*Plant Pathology* (2003) **52**, 326–337

# Stability of partial resistance in potato cultivars exposed to aggressive strains of *Phytophthora infestans*

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Potato cultivars were evaluated for their resistance responses to aggressive strains of *Phytophthora infestans* in field and laboratory experiments. Analysis of variance revealed differential cultivar-by-isolate interactions for both foliar and tuber blight resistance. Differential responses occur as revealed by specific susceptibilities of cultivars to certain pathogen genotypes and changing rank order. In general, severity of late blight epidemics as observed in the haulms did not correlate well with foliar blight resistance ratings as presented in the National List of Recommended Potato Varieties. No significant correlation was found between tuber blight incidence under field conditions and the tuber blight rating in the National List. Also, there was no relation between the field and laboratory tuber blight resistance assessments. A significant association was demonstrated between late blight infection in the foliage and tuber blight incidence under field conditions. The presence of differential interaction, independent of R-gene-based resistance, indicates some adaptation of *P. infestans* to partial resistance and consequently adverse effects on the stability and durability of partial resistance to potato late blight.

*Keywords*: differential interactions, epidemiology, late blight, tuber blight

## Introduction

The oomycete *Phytophthora infestans*, the cause of late blight of potato, is considered one of the most important pathogens of potatoes worldwide. The pathogen affects leaves, stems and tubers, leading to serious yield losses and high costs for chemical control.

To date the vast majority of potato cultivars commonly grown in Western Europe (Colon *et al*., 1995) and North America (Platt & Tai, 1998) are susceptible to late blight. The use of numerous applications of both protective and curative fungicides is common practice in order to control potato late blight, which is expensive and has several adverse effects on the environment. Host resistance should allow a significant reduction of fungicide use while maintaining the present yield and quality standards (Inglis *et al*., 1996). Numerous attempts to achieve durable resistance in potato by the incorporation of R-genes from *Solanum demissum* and *S. stoloniferum* (Black *et al*., 1953; Malcolmson & Black, 1966) proved to be unsuccessful due to rapid adaptation of the pathogen as reviewed by Van der Plank (1971) and Turkensteen (1993).

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*Accepted 10 February 2003*

With the growing public demand for crop protection methods with no adverse effects on health and the environment, breeding for durable resistance against late blight has become a focus for most modern potato-breeding programmes (Colon *et al*., 1995; Inglis *et al*., 1996; Peters *et al*., 1999). Coincidental with these efforts has been the displacement of the US-1 clonal lineage by several more aggressive genotypes of the pathogen in North America (Lambert & Currier, 1997) and the presence of a diverse population of *P. infestans* in Western Europe (Spielman *et al*., 1991). Evidence is accumulating that *P. infestans* is sexually reproducing in many countries in Western Europe (Spielman *et al*., 1991; Drenth *et al*., 1994; Sujkowski *et al*., 1994; Andersson *et al*., 1998; Turkensteen *et al*., 2000). Sexual reproduction and the presence of functional oospores result in high levels of variation in the pathogen, and might lead to increased and more rapid adaptation to certain fungicides and host resistance.

Increased levels of aggressiveness mark the newly established population in Western Europe. Flier *et al*. (1998) studied the variation in aggressiveness to potato tubers in local populations of *P. infestans* in the Netherlands. It was concluded that high levels of aggressiveness to tubers are present in three local populations of the pathogen, and that large variation for aggressiveness is being maintained in these populations. Similar results were obtained when

the variation in aggressiveness to the foliage was evaluated (Flier & Turkensteen, 1999).

In recent years, commercial potato growers repeatedly claimed severe late blight outbreaks in cultivars with high levels of partial resistance and high tuber blight incidences, leading to serious yield losses (Inglis *et al*., 1996; Platt & Tai, 1998). Adequate information on the level of tuber blight resistance is especially important for farmers applying organic or integrated cropping systems. In a recent study, Varis *et al*. (1996) reported that late blight was a serious problem in cultivar Bintje in both integrated and organic systems in Finland. Total yields were 10 and 36% lower, respectively, compared with the conventional cropping system. Similar late blight problems have been reported in organic potato production in the Netherlands (E.T. Lammerts-van Bueren, Louis Bolk Institute, 3972 LA Driebergen, the Netherlands, personal communication). Resistant potato cultivars such as Escort and Santé, which are widely grown in organic farming in the Netherlands, showed considerable levels of tuber blight leading to serious yield losses in recent years. The observation of increased yield losses due to tuber blight has raised doubts about the stability of partial resistance.

The presence of an aggressive, variable population of the pathogen may affect the durability of partial resistance (Nelson, 1979; Latin *et al*., 1981) due to accelerated adaptation of aggressive forms of the pathogen with higher levels of parasitic fitness (Nelson, 1979). A shift towards more aggressive populations of *P. infestans* will cause an overall decrease in resistance of potato cultivars. In addition, differential changes in ranking of partially resistant cultivars after exposure to different genotypes of the pathogen may occur (Leonard & Moll, 1979). The latter effect could serve as an operational definition of instability of field resistance, and is synonymous with the definition of erosion of field resistance according to Nelson (1979). In practice, instability of resistance will change the ranked order of cultivars. In a recent study, Flier *et al*. (2001) explored the presence and relative importance of cultivar-by-isolate interaction in tuber blight incidence and severity. Specificity in cultivar-by-isolate interactions was clearly demonstrated. Additional studies are needed to extend knowledge about host × pathogen differential interaction in the potato–late blight pathosystem to partial resistance in the foliage, and about the specificity of this interaction under field conditions.

The aim of the present study was (i) to evaluate the level of partial resistance of some potato cultivars with respect to the foliage and tubers; and (ii) to evaluate the stability of foliar and tuber blight resistance for partially resistant potato cultivars to selected strains of a sexually reproducing *P. infestans* population. Consequently, the role of specificity is discussed in the interaction between partially resistant potato cultivars and aggressive strains of *P. infestans*. The nature of the host–pathogen interactions was tested under field and climate chamber conditions, and interrelationships were studied between components of partial resistance.

## Materials and methods

### Isolate selection, culturing and inoculum preparation

Information on virulence factors, mating type and data concerning the collection of the isolates is presented in Table 1. Five isolates, all belonging to the new population of *P. infestans* in the Netherlands, were selected (Table 1). IPO82001 serves as a reference isolate, as it has been used for resistance testing by breeders and to obtain foliar resistance ratings for the national list of recommended potato varieties (Ebskamp *et al*., 1999). In earlier tests, isolate IPO82001 was characterized by an intermediate level of aggressiveness to the foliage (Flier & Turkensteen, 1999) and a low level of tuber pathogenicity (Flier *et al*., 1998). IPO98014 is at present one of the most aggressive isolates in the collection, and was obtained from a blighted potato stem found on a potato dump in early spring. Isolates F95573, IPO655-2A and IPO428-2 showed high levels of aggressiveness to tubers in previous whole-tuber inoculation experiments (Flier *et al*., 2001). Isolates taken from liquid nitrogen storage were first inoculated on tuber slices of the general susceptible potato cv. Bintje and incubated in the dark at 15°C for 5–7 days. When sporulating mycelium was present, small tufts of mycelium were placed in a drop of water on the lower epidermis of leaflets of cv. Bintje placed in 9 cm Petri dishes containing 10 mL 2% water agar. The inoculated leaflets were incubated for 7 days in a climate chamber at 15°C with a 16 h light period (Philips fluorescence tubes type

Table 1 Isolates of *Phytophthora infestans* used in inoculation experiments, showing specific virulence spectrum, mating type, year and origin of collection

| Isolate | Race | Mating type | Year of collection | Source |
|---|---|---|---|---|
| F95573[a] | 1,3,4,7,10,11 | A1 | 1995 | Cull pile, Flevoland |
| IPO428-2[b] | 1,2,3,4,5,6,7,8,9,10,11 | A2 | 1992 | Allotment garden, Ede, Gelderland |
| IPO655-2A[b] | 1,2,3,4,5,6,7,8,9,10,11 | A1 | 1992 | Allotment garden, Ede, Gelderland |
| IPO82001[c] | 1,2,3,4,5,6,7,10,11 | A2 | 1982 | Commercial potato crop, Gembloux, Belgium |
| IPO98014[b] | 1,2,3,4,7,11 | A1 | 1998 | Commercial starch potato crop, Drenthe |

[a]Isolate kindly provided by M. Zwankhuizen, Department of Phytopathology, Wageningen University, the Netherlands.
[b]Isolates from the Plant Research International *Phytophthora infestans* collection.
[c]Reference isolate used for foliar blight resistance assessment in the Netherlands.

Table 2 Potato cultivars used in this study, the presence of identified R-genes and known late blight resistance ratings according to the National List of Recommended Potato Varieties

| Cultivar | Purpose | Known resistance | R-genes[c] | Late blight resistance rating[a] | |
|---|---|---|---|---|---|
| | | | | Foliar | Tuber |
| Astarte | Starch | High partial resistance | R3 | 7 | 6 |
| Bintje | Ware | Susceptible | R0 | 3 | 3 |
| Eigenheimer | Ware | Susceptible | R0 | 5 | 3 |
| Hertha | Ware | Partial & R-gene resistance | R1 R3 R10 | 6 | 7 |
| Karnico | Starch | Partial & R-gene resistance | na[d] | 7·5 | 6·5 |
| Kartel | Starch | Partial & R-gene resistance | na | 8[b] | 6·5[b] |
| Pimpernel | Ware | High partial resistance | R0 | 8 | 8 |
| Producent | Starch | Partial & R-gene resistance | R10 | 7 | 8 |
| Santé | Ware | Partial & R-gene resistance | R1 R10 | 4 | 8 |
| Sirtema | Ware | Susceptible | R0 | 4 | 6 |

[a]Rating according to the National List of Recommended Potato Varieties 1999 (Ebskamp *et al.*, 1999).
[b]Ratings according to the National List of Recommended Potato Varieties 1988 (Ebskamp *et al.*, 1998).
[c]Based on unpublished data.
[d]No data available.

33, intensity 12 $Wm^{-2}$). For large-scale inoculum production, greenhouse-grown leaves were cut, placed on wetted filter paper in plastic trays, and inoculated. Trays were wrapped in transparent polythene bags and incubated for 5–7 days as described previously. Inoculum for field infection was prepared by dipping sporulating leaflets in a 10 L bucket filled with tap water, filtering the crude suspension through cheesecloth and adjusting the sporangia concentration to $1{\cdot}0 \times 10^4$ sporangia $mL^{-1}$.

### Response to aggressive isolates

Over a 2-year period, eight potato cultivars (Astarte, Bintje, Eigenheimer, Hertha, Kartel, Pimpernel, Producent and Sirtema) with varying levels of resistance to late blight according to the National List of Recommended Potato Varieties (Ebskamp *et al.*, 1999) (Table 2) were evaluated under field conditions for their response to two aggressive *P. infestans* isolates, F95573 and IPO98014. Field evaluations were performed on a sandy loam soil at the experimental farm at Lienden, the Netherlands.

In both years, certified seed was hand-planted in mid-April using a randomized complete block design with three replicates of four hill plots of 6 m each. Plants were spaced 0·7 m between rows and 0·3 m between hills in a row (≈ 80 plants per plot). Plots had 5 m bare, fallow spacing on all sites to reduce interplot interference and to provide adequate access for sprinkler irrigation and weed control. Silage maize was grown as a buffering crop surrounding the experimental field. All plots received fertilizer according to common practice for ware potato production. A weekly fungicide application of mancozeb (2 kg a.i. $ha^{-1}$) was given to test plots until the third week of July in order to prevent early uncontrolled late blight development. Plots were inoculated during the first week of August. A sporangial suspension ($1{\cdot}0 \times 10^4$ sporangia $mL^{-1}$) of either isolate was applied late in the evening by spraying across the plots at a rate of ≈ 10 mL per plant. An overhead irrigation system (5 mm $h^{-1}$) was used for 2 h per day for 5 weeks to accelerate late blight epidemics in the foliage and enhance infection of the tubers. The percentage of leaf area affected by late blight was estimated for each plot twice a week. Haulms were killed after the first week of September, and tubers were dug and harvested by hand and incubated at 15°C for 2 weeks. Only tubers from hills 2 and 3 were used for tuber blight assessments, in order to avoid a possible bias caused by hills where microclimate and late blight epidemic development might be influenced by the bare fallow. The number of blighted tubers (FPTUB) per plot was assessed visually and the percentage of blighted tubers calculated.

### Stability of partial resistance

The stability of field resistance of three cvs (Bintje, Santé & Pimpernel, 1998) and four cvs (Bintje, Karnico, Santé & Pimpernel, 1999) with varying levels of race-nonspecific resistance to late blight (Table 2) was evaluated for 2 years under field conditions for their response to two highly aggressive *P. infestans* strains (IPO655-2A and IPO98014) and one moderately aggressive isolate, IPO82001. Field evaluations were performed on heavy clay at the IPO experimental farm in Wageningen, the Netherlands.

The experiment consisted of three randomized blocks in both years of evaluation. Plot size was five hills, each 4 m long with 0·7 m between rows and 0·3 m spacing between plants within a row (≈70 plants per plot). Each plot was isolated by 5 m of bare fallow. Silage maize was grown as a buffer crop surrounding the experiment and providing a 5 m buffer between the blocks.

Plots were inoculated in mid-July in both years with a sporangial suspension ($1{\cdot}0 \times 10^4$ sporangia $mL^{-1}$) across the plots. Sprinkler irrigation (5 mm $h^{-1}$) was applied

approximately three times a week for 2 h during the first 3 weeks after inoculation. Disease assessments were recorded twice a week by estimating the percentage leaf area affected by late blight.

Tuber infections were evaluated by digging up tubers from the three middle rows at 5 weeks post-inoculation. Tubers were incubated for 2 weeks at ambient temperature, and subsequently visually examined for the presence of blighted tubers. The percentage of blighted tubers (FPTUB) was calculated for each plot.

### Whole-tuber inoculations

Whole-tuber inoculation experiments were performed using tubers from additional plots growing at the Lienden site (eight cultivars in 1998 and 1999) and Wageningen site (three and four cultivars in 1998 and 1999, respectively). Whole-tuber inoculations were performed at the end of August using tubers from additional plots. For this purpose, tubers were dug by hand to minimize wounding, immediately transferred to the laboratory, and washed to remove adhering soil. Undamaged tubers, about 35 tubers per crate, were placed in plastic seed tuber crates with rose ends facing upward. Tubers were inoculated using isolates IPO82001, IPO655-2A and IPO98014, and subsequently incubated according to the methods described by Flier *et al.* (2001). Three replicate trays were inoculated for each cultivar-by-isolate combination.

After 2 weeks in storage, tubers were visually examined for the presence of tuber blight symptoms. The percentage of infected tubers per crate (WPTUB) was calculated. Tuber rot was evaluated by means of an invasive ability index (IAI) (Flier *et al.*, 1998; Flier *et al.*, 2001). Diseased tubers were cut longitudinally, and disease severity was scored for each individual tuber using the following scale: 0 = no symptoms, 1 =< 2·5% of cut area with symptoms, 2 = 2·5–10%, 3 = 10–25%, 4 = 25–50%, and 5 => 50% of cut area with symptoms.

### Compatibility tests

Detached leaflets of the potato cultivars used in the field experiments were inoculated with five *P. infestans* isolates to determine the compatibility of the isolates used in the field experiments in 1999. Seven days before field inoculation, fully developed lateral leaflets were collected from randomly selected plants (one single leaflet per plant) growing at the Lienden (experiment 1) and Wageningen sites (experiments 1 and 2).

Ten leaflets were inoculated for each cultivar–isolate combination. Individual leaflets were placed in 9 cm Petri dishes filled with 10 mL 2% water agar and inoculated by placing one 10 $\mu$L droplet of sporangial inoculum ($1{\cdot}0 \times 10^4$ sporangia $mL^{-1}$) on the abaxial side of each leaf. Inoculum was prepared from infected leaflets of cv. Bintje according to Flier & Turkensteen (1999). Petri plates with the inoculated leaves were wrapped in transparent polythene bags and incubated in a climate chamber for 1 week at 15°C with a light intensity of 12 $Wm^{-2}$, 16 h light per day. In both experiments lesions were measured three times, between days 3 and 5, using an electronic calliper. The length and width of each lesion was measured, and the average diameter, lesion area and lesion growth rate (LGR) were calculated. Incompatibility was defined here as the mechanism leading to the predominance of unsuccessful infections where the pathogen had been arrested by a hypersensitive reaction by the plant. Therefore a cultivar × isolate interaction leading to an average LGR of 0·0 was regarded as incompatible. In the first test, sporulation (SPOR) was visually assessed using a 0–4 rating scale (0 = no sporulation to 4 = dense sporulation).

In the second experiment, an effort was made to quantify sporulation density. Five leaflets showing single expanding lesions of each cultivar evaluated at the Wageningen site were randomly collected at 7 days post-inoculation. Sporangia were collected by gently dipping each leaflet with a sporulating lesion in 10 mL Isoton II solution (Beckman Coulter BV, Mijdrecht, the Netherlands). Sporangia were counted using a Coulter Counter Z10 (Beckman Coulter BV). Sporulation density and average sporangia production per $cm^2$ lesion area were calculated.

### Data analysis

All statistical tests were performed using the statistical software GENSTAT version 5·2.1 (Payne *et al.*, 1993). Foliar resistance levels of potato cultivars in Wageningen and Lienden were compared in each year by ANOVA on the standardized area under the disease progress curve values (stAUDPC) (Campbell & Madden, 1990). Tuber blight data were analysed using ANOVA and residual maximum likelihood (REML) procedures. The relation between foliar attack (with stAUDPC as a condensate measure) and tuber blight incidence was explored using polynomial linear regression analysis. Spearman rank correlations between the ANOVA estimates for stAUDPC, FPTUB, WPTUB, IAI, LGR and SPOR were calculated to determine their interrelationship. The foliar and tuber blight ratings according to the Dutch National List of Recommended Varieties were transformed by Y = 10 – (rating) in order to permit calculation of positive correlations between listed ratings and the various disease parameters assessed.

## Results

### Response to aggressive isolates

Foliar and tuber resistance against two isolates (I) of late blight varied considerably among eight potato cultivars (C) that were evaluated in field inoculation experiments on an experimental station near Lienden in 1998 and 1999 (Table 3). ANOVA performed on stAUDPC showed significant effects ($P < 0{\cdot}001$) due to cultivars and year of evaluation (Y). Significant contributions of cultivar-by-isolate ($C \times I$; $P = 0{\cdot}042$) and cultivar-by-year ($C \times Y$; $P < 0{\cdot}001$) interactions were also detected. No significant cultivar-by-isolate-by-year interaction was found

Table 3 Resistance response of eight potato cultivars to infection in the haulm and the tuber by two aggressive isolates of *Phytophthora infestans* during 2 years' evaluation at Lienden

| | Foliar blight (stAUDPC) | | | | Tuber blight (% blighted tubers) | | | |
|---|---|---|---|---|---|---|---|---|
| | F95573 | | IPO98014 | | F95573 | | IPO98014 | |
| Cultivar | 1998 | 1999 | 1998 | 1999 | 1998 | 1999 | 1998 | 1999 |
| Astarte | 14·6 | 27·1 | 14·2 | 27·7 | 12·1 | 2·7 | 23·1 | 5·2 |
| Bintje | 12·2 | 27·6 | 14·0 | 28·0 | 14·8 | 10·2 | 36·3 | 14·7 |
| Eigenheimer | 12·5 | 28·4 | 12·7 | 30·8 | 10·7 | 3·7 | 59·3 | 14·3 |
| Hertha | 12·6 | 28·1 | 17·5 | 26·7 | 9·8 | 1·9 | 8·2 | 2·3 |
| Kartel | 0·1 | 4·2 | 3·6 | 0·8 | 0·1 | 0·7 | 1·9 | 0·7 |
| Pimpernel | 14·9 | 29·9 | 12·1 | 31·9 | 4·5 | 0·5 | 19·8 | 2·0 |
| Producent | 13·5 | 25·8 | 13·5 | 22·9 | 0·2 | 1·2 | 0·6 | 1·3 |
| Sirtema | 12·3 | 26·6 | 13·1 | 22·7 | 3·8 | 1·5 | 5·1 | 2·0 |
| $LSD_{cultivar}$ ($P = 0·05$) | | | | 3·4 | | | | 3·8 |
| $LSD_{isolate}$ ($P = 0·05$) | | | | 0·9 | | | | 1·9 |
| $LSD_{cultivar\text{-}isolate\text{-}year}$ ($P = 0·05$) | | | | 5·4 | | | | 7·5 |

StAUDPC = standardized area under the disease progress curve.

($P = 0·365$). Cultivar-by-isolate differential interactions contributed 0·5% of the total variation accounted for by the model. Cultivar Kartel was the most resistant to both *P. infestans* strains (Table 3) but showed surprisingly more resistance to isolate IPO98014 in 1999. All other cultivars showed rather susceptible reactions under field conditions when exposed to these isolates. Moreover, the resistant standard cv. Pimpernel in three out of four tests had stAUDPC values comparable with the susceptible standard cv. Bintje (Table 3). Late blight infection was more severe in 1999 than in 1998 (average stAUDPC values of 24·3 and 12·1, respectively). Both isolates evoked similar levels of disease in the foliage; average stAUDPC values of 18·2 and 18·3, respectively.

Tubers exposed to inoculum produced in the haulm of the eight potato cultivars resulted in significant tuber infection after 2 weeks' incubation following harvest of the tubers (Table 3). The main factors, cultivar, isolate and year, showed highly significant effects ($P < 0·001$). The contribution of C × I, C × Y and isolate-by-year (I × Y) interactions were also significant (ranging from $P = 0·013$ to $P < 0·001$). Again, no significant cultivar-by-isolate-by-year interaction was detected ($P = 0·415$). The C × I interaction accounted for 9·5% of all the variation that could be attributed to the ANOVA model. Starch potato cvs Kartel and Producent showed the lowest overall mean levels of tuber blight attack (0·8% blighted tubers for both cultivars) (Table 3). Bintje and Eigenheimer were the cultivars with the most susceptible tubers (overall means of 19·0 and 22·0%, respectively). Isolate IPO98014 was significantly more aggressive on tubers than isolate F95573 (Table 3). Higher levels of tuber blight attack were observed in 1998 compared with 1999 (with overall means of 12·3 and 4·1% blighted tubers, respectively). Tubers of cv. Pimpernel were quite susceptible to isolate IPO98014 in 1998 when 19·8% of the tubers were infected. Surprisingly, the high tuber blight incidence in Pimpernel was linked to the second lowest foliar blight level (stAUDPC of 12·1) observed for this cultivar in 1998.

## Stability of partial resistance

The level and stability of partial resistance in three (1998) and four (1999) potato cultivars were evaluated in field inoculation studies. The observed levels of resistance to late blight varied from very susceptible to moderately resistant in terms of stAUDPC and percentage blighted tubers (Table 4). Potato haulms were totally killed by late blight within 3 weeks post-inoculation in both years of evaluation. The effects for cultivar, isolate and year were significant ($P < 0·001$). The probability levels of C × I and C × Y interactions were $P = 0·018$ and $P < 0·001$, respectively. In contrast to the results obtained at Lienden, C × I × Y interaction contributed significantly ($P = 0·003$) to the observed variation in foliar resistance. On average, 5·6 and 1·6% of the variation could be explained by C × I and C × I × Y interaction, respectively. Bintje was the most susceptible cultivar, with an overall mean stAUDPC of 52·1, while cvs Santé and Pimpernel showed intermediate levels of resistance in the foliage with overall mean stAUDPC values of 21·9 and 24·9, respectively (Table 4). Cultivar Karnico was the most resistant cultivar, with an overall mean stAUDPC value of 1·9 (1999 data only). Isolates IPO655-2A and IPO98014 showed similar levels of aggressiveness, while IPO82001 caused less severe late blight epidemics in the foliage.

As in Lienden, average late blight epidemics in Wageningen were more severe in 1999 compared with 1998. Remarkable differences in stability of foliar resistance were observed for the four cultivars tested in 1999. Both cvs Karnico and Santé showed a fairly stable reaction pattern when exposed to three *P. infestans* strains, while cvs Bintje and Pimpernel showed a surprisingly high level of foliar susceptibility when exposed to the highly aggressive strains IPO655-2A and IPO98014 (Table 4).

Table 4 Resistance response of four potato cultivars to infection in the haulm and the tuber by three isolates of *Phytophthora infestans* during 2 years' field evaluation at Wageningen

| | Foliar blight (stAUDPC) | | | | | | Tuber blight (% blighted tubers) | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Isolate | IPO82001 | | IPO655-2A | | IPO98014 | | IPO82001 | | IPO655-2A | | IPO98014 | |
| Cultivar | 1998 | 1999 | 1998 | 1999 | 1998 | 1999 | 1998 | 1999 | 1998 | 1999 | 1998 | 1999 |
| Bintje | 35·7 | 40·5 | 46·3 | 70·9 | 45·5 | 73·6 | 10·5 | 5·9 | 14·5 | 2·5 | 14·3 | 1·6 |
| Santé | 24·8 | 21·1 | 22·6 | 22·1 | 21·1 | 20·0 | 3·3 | 1·4 | 7·0 | 3·3 | 5·4 | 3·1 |
| Pimpernel | 6·9 | 24·6 | 13·6 | 38·9 | 22·4 | 43·0 | 15·7 | 16·7 | 6·3 | 2·3 | 11·3 | 3·9 |
| Karnico | nd[a] | 1·9 | nd | 1·2 | nd | 2·6 | nd | 5·8 | nd | 6·2 | nd | 2·6 |
| $LSD_{cultivar}$ ($P = 0·05$) | | | | | | 7·3 | | | | | | 4·6 |
| $LSD_{isolate}$ ($P = 0·05$) | | | | | | 5·5 | | | | | | 3·5 |
| $LSD_{cultivar\text{-}isolate\text{-}year}$ ($P = 0·05$) | | | | | | 8·1 | | | | | | 8·2 |

StAUDPC = standardized area under the disease progress curve.
[a]Not determined.

Table 5 Percentage blighted tubers and tuber blight severity (as presented as a 1–4 invasive ability index (IAI)) of eight potato cultivars evaluated in whole-tuber inoculation experiments with four aggressive strains of *Phytophthora infestans* in two successive years at Lienden

| | Blighted tubers (%) | | | | | | | | Tuber blight severity (IAI) | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | F95573 | | IPO428-2 | | IPO655-2A | | IPO98014 | | F95573 | | IPO428-2 | | IPO655-2A | | IPO98014 | |
| Cultivar | 1998 | 1999 | 1998 | 1999 | 1998 | 1999 | 1998 | 1999 | 1998 | 1999 | 1998 | 1999 | 1998 | 1999 | 1998 | 1999 |
| Astarte | 39·3 | 51·6 | 17·5 | 35·2 | 6·2 | 7·7 | 23·2 | 40·1 | 1·8 | 2·3 | 2·2 | 2·2 | 1·2 | 2·6 | 1·6 | 2·1 |
| Bintje | 70·6 | 82·4 | 74·8 | 74·6 | 22·0 | 6·8 | 57·7 | 67·7 | 2·4 | 3·4 | 2·9 | 2·9 | 2·1 | 2·5 | 2·1 | 3·1 |
| Eigenheimer | 89·6 | 82·7 | 78·0 | 80·4 | 13·6 | 12·2 | 75·4 | 74·3 | 2·2 | 3·0 | 1·9 | 3·0 | 1·3 | 2·8 | 1·6 | 2·8 |
| Hertha | 89·8 | 64·5 | 44·2 | 54·0 | 7·2 | 1·0 | 67·7 | 71·2 | 2·1 | 3·4 | 2·0 | 2·9 | 1·0 | 2·5 | 1·8 | 3·0 |
| Kartel | 1·9 | 0·8 | 0·9 | 0·0 | 0·0 | 0·0 | 6·4 | 3·6 | 1·3 | 1·7 | 1·2 | 0·0 | 0·0 | 0·0 | 2·1 | 1·0 |
| Pimpernel | 34·5 | 75·7 | 35·2 | 66·1 | 0·0 | 0·0 | 50·1 | 72·5 | 1·7 | 1·8 | 2·3 | 1·8 | 0·0 | 0·0 | 1·9 | 2·2 |
| Producent | 21·1 | 50·5 | 4·4 | 7·1 | 0·0 | 0·0 | 3·6 | 11·9 | 2·3 | 1·7 | 1·2 | 2·3 | 0·0 | 0·0 | 1·7 | 2·4 |
| Sirtema | 53·2 | 54·7 | 57·0 | 63·8 | 4·6 | 1·1 | 40·7 | 25·3 | 1·8 | 3·2 | 2·6 | 3·3 | 1·6 | 2·6 | 2·0 | 2·8 |
| $LSD_{cultivar}$ ($P = 0·05$) | | | | | | | | 7·4 | | | | | | | | 0·4 |
| $LSD_{isolate}$ ($P = 0·05$) | | | | | | | | 5·2 | | | | | | | | 0·3 |
| $LSD_{cultivar\text{-}isolate\text{-}year}$ ($P = 0·05$) | | | | | | | | 20·9 | | | | | | | | 1·1 |

Tuber blight attack at Wageningen showed less pronounced differences between cultivars and isolates compared with the Lienden site. ANOVA revealed significant differences among cultivars ($P = 0·026$) and year of evaluation ($P = 0·002$). Although 27·0% of the total explained variation was accounted for by cultivar-by-isolate interaction, no significant effect was demonstrated. Cultivars Bintje and Pimpernel showed a similar susceptibility of tubers to late blight attack (with overall means of 8·2 and 9·3% blighted tubers, respectively) (Table 4). On average, cvs Santé and Karnico showed the most resistant reaction (overall mean 3·9 and 4·9%, respectively). All three isolates showed similar average levels of aggressiveness to tubers. The interaction between isolate IPO82001 and cv. Pimpernel was marked by remarkably high incidences of tuber blight in both years, similar to the results obtained with cv. Pimpernel and isolate IPO98014 in 1998 at Lienden.

In concordance with the results obtained at the Lienden site, average tuber blight incidence at Wageningen was higher in 1998 compared with 1999. An increase in the average percentage of blighted tubers as observed in 1998 tended to be associated with slower late blight epidemics in the foliage (as measured by stAUDPC values) in both experiments.

## Whole-tuber inoculations

Large differences among cultivars and isolates were found in whole-tuber tests with tubers from both locations, Lienden and Wageningen (Tables 5 and 6, respectively). General immunity to tuber infection was not observed for the cultivars evaluated in the whole-tuber tests.

### *Tuber inoculations (Lienden site)*

In 1998, percentage of blighted tubers varied between 0% for cvs Kartel, Pimpernel and Producent in combination with IPO655-2A and 89·8% for cv. Hertha inoculated with F95573 (Table 5), and ranged in 1999 from 0% (cvs Kartel, Pimpernel and Producent inoculated with IPO428-2 IPO655-2A and IPO655-2A, respectively) to a high of 82·7% (cv. Eigenheimer inoculated with F95573) (Table 5). ANOVA performed on percentage blighted tubers (after angular transformation) for the 1998 and

Table 6 Percentage blighted tubers and tuber blight severity (as presented as a 1–4 invasive ability index (IAI)) of four potato cultivars evaluated in whole-tuber inoculation experiments with two aggressive strains (IPO655-2A, IPO98014) and a reference isolate (IPO82001) of *Phytophthora infestans* in two successive years at Wageningen

| | Blighted tubers (%) | | | | | | Tuber blight severity (IAI) | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | IPO82001 | | IPO655-2A | | IPO98014 | | IPO82001 | | IPO655-2A | | IPO98014 | |
| Cultivar | 1998 | 1999 | 1998 | 1999 | 1998 | 1999 | 1998 | 1999 | 1998 | 1999 | 1998 | 1999 |
| Bintje | 16·1 | 67·2 | 8·6 | 45·2 | 23·4 | 80·3 | 2·8 | 2·0 | 1·7 | 2·2 | 1·7 | 2·6 |
| Santé | 7·7 | 84·6 | 5·6 | 71·0 | 18·3 | 79·7 | 2·8 | 1·6 | 1·8 | 1·2 | 3·0 | 2·0 |
| Pimpernel | 13·8 | 78·3 | 4·5 | 90·3 | 35·0 | 90·3 | 1·9 | 1·5 | 1·7 | 1·8 | 2·4 | 2·6 |
| Karnico | nd[a] | 66·7 | nd | 26·2 | nd | 73·5 | nd | 2·2 | nd | 2·1 | nd | 2·4 |
| $LSD_{cultivar}$ ($P = 0·05$) | | | | | | 5·6 | | | | | | 0·4 |
| $LSD_{isolate}$ ($P = 0·05$) | | | | | | 4·8 | | | | | | 0·3 |
| $LSD_{cultivar\text{-}isolate\text{-}year}$ ($P = 0·05$) | | | | | | 9·6 | | | | | | 0·7 |

[a]Not determined.

1999 Lienden data showed significant effects due to cultivars ($P < 0·001$), isolates ($P < 0·001$) and years ($P = 0·013$). Significant interaction terms were found for C × I ($P < 0·001$) and C × Y ($P = 0·002$). A total of 89·2% of the observed variation could be attributed to the model, and 14·2% of the explained variance was due to the C × I differential interaction term. Isolate F95573 caused the highest average percentage of blighted tubers, closely followed by IPO98014 and IPO428-2. Isolate IPO655-2A proved to be the least aggressive tuber blight strain. Tubers of cv. Kartel showed high resistance after inoculation with all isolates except IPO98014 when up to 6·4% blighted tubers were recorded. Remarkably high incidences of tuber infection were also observed in the specific interaction between Producent and F95573.

ANOVAs for the 1998 and 1999 IAI Lienden data revealed significant cultivar, isolate and year effects ($P < 0·001$) and a C × Y interaction effect ($P = 0·001$). No significant C × I interaction term was observed, although 9·7% of the explained variance could be attributed to cultivar-by-isolate interaction. The model accounted for 68·3% of the observed variation in tuber blight severity. Non-zero values for IAI varied from 1·2 (cvs Astarte, Kartel and Producent in combination with IPO655-2A, IPO428-2 and IPO428-2, respectively) to 2·9 (cv. Bintje inoculated with IPO428-2) in 1998, and from 1·0 (cv. Kartel inoculated with IPO98014) to 3·4 (cvs Bintje inoculated with F95573) in 1999 (Table 5). The average IAI for isolate IPO655-2A was significantly lower than for the other three isolates of *P. infestans*.

*Tuber inoculations (Wageningen site)*

The whole-tuber inoculation tests with tubers from Wageningen showed similar levels of variation for tuber attack (Table 6) to those found using tubers from the location at Lienden. The ANOVA on the percentage blighted tubers showed highly significant effects of cultivar, isolate, year and all two-way interaction terms. Cultivar-by-isolate-by-year interaction also contributed to the observed tuber blight incidences in 1998 and 1999 ($P = 0·005$), although only 1·8% of the variance accounted for could be assigned to this interaction term. The model accounted for 95·2% of the observed variation, and 9·7% of the explained variance could be attributed to C × I differential interaction. The percentage of blighted tubers ranged between a low 4·5% in 1998 for cv. Pimpernel inoculated with IPO655-2A and a high 90·3% in 1999 for cv. Pimpernel inoculated with either IPO655-2A or IPO98014. In 1999, tubers of cv. Karnico were remarkably susceptible to inoculation with isolate IPO82001 and IPO98014. In general, tuber blight incidences were high in both years of whole-tuber inoculations.

For IAI, only 52·8% of the observed variation could be attributed to the model used in the ANOVA. Significant effects were detected for cultivars ($P = 0·032$), isolates ($P = 0·009$) and C × Y interaction ($P = 0·015$). No significant effect was detected for C × I interaction ($P = 0·231$), although 20·5% of the variance accounted for could be attributed to cultivar-by-isolate interaction. Tuber blight severity varied from an IAI of 1·5 for cv. Pimpernel in combination with IPO82001 in 1999 to 3·0 for cv. Santé inoculated with IPO98014 in 1998.

## Compatibility tests

Infection experiments using detached leaflets collected from field-grown plants at Lienden and Wageningen showed highly significant ($P < 0·001$) effects of cultivar, isolate and C × I differential interaction when LGR and SPOR were analysed. The model accounted for most of the variation observed (ranging from 79·6 to 85·9%), and the differential interaction between cultivars and isolates accounted for 11·0–13·6% of the variation that could be attributed to the model used. Incompatible combinations that might be attributed to the action of R-genes were only detected in the case of isolate IPO82001 in combination with cvs Astarte and Kartel (Table 7). LGR ranged from zero growth for cvs Astarte and Kartel in combination with IPO82001 to a high 7·9 mm $day^{-1}$ for cv. Hertha in combination with IPO655-2A (Table 7). Sporangia production, as measured by SPOR, varied from 0·0 (cvs Kartel, Hertha and Astarte in combination with IPO82001

Table 7 Radial lesion growth rates (mm day$^{-1}$) and sporulation density (presented as a 0–4 index value) of four aggressive strains and a reference isolate of *Phytophthora infestans* assessed by detached leaflet inoculations with leaves collected from potato cultivars growing at two experimental sites in 1999

| | | LGR (mm day$^{-1}$) | | | | | SPOR (index) | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Location | Cultivar | F95573 | IPO428-2 | IPO655-2A | IPO82001 | IPO98014 | F95573 | IPO428-2 | IPO655-2A | IPO82001 | IPO98014 |
| Lienden | Astarte | 4·9 | 4·8 | 4·8 | 0·0 | 5·0 | 2·0 | 3·0 | 3·2 | 0·0 | 3·8 |
| | Bintje | 5·4 | 5·9 | 6·6 | 0·8 | 5·6 | 2·4 | 3·0 | 3·0 | 0·6 | 3·8 |
| | Eigenheimer | 5·9 | 4·6 | 6·2 | 1·9 | 6·9 | 2·6 | 3·2 | 3·4 | 0·6 | 4·0 |
| | Hertha | 6·2 | 6·4 | 7·9 | 2·1 | 6·2 | 3·0 | 1·8 | 3·0 | 0·0 | 2·8 |
| | Kartel | 0·7 | 0·3 | 1·0 | 0·0 | 1·5 | 0·2 | 0·0 | 0·4 | 0·0 | 0·8 |
| | Pimpernel | 4·4 | 5·7 | 4·8 | 1·1 | 5·3 | 3·0 | 3·0 | 3·0 | 1·2 | 3·2 |
| | Producent | 4·7 | 2·1 | 2·7 | 1·2 | 2·7 | 3·0 | 3·6 | 3·2 | 1·2 | 3·8 |
| | Sirtema | 6·2 | 5·9 | 6·5 | 2·0 | 6·2 | 2·2 | 1·2 | 1·4 | 1·0 | 2·2 |
| $LSD_{cultivar\text{-}isolate}$ ($P = 0·05$) | | | | | | 1·6 | | | | | 0·7 |
| Wageningen | Bintje | 6·3 | 6·1 | 5·9 | 2·4 | 6·7 | 3·2 | 3·8 | 3·8 | 1·6 | 4·0 |
| | Karnico | 5·1 | 2·7 | 5·3 | 0·8 | 5·8 | 3·0 | 2·0 | 3·0 | 0·8 | 3·0 |
| | Pimpernel | 5·3 | 5·8 | 5·4 | 2·6 | 5·6 | 1·4 | 2·4 | 2·8 | 1·2 | 3·0 |
| | Santé | 6·0 | 2·8 | 6·1 | 1·0 | 6·7 | 3·0 | 2·0 | 3·4 | 1·2 | 4·0 |
| $LSD_{cultivar\text{-}isolate}$ ($P = 0·05$) | | | | | | 1·1 | | | | | 0·6 |

LGR = lesion growth rate; SPOR = sporulation.

and Kartel inoculated with IPO428-2) to 4·0 (cvs Eigenheimer, Bintje and Santé inoculated with IPO98014) (Table 7).

Sporangia production varied considerably in a detached leaflet experiment aiming to quantify sporulation density more precisely in the cultivars Bintje, Karnico, Pimpernel and Santé (Fig. 1). ANOVA for this compatibility experiment showed significant contributions to observed variation in LGR by cultivars and isolates ($P < 0·001$) as well as the differential interaction between cultivars and isolates ($P = 0·023$). The percentage variance accounted for by the model was 64·8%; 8·4% of the explained variance could be attributed to C × I interaction. LGR varied between 2·2 mm day$^{-1}$ for the combination of cv. Pimpernel and IPO82001 and 4·7 mm day$^{-1}$ for cv. Bintje in combination with IPO655-2A and IPO98014 (Fig. 1). ANOVA using the $\log_e$-transformed data for sporulation density revealed significant effects of cultivars ($P = 0·016$) and C × I differential interaction ($P = 0·007$). The amount of variation accounted for was 57·2%, and 43·1% of this variation could be attributed to cultivar-by-isolate interaction. Spore production was also variable, ranging from $2·9 \times 10^4$ sporangia cm$^{-2}$ for cv. Santé and IPO98014 to $10·8 \times 10^4$ sporangia cm$^{-2}$ for cv. Santé and IPO655-2A (Fig. 1). Isolate IPO82001 showed a higher LGR on cv. Karnico in the second experiment compared with the first, with 0·8 and 3·2 mm day$^{-1}$, respectively. When exposed to different *P. infestans* strains, cultivars showed a variable expression of components of rate-reducing resistance. The cvs Pimpernel and Bintje showed remarkable differences in LGR when exposed to isolates IPO82001, IPO655-2A and IPO98014, while SPOR seems more or less fixed at a certain level. Cultivar Santé showed a striking increase (ranging from 2·9 to $10·8 \times 10^4$ sporangia cm$^{-2}$) in SPOR, while maintaining a stable LGR of ≈ 3·5 mm day$^{-1}$ following infection with isolates IPO655-2A, IPO98014 and IPO82001. Cultivar Karnico appeared to express the most stable expression for both components tested, with relatively small differences in LGR (ranging from 2·7 to 3·3 mm day$^{-1}$) and SPOR (ranging from 3·7 to $5·8 \times 10^4$ sporangia cm$^{-2}$). However, this stability in sporulation density was not observed in the case of IPO82001 in the first experiment using a SPOR index.

## Correlations

The relationships between the various measures for foliar and tuber blight resistance were explored by means of Spearman rank correlations. The foliar resistance ratings in the Dutch National List of Recommended Potato Varieties were not correlated with the actual stAUDPC values from the Lienden and Wageningen sites. The Spearman rank correlation coefficient was 0·138, not significantly different from zero ($P = 0·67$). The foliar disease ratings were associated with both LGR ($r = 0·569$, $P = 0·05$) and SPOR ($r = 0·625$, $P = 0·03$). Neither LGR nor SPOR was significantly correlated with observed foliar blight resistance as measured by stAUDPC values ($r = 0·529$ and 0·372, respectively).

The tuber resistance ratings were found to be poorly correlated with tuber blight incidence under field conditions ($r = 0·593$, $P = 0·04$). No correlations between the tuber resistance rating and percentage blighted tubers or IAI in the whole tuber assay were detected. The tuber blight incidence observed under field conditions was

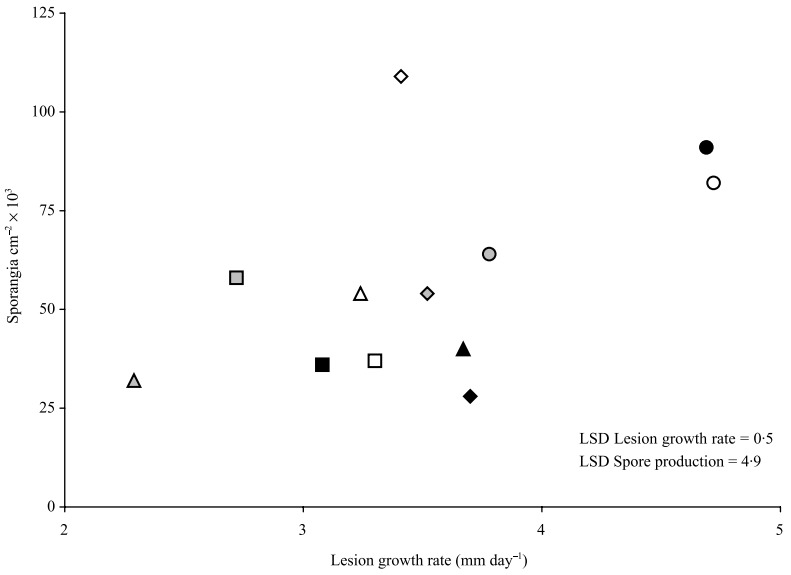


Figure 1 Relationship between sporulation capacity (sporangia cm$^{-2}$ × 10$^4$) and the lesion growth rate in mm day$^{-1}$ for four potato cultivars inoculated with three isolates of *Phytophthora infestans* in a detached-leaflet test. Cultivars are represented by circles (Bintje); squares (Karnico); triangles (Pimpernel) and diamonds (Santé); isolates are distinguished by marker patterns; white, grey and black represent IPO655-2A, IPO82001 and IPO98014, respectively.

associated with the percentage blighted tubers obtained by the whole-tuber test ($r$ = 0·648, $P$ = 0·02).

No clear relationship between stAUDPC and percentage blighted tubers could be established for the Lienden as well as the Wageningen data when applying rank correlations. No significant correlation coefficients were demonstrated between foliar and tuber blight other than a correlation coefficient ($r$ = 0·705, $P$ = 0·01) between the foliar resistance rating in the national list and tuber blight severity as measured by IAI in the whole tuber experiments.

## Discussion

Cultivars used in this study differed considerably for partial late blight resistance in the haulm as well as tubers. The level of tuber infection was not found to be closely related to foliar blight resistance, which is in agreement with earlier studies (Wastie, 1991), although other reports have claimed a good correlation between foliar disease and results based on tuber inoculations (Stewart *et al*., 1996; Platt & Tai, 1998). Whole-tuber inoculation assays led, on average, to higher incidences of tuber infection compared with the field experiments. The whole-tuber test rules out avoidance or escape mechanisms such as zoospore suppressiveness of acidic soils (Andrivon, 1995) or escape from infection through long stolons (e.g. in the case of cv. Pimpernel) that may lead to low levels of tuber blight.

Stewart *et al*. (1996) stated that late blight resistance in foliage and tuber is determined by the same genes or by different linked genes, but the lack of association between levels of foliar and tuber blight observed under field conditions might be explained by the influence of environmental variation and temporal or spatial escape mechanisms of tubers (Bain & Möller, 1999). The results here provide strong indications for the presence of specificity between *P. infestans* isolates and potato cultivars with partial resistance. The presence of differential interaction between potato cultivars and *P. infestans* isolates was confirmed at nearly all phases of host–pathogen interaction. The observations are in agreement with Caten (1974) who stated that differential interactions between pathogen isolates and nonimmune host varieties are a common feature of host–pathogen systems. Support for this view was presented by Leonards-Schippers *et al*., 1994) who identified at least one 'isolate-specific' quantitative trait locus for quantitative late blight resistance in diploid potato lines by means of interval mapping. There is doubt over the existence of forms of resistance totally independent of the invading strain. It is very unlikely that R-genes are to be held responsible for the observed specificity, as compatibility studies using detached leaves did not indicate the presence of incompatibility between cultivars and the isolates used in the field evaluations. In addition, R-genes do not appear to inhibit the growth of *P. infestans* after tuber infection, although the *R*1 resistance gene has been reported to confer a strong hypersensitive reaction in the cortical region after inoculation with incompatible isolates (Lapwood & McKee, 1961; Toxopeus, 1961). Recent work (Flier *et al*., 2001) indicates that a different class of resistance genes with a quantitative effect might be involved in the resistance reaction in the outer cortex region of potato tubers.

Evidence for the presence of specificity in potato tuber blight has been reported by de Bruyn (1947); Caten (1974); Bjor & Mulelid (1991); Peters *et al*. (1999). However, reports on specificity in foliar late blight epidemics of partially resistant potatoes are scarce (Latin *et al*., 1981; James & Fry, 1983) and the results obtained by Latin *et al*. (1981) have been questioned (Kulkarni & Chopra, 1982). In laboratory studies, James & Fry (1983) were able to increase slightly the level of foliar pathogenicity of isolates by repeated sequential cycles of culturing on two cultivars. However, they did not find evidence for differential adaptation as the gain in aggressiveness was not limited to

the cultivar in which the cycling had occurred. They concluded that specificity, measured as cultivar-by-isolate interaction, was very limited and of no practical importance. Others have pointed out that the cultivar-by-isolate interaction described by Latin *et al*. (1981) could be confounded with environmental interaction (Kulkarni & Chopra, 1982; Fry & Spielman, 1991). In the data reported here, such a confounding effect was observed at Wageningen in 1999 where cvs Pimpernel (National List rating 8) and Santé (National List rating 4) were of equal susceptibility to reference isolate IPO82001, which is used for the National List resistance testing. However, there are several differences in experimental design between evaluation of cultivar resistance for the National List and the experiments presented here that might explain the observed differences in resistance rating. For example, National List evaluation of foliar late blight resistance is based on micro-plots (six plants) and sprinkler irrigation is being applied on a daily basis. National List resistance ratings are based on multiple year averages to compensate for year effects. It appears that interpretation of differential interaction and adaptation data is not unambiguous due to year differences associated with field trials of this kind.

More recently, Inglis *et al*. (1996) compared cultivar rankings in response to foliar infection with new isolates of *P. infestans* and rankings obtained with isolates that had been predominant in the USA before 1990. Cultivar rankings were found to be nearly identical to the previously obtained data. These data provide additional support for the view that erosion of partial resistance is of little importance.

All published reports on the role of specificity for stability of partial resistance to potato late blight are based on studies concerning either the asexually reproducing US-1 clonal lineage, which until recently appeared to be pan-globally distributed (Spielman *et al*., 1991), or new, immigrant isolates of the pathogen. No data exist on the contribution of cultivar-by-isolate interaction with reference to highly variable, sexually reproducing *P. infestans* populations that have been reported for Central Mexico (Goodwin *et al*., 1992) and Western Europe (Drenth *et al*., 1994). Specificity and adaptation to late blight resistance is more likely to occur when genetic variation is being maintained at a very high level (McDonald & Linde, 2002). Consequently, adaptation of isolates to partial resistance to late blight is far more likely to occur in areas with sexually reproducing *P. infestans* populations compared with clonally propagating populations. The specific susceptible response of the foliage of cv. Pimpernel to the new population isolates IPO98014 and IPO655-2A, and the remarkably high incidences of tuber infection in several starch potato cultivars following inoculation with current isolates, appear to support the idea that adaptation to partial resistance is more likely to occur in sexually reproducing pathogen populations.

The order of magnitude of cultivar-by-isolate specificity relative to the differences in cultivar resistance and aggressiveness of isolates determines the potential ability of the pathogen population to adapt to partial resistance, and therefore the stability of such resistance (Caten, 1974). It has been stated that only a small portion of the observed variation in experiments can be attributed to cultivar-by-isolate interaction when ANOVA is used to evaluate experimental data (Parlevliet & Zadoks, 1977; Carson, 1987). Carson (1987) evaluated six genetic models of host–pathogen interaction featuring partial resistance. All models that allowed for substantial cultivar-by-isolate interactions resulted in a small cultivar-by-isolate interaction estimate in the ANOVA of disease reaction. The percentage variance accounted for by C × I ranged from 1·6 to 6·5% for the $\log_e$-transformed multiplicative and interactive multiplicative models, respectively (Carson, 1987). As a consequence, the relative importance of cultivar-by-isolate interaction will be underestimated when ANOVA is applied to experimental data, and the detection of significant cultivar-by-isolate interaction in field or greenhouse experiments requires fairly small estimates for experimental error. Approximately 10% of the total variation in the experiments reported here could be explained by cultivar-by-isolate interactions, which is in the expected order of magnitude compared with the model-based studies of Parlevliet & Zadoks (1977) and Carson (1987).

The presence of specificity implies that screening for partial resistance and predicting the stability of partially resistant potato cultivars using only one isolate may lead to the selection of breeding lines which will not express stable forms of partial resistance. The authors believe that proper screening for partial resistance should involve two stages. First, the breeding lines should be exposed to a well defined virulent (R-gene-compatible) and aggressive isolate of *P. infestans*. Potato clones with an outstanding performance in this first test, which should take place for at least two seasons, should then be exposed to a highly variable population of *P. infestans*. This could be either a naturally existing population or a mix of many genotypes with a broad genetic base. Only clones that express stable resistance to the variable pathogen population should be selected, and compatible isolates should be collected from those clones for additional stability tests. This approach might reduce the risk of selection for nonstable forms of resistance, but cannot completely exclude the possibility that erosion will take place after introduction of the new cultivar. As a consequence, continuation of late blight testing for the National List using low aggressive isolates IPO82001 and VK 6C (Flier *et al*., 2001) can no longer be recommended. Instead, an isolate showing a high level of aggressiveness to the foliage and tubers combined with a fairly complex virulence spectrum should be used, e.g. isolate IPO98014, F95573 or IPO428-2.

From the results of this study, it is concluded that specificity plays a significant role in interactions between isolates of *P. infestans* and potato cultivars. This study demonstrates that erosion of partial resistance in potato cultivars occurs under field conditions, as shown in the case of the partially resistant cv. Pimpernel tested against isolate IPO98014. The presence of specificity in interactions between *P. infestans* and partially resistant potato cultivars supports the concept of 'erosion of resistance'

alluded to by Niederhauser (1962) and Nelson (1979), and will affect the stability and durability of partial resistance against late blight in potatoes. This is in agreement with substantial anecdotal evidence for erosion of partial resistance in potato in the Netherlands in recent years. This highlights the need for better insight into the adaptive ability of the pathogen in order to predict the relative durability of partial resistance in potato cultivars when exposed to variable *P. infestans* populations.

## Acknowledgements

We thank Maarten Holdinga and the personnel at the experimental farms for their great help with the field experiments and tuber blight assessments. This work was supported by a grant from the Netherlands Ministry of Agriculture, Nature Management and Fisheries.

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