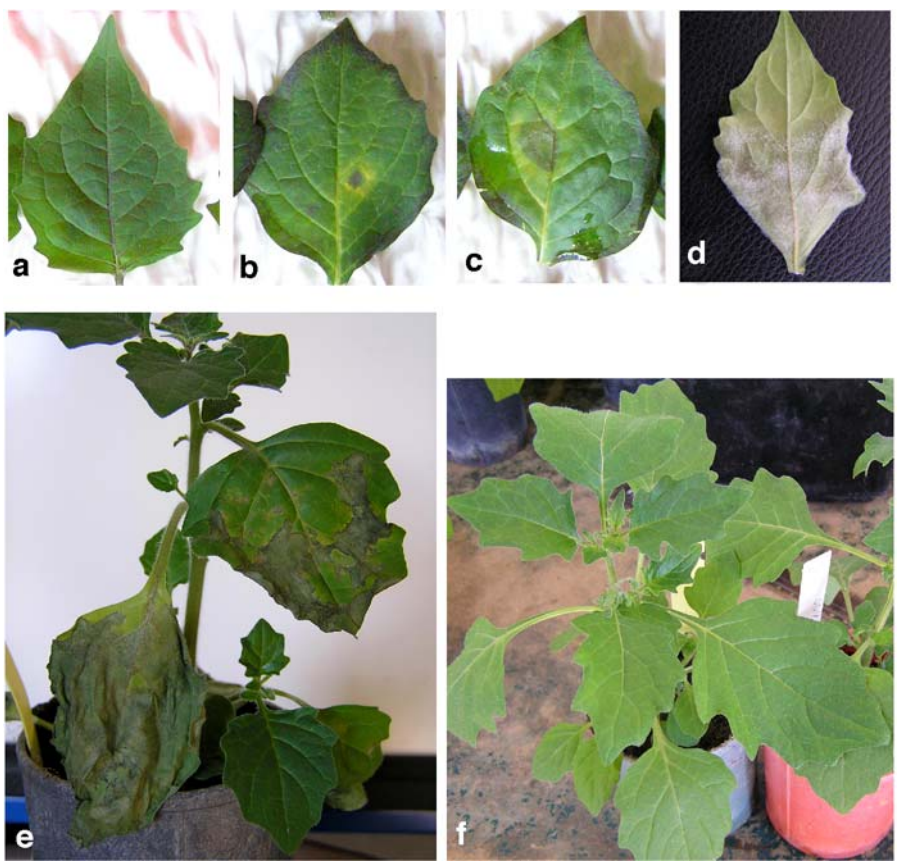

Fig. 1 The detached leaf assay; symptoms of infection caused by *P. infestans* on *S. nigrum* leaves: **a** The isolate MP 324 on accession N19 (lack of symptoms). **b** The isolate MP 324 on accession N12 (necroses of the size less or equal to the area of inoculation drop, without sporulation). **c** The isolate MP 324 weakly sporulating on accession N15. **d** The isolate MP 637 intensively sporulating on accession 28. The whole plant assay: **e** infected *S. nigrum* plant of accession 28 with *P. infestans* isolate MP 324, **f** highly resistant *S. nigrum* plant of accession 8

sions of *S. nigrum* showed symptoms of infection in our studies, though the variability in the reaction of leaves from the same plant within the same test and among tests suggested a high level of resistance, which in some circumstances might have been overcome by the pathogen. The sporulation of *P. infestans* on *S. nigrum* leaves is often less than on susceptible potato leaves, which means that factors other than *R* gene(s) may be involved in the resistance of *S. nigrum*. A similar observation was presented in the study by Flier et al. (2003), where mean sporulation densities were 2,704 sporangia cm^{-2} for *S. nigrum* (Sn001) and 47,046 sporangia cm^{-2} for cv. Bintje susceptible to *P. infestans*. Three *S. villosum* accessions, and one of *S. scabrum* were highly resistant to infection with either of the two *P. infestans* isolates in all experiments conducted.

Two different isolates of *P. infestans* were used in this study, and 6 genotypes out of 39 tested, showed different reactions depending on the isolate. The differential interaction of the isolates and the accessions might be either due to the presence or absence of the virulence to *R*6 or *R*8, respectively, or due to the presence or absence of the virulence to unidentified *R* genes. This interaction supports the opinion of Flier et al. (2003) about *R* gene-based resistance to *P. infestans* in *S. nigrum*. Flier et al. (2003) observed interactions for 3 genotypes of *S. nigrum* out of 8 tested with 2 or 3 *P. infestans* isolates, but did not observe any interactions for 2 extremely resistant *S. nigrum* genotypes with 12 different isolates, and for 1 susceptible genotype of *S. nigrum* (Sn001) with 9 different isolates of *P. infestans*, including the isolate representing race 0. Studies on the inheritance of resistance to *P. infestans* of F2 progeny obtained after crossing susceptible and resistant *S. nigrum* parents, may give more information about the nature of resistance.

The comparison of the results obtained after inoculation of detached leaves with the results obtained after inoculation of whole plants showed no major differences between the two tests. Eight *S. nigrum* accessions, two of *S. villosum*, and one of *S. scabrum*, which were highly resistant in the detached leaf assay, were also highly resistant in the whole plant assay. Nine accessions of *S. nigrum* infected in the detached leaf assay were also infected when whole plants were inoculated. However, two exceptions occurred when the detached leaves, but not the plants were infected. This might possibly be explained by the younger age of the plants tested in the whole plant assay.

To assess the influence of greenhouse- and field-growing conditions on *S. nigrum* plants on disease development in the detached leaf assay, plants of selected accessions were grown in the greenhouse and in the field simultaneously. It has been shown that in some cases leaves from field-grown plants gave a resistant reaction in contrast to the leaves from greenhouse-grown plants, which were susceptible to *P. infestans*. Even though the leaves for the detached leaf assay were collected from the middle part of the plant, there were some differences in the reaction of the leaves within the same plant. In studies by Carnegie and Colhoun (1982) on potato–*P. infestans* interactions, in some cultivars, leaflets of the same leaf showed reactions varying from hypersensitivity, which commonly occurred on upper and middle leaves of potato, to normal lesions. The authors suggested that a slight change in the physiological state of a leaflet could affect the establishment of a lesion.

The isolates used in our study represented the new population of *P. infestans*, which is very diverse in Poland (Zarzycka 1997; Śliwka et al. 2007). Our studies extended the range of *S. nigrum* accessions tested under laboratory conditions, and showed that 23 out of 39 *S. nigrum* accessions, originating from the UK, France, Germany, Poland, Romania and Russia, were susceptible to Polish *P. infestans* isolates. All isolates obtained during 2001 from black nightshade weeds found among diseased potatoes in Wales, UK were determined to be part of the new population by genetic finger printing analysis by Deahl et al. (2004). Also, the current population of *P. infestans* in The Netherlands was pathogenic on *S. nigrum*. Moreover, oospores were found on the leaves of *S. nigrum* in the field and also after artificial inoculation with A1 and A2 *P. infestans* strains by Flier et al. (2003).

The results of our research confirm that *S. nigrum* is a host of *P. infestans*, because non-host resistance is defined as immunity displayed by an entire plant species against all genetic variants of a pathogen species (Heath 2000). Flier et al. (2003) suggested a reconsideration of the present status of *S. nigrum* as a non-host plant to *P. infestans* based on the presence of field infections and results obtained in detached leaf inoculation studies.

Even though in our studies about 60% of *S. nigrum* accessions were infected with one or two different *P. infestans* isolates, the natural conditions in Poland are often much less favourable for pathogen development

than the conditions provided in the laboratory: highly aggressive and virulent *P. infestans* isolates, high humidity and the optimal temperature for *P. infestans* growth. Therefore, it is concluded that the role of *S. nigrum* in potato late blight epidemics is minor. Flier et al. (2003) also stated that based on the nationwide late blight survey in The Netherlands in 1999–2000, which showed that infection of *S. nigrum* was a relatively rare event, diseased plants do not contribute significantly to the overall late blight disease pressure present in potato production areas.

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