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Foliar aggressiveness of *Phytophthora infestans* in three potato growing regions in the Netherlands

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Abstract

Thirty-six isolates of *Phytophthora infestans* originating from three different potato growing regions in the Netherlands were tested for their aggressiveness to leaves of potato cultivar Bintje under controlled conditions. Measurements of latent period, maximal growth rate, infection efficiency and sporulation intensity were made and a composite aggressiveness index was calculated. Large variation in aggressiveness was present among isolates for each regional *P. infestans* population studied. The three populations differed significantly in latent period, but not for maximal growth rate and infection efficiency. Phenotypic variation existed for all components of aggressiveness and the aggressiveness index in *P. infestans* from each regional source. No association was found between mating type and aggressiveness. It is concluded that high levels of variation for aggressiveness are being generated and maintained through sexual reproduction in *P. infestans* strains from regional potato growing practices.

Abbreviations: LP10 – latent period; MGR – maximal growth rate; SPOR – sporulation density; AI – aggressiveness index = $1/\text{LP10} \times \text{MGR} \times \text{IEI} \times \text{SPOR} \times 10^4$.

Introduction

Late blight, caused by the oomycete *Phytophthora infestans* (Mont.) de Bary, is one of the most devastating threats to the potato crop in the world. Crop losses due to late blight have been estimated to account for 10–15% of the total global annual potato production (Anonymous, 1996). The economic value of the crop lost and the costs of crop protection amount to 3 billion US$ annually (Anonymous, 1996). In the Netherlands, each year large amounts of fungicides, with a total value of approximately 55 million US$ are applied to control the disease (Davidse et al., 1989). With increasing public concern about the environmental consequences of pesticide use, more sustainable and consumer friendly disease control measures are desired.

For more than a century, the genetic structure of *P. infestans* in Western Europe was highly uniform with only limited race diversity. As only A1 mating type strains were present, the fungus was forced to propagate asexually by means of sporangiospores and zoospores during the potato growing season, while its survival during the winter depended entirely on hibernating mycelium in potato tubers (van der Zaag, 1956). As a consequence, only a few closely-related strains of the fungus were found (Drenth et al., 1994).

The situation became different with the introduction of a new population of *P. infestans* to Western Europe (Spielman et al., 1991; Fry et al., 1991, 1993; Drenth et al., 1994). Most likely this new population originated from Mexico and was introduced to the European mainland shortly before 1980 (Spielman et al., 1991). An impressive increase in

genetic variation was demonstrated at the molecular level (Drenth et al., 1993), and this was accompanied by an increase in race diversity and the appearance of 'new' virulence factors in the Netherlands (Drenth et al., 1994). However, only a little attention has been paid to assess the level of variation of aggressiveness in the current population of *P. infestans* (Day and Shattock, 1997). The old population of *P. infestans* showed some variation in aggressiveness (Caten, 1970). However, no significant differences were found when *P. infestans* isolates from a Mexican population were compared with isolates from the United States and Wales (Tooley et al., 1986).

The objective of this study was to compare aggressiveness of *P. infestans* isolates sampled from three regions of the Netherlands with typical potato growing practices by means of a bioassay and to determine the variation amongst isolates and between regional sources of the pathogen.

Materials and methods

Origins of isolates

In 1995, isolates from single lesions were sampled from the following three regions; (a) a main starch potato growing region in the south-east of the Province of Drenthe on sandy peat soils, (b) the ware and seed potato production area in Southern Flevoland on clay soils and (c) an allotment garden complex at Ede on a sandy soil. The three regional sources are isolated from each other by spatial effects, potato growing practice and potato cultivars. The isolates collected in Flevoland were kindly provided by Dr. M. Zwankhuizen from the Department of Phytopathology, Wageningen Agricultural University, the Netherlands. Since this study deals with variation in aggressiveness between isolates within regions and variation between regions, 12 non-identical isolates were randomly selected from each of the three potato growing regions. For Drenthe and Ede, this selection was made based on physiological race and mating type. For the isolates collected in Southern Flevoland, isolate selection was based on RG57 RFLP fingerprint patterns (Zwankhuizen et al., 1998). In Table 1, a list of the isolates used in this study is given.

Culturing and preparation of inoculum

Isolates were stored in a liquid nitrogen storage system, for which purpose sporangium suspensions from single lesions were prepared in a 15% dimethylsulphoxide solution. Spore suspensions were transferred into 1.8 ml cryovials, cooled down to $-40\,^{\circ}$C at a rate of approximately $0.5\,^{\circ}\mathrm{C\,min^{-1}}$ using a Neslab CC 60 II immersion cooler and an alcohol bath and transferred to liquid nitrogen. Isolates taken from long-term storage

Table 1. Virulence and mating type of 36 isolates of *Phytophthora infestans* originating from three different potato growing regions in the Netherlands

Southern Flevoland, ware and seed potato region			Ede, allotment garden complex			Drenthe, starch potato region		
Isolate	Race[1]	Mating type[2]	Isolate	Race	Mating type	Isolate	Race	Mating type
F95100	1.3.4.7.10.11	A1	I95004	3.4.10.11	A1	I95117	3.4	A1
F95104	1.3.4.10.11	A1	I95018	1.2.3.4.5.7.10.11	A1	I95130	3.4.7.10.11	A1
F95130	1.3.4.7.10.11	A1	I95023	1.3.4.5.6.7.10.11	A2	I95131	1.3.4.6.7.10	A2
F95162	1.2.3.4.7.11	A1	I95024	1.4.7.10.11	A2	I95138	1.10	A1
F95301	1.2.3.4.6.7.10.11	A1	I95032	3	A1	I95146	1.3.7.10.11	A2
F95305	1.3.10.11	A1	I95039	1.3.4.7.8.10.11	A2	I95150	1.3.4.7.10.11	A1
F95516	1.3.4.7.10.11	A1	I95050	1.3.4.5.7.8.10.11	A2	I95155	3.4.7.10.11	A1
F95528	1.3.4.7.10.11	A1	I95052	1.3.4.5.6.7.8.10.11	A2	I95161	1.3.4.7.8.10.11	A1
F95555	3.4.7.11	A1	I95054	4	A2	I95175	1.3.4.6.7.8.10.11	A1
F95573	1.3.4.7.10.11	A1	I95057	1.3.4.7.8.10.11	A2	I95181	1.3.4.6.7.8.10.11	A2
F95587	1.2.3.4.6.7.10.11	A1	I95062	1.3.4.7.10.11	A1	I95188	1.3.4.6.7.10.11	A2
F95624	1.2.3.4.10.11	A2	I95066	1.3.4.7.11	A1	I95197	1.4.10.11	A1

Reference isolate I82001, race 1.2.3.4.5.6.7.10.11; A2 mating type.

[1]Physiological race determined with R-gene differentials R1 to R11.

[2]Mating type assessed after pairing of the isolates with tester strains 80029 (A1) and 88133 (A2) on leaf discs of cultivar Bintje.

were first cultured on tuber slices of the general susceptible potato cultivar Bintje by incubation in the dark at 15 °C for 5–7 days. When sporulating mycelium was present, small pieces of mycelium were placed on the lower epidermis of leaflets of cultivar Bintje placed with the abaxial side up in 9 cm Petri dishes containing 10 ml 2% water agar. Inoculated leaflets were kept in a climate chamber at 15 °C with a 16 h light period by means of fluorescence tubes type 33 at an intensity of 12 W m^{-2}. Leaflets densely covered with sporulating mycelium were obtained after seven days of incubation.

Sporangial inoculum was prepared by washing these leaves in 20 ml of tap water. The crude suspension was washed and collected on 15 μm nylon filter. After resuspension, the concentration was adjusted to 20,000 sporangia per ml using a Coulter Counter Z1 (Coulter Electronics Inc.) and kept at 18 °C. The suspensions were used as inoculum within 30 min after preparation.

Race and mating type determination

The R-gene differential set of potato clones for race identification consisted of: r0 (Bintje), R1, R2, R3, R4, R5, R6, R7, R8, R9, R10, R11, R1R2, R1R3, R1R4, R2R3, R2R4 and R1R2R3 (Black et al., 1953; Malcolmson and Black, 1966). Potato tubers of each differential line were planted in 12 l plastic pots containing loam-based compost. Plants were grown under greenhouse conditions with at least 16 h light a day augmented with Philips Son-T Agro illumination. The greenhouse temperature was kept at 18 °C with a RH of 80%.

For race determination, detached leaflets of the differentials were placed abaxial side up in 9 cm diameter plastic Petri dishes containing 10 ml 2% water agar. The leaflets were sprayed with a sporangial suspension (10^4 sporangia ml^{-1}) by means of a spraying nozzle at a pressure of 0.5 kg m^{-2} until runoff. Inoculated leaflets were incubated in a growing chamber at 15 °C in the dark for 24 h. Subsequently the remaining fluid was allowed to evaporate by placing the petri dishes without lids in a laminar flow cabinet for 30 min. Incubation was continued in a climate chamber at 15 °C with a photo period of 16 h provided by fluorescence tubes type 33 (Philips) at an intensity of 12 W m^{-2}. At day 4, 5 and 6 development of lesions was scored. When sporulation was clearly visible on an R-gene differential leaflet the disease reaction was considered compatible.

Mating type of the isolates was determined by pairing with the A1 and A2 tester strains 80029 and 88133, respectively (Drenth et al., 1994), on 14 mm leaf discs of cultivar Bintje, placed in 9 cm Petri dishes on 2% water agar. Leaf discs were inoculated with the isolate to be tested and one of the tester strains by placing small mycelial plugs in 10 μl droplets of tap-water, 7 mm apart. Leaf discs were incubated at 15 °C with a photoperiod of 16 h for two weeks after which the leaf tissue was decolourised in 70% ethanol at 50 °C and microscopically examined for the presence of oospores.

Aggressiveness assessment; bioassay

The bioassay comprised three experiments and each experiment involved thirteen isolates, i.e. twelve isolates from one of the three regions sampled, and the reference isolate I82001. The aggressiveness assay for each isolate was performed using three replicates, each replicate (experimental unit) consisting of 50 leaf discs of cultivar Bintje with a diameter of 14 mm. A single leaf disc was placed abaxial side up in each cell of two 25-cell replicate plates (Greiner no. 638102) supplied with 1 ml 2% water agar per cell. Leaf discs were cut by means of a cork borer, using only young full-grown leaflets of plants grown under the greenhouse conditions described before. Thus, a total of 5850 leaf discs were inoculated.

Inoculation was performed by placing a 10-μl droplet of a sporangial suspension of 2.0×10^4 sporangia ml^{-1} at the centre of each disc. The plates with the inoculated leaf discs were placed in plastic trays, which then were enclosed in a transparent polythene bag to avoid desiccation. The trays were placed in the dark in a climate chamber at 15 °C. After 24 h, droplets were removed with the help of filter paper and incubation was continued at 15 °C and 16 h photo period for 8 days. The presence or absence of sporangiophores was examined at 72 h after inoculation, and subsequently at intervals of approximately 12 h and the fraction of sporulating leaf discs for each experimental unit was calculated. In addition, sporulation density was examined at 72 h of sporulation. To this, sub-samples of six sporulating leaf discs were taken from each experimental unit. The sporangia were released from the sporangiophores by shaking the leaf discs in 1 ml of Isoton II electrolytic buffer (Coulter Electronics Inc.), supplemented with 1% formaldehyde, using a vortex mixer. After dilution, spore density was measured in

three subsamples of 0.5 ml by means of a Coulter counter.

Aggressiveness assessment; statistical analysis

All statistical analyses were performed using Genstat 5 version 3.1 (Payne et al., 1993).

For each experimental unit the fraction of sporulating leaf discs was fitted to the Gompertz growth model to find parameter estimates. Three growth defining parameters were calculated from the curve equations. The latent period (LP10) was calculated as the period measured in hours after inoculation in which 10% of the total sporulating discs became apparent. In addition, LP50 and LP90 values were calculated but appeared to be less informative and therefore excluded. The maximal curve growth rate (MGR) was calculated as the first derivative of the fitted curve at the point of inflexion. This parameter is a derived measure for the speed with which the maximum number of infections was achieved. The infection efficiency index (IEI) was calculated as the fitted asymptotic value of leaf discs with the pathogen sporulating after 8 days. Sporulation intensity (SPOR) was calculated as the natural logarithm of the average number of sporangia per cm^2 infected leaf tissue, based on 18 affected leaf discs per isolate. A composite aggressiveness index (AI) was calculated for each isolate using the formula $AI = 1/LP10 \times MGR \times IEI \times SPOR \times 10^4$. The aggressiveness index in this form combines information about infection efficiency, latent period, speed of appearance of sporulating lesions and sporulation density in a single value. This index presents the epidemiological potential of an isolate concerned. The multiplication factor 10^4 was introduced for scaling purposes. Similar pathogenicity/aggressivity indices have been used for this and other pathogens (Crute et al., 1987; Day and Shattock, 1997; Thakur and Shelly, 1993).

A mixed model analysis of variance was performed on the assessed parameters as well as sporulation intensity and aggressiveness index. Isolates within regions were assumed to be a random sample of the underlying population of genotypes of each sampled region. Restricted Maximal Likelihood (REML) analysis was used to obtain estimates for variance components and mean values of the parameters concerned for the three regional populations of the pathogen. The ratio between the average estimated variance components due to phenotypic variation between isolates ($\sigma^2_{\text{average}}$) and random error components (σ^2_e) was used to examine whether significant phenotypic variation for a given component existed in the regional populations (Searle et al., 1992). Wald tests (Payne et al., 1993) were used for testing contrasts between fixed model terms. Spearman rank correlation coefficients were calculated between the assessed components LP10, MGR, IEI, SPOR, AI and mating type as well as the number of virulence factors.

Results

Phenotypic variation for the assessed aggressiveness components and the aggressiveness index was found to be present (Table 2). Remarkable differences in infection efficiency, latent period and maximal growth rate were detected when individual isolates were compared but the average values for the aggressiveness components of the regional populations were similar for most components except LP10 (Table 2). A significant difference ($P = 0.05$) between regional populations could only be detected for the latent period. On average, isolates originating from the allotment gardens at Ede showed a longer average latent period when compared to isolates from Drenthe and Southern Flevoland. Furthermore, results indicate that the average aggressiveness index of the Ede population is slightly lower compared to the other regional populations. A marginally significant difference ($P = 0.10$) was found when the t test approximation was used (Table 2). The more appropriate Wald test did not detect significant contrasts.

The populations did not differ significantly for the MGR, as defined by the first derivative of the fitted curve at the point of inflexion, the infection efficiency index or sporulation density (Table 2). Substantial variation for traits related to aggressiveness was detected within the three regional populations of *P. infestans*. The estimated variance components for LP10, MGR, IEI, SPOR and AI are presented in Table 3. The ratio $\sigma^2_{\text{average}}/\sigma^2_e$ was calculated to measure the relative amount of variability due to phenotypic differences between the pooled group of isolates assessed. The phenotypic variation for all assessed aggressiveness components was found to be significantly ($P < 0.001$) larger than the matching random error component of variance (Table 3).

Rank correlation coefficients were calculated among the aggressiveness components, aggressiveness index, mating type and the number of virulence factors in order to determine whether associations existed

Table 2. Estimated components of aggressiveness and composite aggressiveness index of *P. infestans* isolates originating from three different potato growing regions in the Netherlands

Isolate/Region	Component[1]				
	LP10	MGR × 10^3	IEI	SPOR	AI
Southern Flevoland					
F95100	106.8	8.0	0.44	4.95	1.6
F95104	107.1	16.2	0.77	5.16	2.7
F95130	121.7	4.8	0.12	5.23	0.2
F95162	89.3	16.2	1.00	5.59	10.3
F95301	94.7	41.2	0.99	5.21	22.6
F95305	110.6	22.5	0.72	5.16	7.6
F95516	85.9	20.3	0.92	5.19	11.2
F95528	81.5	24.5	1.00	4.83	14.5
F95555	88.6	13.6	0.48	4.84	3.6
F95573	84.4	15.0	0.97	5.01	8.6
F95587	106.5	4.7	0.40	5.18	0.9
F95624	130.1	5.8	0.30	5.12	0.7
$\text{Average}_{\text{Flevoland}}$	100.6	15.3	0.68	5.14	7.0
Ede					
I95004	136.9	22.8	0.56	5.23	4.9
I95018	113.4	34.8	0.77	6.27	14.8
I95023	99.0	26.2	0.98	5.12	13.4
I95024	92.1	2.0	0.17	5.16	0.2
I95032	106.2	17.6	0.55	5.29	4.8
I95039	94.7	19.5	0.80	4.85	8.0
I95050	115.9	5.8	0.11	4.95	0.3
I95052	98.2	18.7	0.74	4.94	6.9
I95054	123.6	10.3	0.37	5.05	1.5
I95057	116.7	5.5	0.25	5.07	0.6
I95062	125.8	11.7	0.24	5.05	1.1
I95066	144.5	18.3	0.72	4.87	4.4
$\text{Average}_{\text{Ede}}$	113.9	16.1	0.52	5.23	5.1
Drenthe					
I95117	92.0	23.4	0.97	5.51	13.6
I95130	85.7	28.3	0.98	5.46	17.7
I95131	115.3	5.1	0.18	4.78	0.4
I95138	109.2	4.4	0.15	4.87	0.3
I95146	102.2	21.7	0.83	5.06	9.0
I95150	96.5	9.6	0.34	5.44	1.8
I95155	91.0	4.4	0.31	5.26	0.8
I95161	81.2	31.4	0.99	5.38	20.7
I95175	100.8	17.4	0.69	4.91	5.9
I95181	119.6	45.5	0.78	4.89	14.4
I95188	87.4	22.6	0.96	4.85	12.1
I95197	77.2	27.8	0.95	4.87	16.7
$\text{Average}_{\text{Drenthe}}$	96.5	20.1	0.68	5.17	9.5
I82001	109.7	10.7	0.71	4.72	3.6
$\text{S.E.D}_{\text{average}}$	6.0	4.5	0.13	0.12	2.6

[1]LP10 = latent period, MGR = maximal growth rate, IEI = infection efficiency index, SPOR = sporulation density, AI = aggressivity index = 1/LP10 × MGR × IEI × SPOR × 10^4.

Table 3. Variance components of aggressiveness components using Restricted Maximal Likelihood (REML) estimators. Variance components are based on a sample of 12 isolates from three regional populations of *P. infestans*

	Component[1]				
	LP10	MGR × 10^5	IEI × 10^3	SPOR	AI
Region					
Drenthe	158	10.3	110.6	0.08	52.2
Flevoland	224	14.7	97.4	0.03	44.2
Ede	261	7.8	81.1	0.14	21.6
$\sigma^2_{\text{average}}$[2]	214	10.9	96.4	0.08	39.3
σ^2_{e}[3]	60	3.8	6.1	0.03	8.2
$\sigma^2_{\text{average}}/\sigma^2_{\text{e}}$	3.6*	2.9*	15.8*	2.9*	4.8*

*Variance ratio significantly ($P < 0.001$) larger than one, based on a F distribution with 33 and 72 degrees of freedom respectively.
[1]LP10 = latent period, MGR = maximal growth rate, IEI = infection efficiency index, SPOR = sporulation density, AI = aggressivity index = 1/LP10 × MGR × IEI × SPOR × 10^4.
[2]Average aggressiveness variance component.
[3]Random error variance component.

Table 4. Spearman rank correlation coefficients among aggressiveness components, composite aggressiveness index, mating type and the number of virulence factors for isolates sampled

	Component[1]				
	LP10	MGR	IEI	SPOR	AI
MGR	−0.33*				
IEI	−0.61**	0.81**			
SPOR	−0.12	0.14	0.13		
AI	−0.55**	0.95**	0.93**	0.17	
MT	−0.11	−0.01	−0.03	−0.19	0.00
VIR	0.16	−0.04	−0.05	−0.34*	−0.03

*Denotes a significant (unequal to zero) correlation at $P = 0.05$ with 37 degrees of freedom when applying the t approximation method.
**Denotes a significant (unequal to zero) correlation at $P < 0.01$ with 37 degrees of freedom when applying the t approximation method.
[1]LP10 = latent period, MGR = maximal growth rate, IEI = infection efficiency index, SPOR = sporulation density, AI = aggressivity index = 1/LP10 × MGR × IEI × SPOR × 10^4, VIR = number of virulence factors.

between the parameters assessed (Table 4). As the sampled *P. infestans* populations from the three regions concerned did not seem to differ much either with respect to their average value of aggressiveness components or components of variance, correlations were

calculated with the pooled data set of the three sampled populations.

A negative correlation was found between the latent period and the maximum growth rate ($P = 0.05$) and infection efficiency index ($P < 0.01$). A positive correlation was calculated between maximum growth rate and infection efficiency index ($P < 0.01$). Mating type was neither correlated with any of the aggressiveness components assessed, nor with race complexity. A small, yet significant ($P = 0.05$) negative rank correlation was found between race complexity and sporulation density.

Discussion

The bioassay used to estimate the components of aggressiveness in *P. infestans* isolates is characterised by an extremely low level of environmental variation. Accurate measurement of aggressiveness under controlled conditions is very useful in ecological and genetic studies since it by-passes many problems encountered when measuring relative fitness between isolates under field conditions (James and Fry, 1983; Tooley and Fry, 1985).

From our data, it can be concluded that a large amount of variation for aggressiveness to the foliage is present in regional *P. infestans* populations. Regional populations of *P. infestans* differed significantly for the latent period but not for maximal growth rate or infection efficiency. Isolates from the allotment garden complex at Ede showed a longer average latent period compared to isolates originating from Drenthe and Southern Flevoland. Only a marginally significant difference was found for the composite aggressiveness index, the latter difference can be assigned, to a large extent, to the difference in average latent period. The difference in latent period between regions might be explained by the presence of 'tomato-adapted types' (Legard et al., 1995) at Ede, whereas isolates from the other two regions were 'tomato-unadapted'.

Variation for aggressiveness seems evenly distributed over regional populations of the pathogen since variation in aggressiveness is present amongst isolates in each regional population, whilst no significant differences in average variance components between regional populations were detected. The presence of high levels of variation for aggressiveness in local populations of *P. infestans* is most likely to be credited to the occurrence of sexual reproduction. The aggressiveness related factors, latent period, maximum growth rate and the infection efficiency index were correlated and a small, but significant association (-0.34) was found between sporulation density and race complexity. However, the relevance of the association between spore production and race complexity is doubtful since the value of the calculated rank correlation coefficient is rather small. It is therefore concluded that no clear indications for fitness costs related to the accumulation of unnecessary virulence factors are present as no association between race complexity and aggressiveness was found to be present. Our study, in accordance with many previous studies, does not support the concept of 'stabilising selection' (Vanderplank, 1968).

No association was found between any component of aggressiveness or the aggressiveness index and mating type. The absence of a specific association between mating type and aggressiveness in the Dutch population of *P. infestans* might be explained by the presence of sexual reproduction of the pathogen in the Netherlands (Drenth et al., 1994). The process of random assortment during meiosis guarantees that any association between mating type and aggressiveness will be broken after a few cycles of sexual reproduction, provided that this association is not based on tight genetic linkage.

Large differences for aggressiveness were found to be present between isolates. These factors are clearly associated with parasitic fitness (Nelson, 1979), as they influence the relative ability of a genotype to persist successfully over time. Aggressiveness is typically involved in epidemiological success, a case of short-term parasitic fitness. However, short-term reproductive success is not necessarily equivalent to long-term parasitic fitness, which reflects the ultimate reproductive success and survival over a longer period of time. For asexually reproducing populations of *P. infestans* in the Netherlands, hibernation in infected tubers during the crop-free season is the sole mechanism for survival and, consequently, a principal factor involved in long-term parasitic fitness (Shattock, 1977). As components of aggressiveness to the foliage were not found associated with either the rate of tuber infection or the successive invasion of tuber tissue (Flier et al., 1998), long-term reproductive success and survival appears to be a complex trait, being influenced by many biological and environmental factors. The relative importance of oospores as an alternative means of survival in partially sexual populations of *P. infestans* is still not well established (Andrivon, 1995). Viable oospores of *P. infestans*

were collected from allotment gardens in 1992 and from farmers' fields in the starch potato region in Drenthe in 1993, 1994 and 1998 (L.J. Turkensteen, unpubl.). These observations, combined with observed mating type ratios and the amount of variation in aggressiveness present in regional populations of the pathogen suggest that oospores play a considerable role in late blight epidemics in the Netherlands. Sexual reproduction also serves as the prime process for recombination of existing genetic variation for parasitic fitness, thus leading to maximal variability and aggressive strains. However, whether the more aggressive isolates may also serve as superior mates for maximal oospore production is to be questioned.

Taking into account the small sample size in this study, the most aggressive strain is not necessarily present within this sample. The components of aggressiveness were found to be only weakly to moderately correlated (Table 4), which implicates that any combination of such components may occur in nature. Combining components with the highest aggressiveness values in a single strain of *P. infestans* appears to be possible. However, the discrepancy between short-term epidemiological success and long-term reproductive success and survival makes it extremely difficult to predict the possibility of adaptation of highly aggressive strains of *P. infestans* to partially resistant potato cultivars. Moreover, erosion of quantitative resistance is not the action of increased levels of aggressiveness against all cultivars, but based on differential interactions with certain components of resistance in the host (Vanderplank, 1968).

Taking into account that we have only tested a limited sample of isolates from three regional populations, we conclude that large amounts of variation for aggressiveness are being maintained in regional populations of *P. infestans* in the Netherlands. Thus, adaptation of the pathogen to partially resistant potato varieties cannot be excluded. Our knowledge about both short-term and long-term parasitic fitness, and their interactions with resistant hosts and the environment is poor. More information is needed to provide reliable model based predictions on the stability of partial resistance against late blight.

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