Euphytica (2005) 143: 75–83
DOI: 10.1007/s10681-005-2658-0

Dissection of foliage and tuber late blight resistance in mapping populations of potato

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Received 19 January 2005; accepted 22 February 2005

Key words: allelic diversity, late blight, *Phytophthora infestans*, race-specific resistance, tuber resistance

Summary

The devastating late blight pathogen *Phytophthora infestans* infects foliage as well as tubers of potato. To date, resistance breeding has often focused on foliage blight resistance, but tuber blight resistance is becoming more and more important in cultivated potatoes. In this study, a reliable tuber assay for resistance assessment was developed and foliage and tuber blight resistance (*R*) was compared in four mapping populations. In the RH4X-103 population, tuber blight resistance inherited independently from foliage blight resistance. Three specific *R* genes against *P. infestans* were segregating. The *Rpi-abpt* and *R3a* genes function as foliage-specific *R* genes, whereas the *R1* gene acts on both foliage and tuber. In the segregating populations SHRH and RH94-076, tuber and foliage blight resistance correlated significantly, which suggests that resistance in foliage and tuber is conferred by the same gene (could be *R3b*) and quantitative trait loci (QTL), respectively. In the CE population neither tuber nor foliage resistance was observed.

Introduction

Late blight caused by the oomycete *Phytophthora infestans* is a devastating disease in potato (*Solanum tuberosum* L.). The economic value of the crop protection and losses by the disease has reached several billion US dollars annually (Kamoun, 2001). Although numerous chemicals are applied to control late blight, introduction of resistance (*R*) genes from wild *Solanum* species into potato cultivars is considered the most promising and environmentally safe approach to achieve late blight resistance.

For late blight resistance in foliage, eleven *R* genes from *S. demissum* have been introduced into cultivated potatoes. Five genes, *R1*, *R2*, *R3*, *R6* and *R7* were mapped and shown to confer race-specific resistance (Leonards-Schippers et al., 1992; Li et al., 1998; El-Kharbotly et al., 1994, 1996). Also in other wild species such as *Solanum microdontum*, *Solanum berthaultii*, *Solanum pinnatisectum* and *Solanum bulbocastanum*, *R* genes and quantitative trait loci (QTL) have been localized as new sources for foliage resistance against *P. infestans* (Sandbrink et al., 2000; Ewing et al., 2000; Kuhl et al., 2001; Naess et al., 2000; van der Vossen et al., 2003, 2004).

The genetics of tuber blight resistance has not extensively been studied. The inheritance of tuber blight resistance was proven by three different testcrosses in potato: resistant × resistant, resistant × susceptible and susceptible × susceptible (Toxopeus, 1961; Wastie et al., 1987), as the mean percentage of susceptible tubers was significantly different among the three testcrosses. The inheritance of tuber bight resistance was then explored using combining ability

analysis by Stewart et al. (1992). In 1999, there were the first contemporary reports on mapping QTL for tuber blight resistance. Oberhagemann et al. (1999) analyzed five populations derived from crosses between heterozygous potato clones devoid of any known major *R* genes in foliage. One major QTL for tuber blight resistance was observed near marker GP179 on chromosome 5 in three populations. This QTL was closely linked to foliage blight resistance, foliage maturity and vigour. In general, cultivars with a good level of foliage blight resistance show a good level of tuber blight resistance (Collins et al., 1999), but this is depending on the plant genotypes (Świeżyński & Zimnoch-Guzowska, 2001). To date, no *R* genes against late blight were identified to specifically act in tuber or foliage.

Tuber resistance against *P. infestans* is an agriculturally important trait. For instance, when cut potato seeds are planted, one or two cycles of late blight transmission may occur between cutting and emergence (Lambert et al., 1998). A higher degree of resistance in seed tubers is expected to lower the infection pressure in the field (Toxopeus, 1958; Wastie et al., 1991). Toxopeus (1958, 1961) reported that important barriers to prevent the pathogen from penetrating the tuber are the tuber skin and the cambial layer just below the tuber skin. Also the periderm, the cortex and the medulla are thought to be involved in tuber blight resistance (Flier et al., 2001). Therefore the expression of tuber blight resistance is largely dependent on inoculated tissues (Świeżyński & Zimnoch-Guzowska, 2001).

In this study, four mapping populations bearing various *R* genes and QTL from different sources were used to investigate the inheritance of, and the relation between tuber and foliage blight resistance. Most *R* genes and QTL appeared to be active in both foliage and tuber. In one mapping population, foliage specific *R* genes were identified, including a novel *R* gene derived from *S. bulbocastanum*.

Materials and methods

Plant material

The parents and progeny of four mapping populations, SHRH, RH4X-103, RH94-076 and CE were used in this study (Table 1). The diploid SHRH population is widely used in potato genetic mapping at the Laboratory of Plant Breeding and Nematology, Wageningen University, The Netherlands and used for an ultra high density (UHD) map with more than 10,000 AFLP (Amplified Fragment Length Polymorphism) markers (Rouppe van der Voort et al., 1997a, 1997b and 1999; Huang et al., 2004; H. van Os, unpublished). The UHD map is available in the web (http://www.dpw.wageningen-ur.nl/uhd/). For this population, 14 resistant and 16 susceptible genotypes were chosen based on the results of inoculation with isolate IPO-0 in foliage (Huang et al., 2004). The tetraploid RH4X-103 population is derived from a cross between 707TG11-1 and RH89-039-16. 707TG11-1 was obtained from ABPT material, which was produced via bridge crosses as quadruple hybrids with four *Solanum* species: *S. acaule*, *S. bulbocastanum*, *S. phureja* and *S. tuberosum* (Hermsen & Ramanna, 1973). For this population, 15 resistant and 15 susceptible genotypes were chosen based on the results of inoculation with *P. infestans* isolate 90128 in foliage (T.H. Park, submitted). The diploid RH94-076 population is derived from a cross between RH90-038-21, an interspecific hybrid between *S. microdontum* and *S. tuberosum* and RH88-025-50, an interspecific hybrid between *S. phureja* and *S. tuberosum*. For this population, 15 genotypes with the highest and 15 genotypes with the lowest AUDPC (Area Under Disease Progress Curve) value, which were evaluated with a complex *P. infestans* isolate IPO-82001 in a field experiment (C. Celis, unpublished), were selected. The diploid CE population is derived from a cross between C (USW5337.3) and E (77.2102.37). Clone C is an

Table 1. Mapping populations used in this study. Parents with known *R* genes or QTL in foliage, wild *Solanum* species origin of resistance and genetic location of the *R* gene or QTL are presented

Population	Maternal clone (*R* gene)	Paternal clone	Resistance source	*R* gene/QTLs and location	Reference
SHRH	SH83-92-488 (R3)	RH89-039-16	*S. demissum*	*R3* on chromosom 11	Huang et al. (2004)
RH4X-103	707TG11-1 (*Rpi-abpt*)	RH89-039-16	*S. bulbocastanum*	*Rpi-abpt* on chromosome 4	T.H. Park (submitted)
RH94-076	RH90-038-21 (QTL)	RH88-025-50	*S. microdontum*	QTLs on chromosome 4	C. Celis (unpublished)
CE	USW5337.3	77.2102.37	None	None	Jacobs et al. (1995)

interspecific hybrid between *S. phureja* and *S. tuberosum*. Clone E was obtained from a cross between the clone C and *S. vernei – S. tuberosum* backcross clone (Jacobs et al., 1995). Thirty genotypes were randomly selected. Potato cultivars Nicola and Bintje were used as resistant and susceptible controls, respectively, in all experiments.

Isolates of P. infestans and preparation of inoculum

The *P. infestans* isolates used in this study are presented in Table 2. The isolates were cultured on rye sucrose agar medium in the dark at 15 °C for 1–2 weeks (Caten & Jinks, 1968). Sporulating mycelium was flooded with cold water and the sporangiaspore suspension was incubated at 4 °C for 3 h. After the release of the zoospores, the inoculum was adjusted to a concentration of 5×10^5 zoospores/ml (Vleeshouwers et al., 1999).

Resistance assays

The wounded tuber assay was developed based on the method described by Roer & Toxopeus (1961). Intact tubers of similar size were taken from cold storage. They were washed in tab water, sterilized in 5% sodium hypochlorite for 5 min and rinsed in tap water twice. Holes of 5 mm depth were made on the surface of the tubers and a 10 μl droplet of inoculum was applied in the wound. The tubers were incubated in a closed tray with 100% relative humidity in the dark at 15 °C and resistance was evaluated at 5–14 days after inoculation. After the evaluation, the tubers were cut and kept in the same condition for three additional days.

Two types of tuber slice methods were performed, i.e. the medulla slice assay and the cortex slice assay as described by Dorrance & Inglis (1998). Tuber slices of about 7 mm thickness were taken from the medulla and the cortex, i.e. the central and the outer part of tubers, respectively. The slices were placed individually in 9 cm petri-dishes and spot-inoculated with a 10 μl droplet of inoculum on the middle upper side of the slices. They were incubated in the dark at 15 °C and evaluated at 3–7 days after inoculation.

Foliage blight resistance was determined by a detached leaf assay. Fully expanded and healthy leaves collected from greenhouse plants were placed randomly on wet paper in trays with high relative humidity. The leaflets were inoculated by pipetting 10 μl droplet of inoculum on the abaxial side and incubated in the climate chamber at 15 °C. The symptoms were evaluated at 3–14 days after inoculation.

Table 2. Isolates of *P. infestans* and virulence factors

Isolate	Race	Source
IPO-0	0	W. Flier, Plant Research International, The Netherlands
90128	1.3.4.7.8.11	F. Govers, Wageningen University, The Netherlands
99018	1.4	F. Govers, Wageningen University, The Netherlands
H30P04	3.7	F. Govers, Wageningen University, The Netherlands

DNA isolation and molecular marker analysis

DNA isolation was performed with fresh leaf tissue using the Retsch machine (Retsch Inc., Haan, Germany) in which DNA of 96 samples can be isolated simultaneously. The fresh leaf tissue was grinded in the presence of a 2% CTAB buffer composed of Tris (pH 7.5), 5 M NaCl and 0.5 M EDTA (pH 8.0).

Markers linked to the resistance locus were identified by a bulked segregant analysis (BSA) as described by Michelmore et al. (1991) using the AFLP method (Vos et al., 1995). AFLP bands were separated on a 6% polyacryl amide gel in a Li-cor sequencer (Li-cor, Lincoln, NB, U.S.A.). From pre-amplified products, the bulks for resistant and susceptible genotypes were composed according to the phenotypic data obtained from the resistance assay. Each bulk consisted of pre-amplified products of eight genotypes. In the BSA analysis, the resistant parent, the susceptible parent, the resistant bulk and the susceptible bulk were screened with 256 primer combinations. Candidate markers, which seemed to be linked to the resistance gene, were selected on the basis of absence/presence of bands. Candidate markers were tested for confirmation of linkage on 16 individual genotypes used for resistant and susceptible bulk composition.

For linkage analysis and characterization of resistances in the RH4X-103 population, PCR-based markers were used to detect different known *R* genes (T.H. Park, submitted; Ballvora et al., 2002; Meksum et al., 1995; Huang et al., in press). The markers are listed in Table 3.

Table 3. List of primers of PCR based-markers used in this study

Marker	PCR primer (5′-3′)[a]	Temperature (°C)[b]	Enzyme[c]	Reference
GP179	GGTTTTAGTGATTGTGCTGC AATTTCAGACGAGTAGGCACT	55	*BssKI*	Meksem et al. (1995)
Th2	ATTCATCGTCATCGCCTTTA CCTTTGTATCATTCGCAGTT	56	a.s.[d]	T.H. Park. (submitted)
76_2S	CACTCGTGACATATCCTCACTA CAACCCTGGCATGCCACG	50–55	a.s.	Ballvora et al. (2002)
SH23_2	ATCGTTGTCATGCTATGAGATTGTT CTTCAAGGTAGTGGGCAGTATGCTT	64–50	a.s.	Huang et al. (in press)

[a]Nucleotide sequence of primers. Both forward and reverse primers are shown.
[b]Annealing temperature. For 76_2S, the annealing temperature was 50 °C for the first 7 cycles and 55 °C for the last 30 cycles. For SH23_2, a touch-down program was applied. For the first 12 cycles, the annealing temperature was gradually decreasing from 64 °C to 50 °C and it was kept at 50 °C for the last 20 cycles.
[c]Restriction enzyme that reveals polymorphism between resistant and susceptible linked alleles of the marker.
[d]a.s. means allele specific marker showing polymorphism without digestion.

Results

Tuber blight assessment

To optimize the method for tuber blight resistance assessment and to compare late blight resistance between foliage and tuber, the parents of four mapping populations (Table 1) were inoculated with the *P. infestans* isolates IPO-0, H30P04 and 90128 (Table 2) on tuber medulla slices, cortex slices and wounded tubers. No difference in resistance outcome was found between the different methods. However, the wounded tuber assay was selected for further experiments, because it showed systematically clear phenotypes and more reliable patterns. On the fifth day after inoculation, resistant genotypes did not show any disease symptom (Figure 1a), but massive mycelium was visible at the inoculation site on the wound of susceptible genotypes (Figure 1b). The difference between resistant and susceptible became clearer when the tubers were cut. Resistant genotypes showed a sharp border, which looked like a hypersensitive response (HR; Figure 1a), whereas in susceptible genotypes the tissue was browning that expanded from the inoculation site (Figure 1b). After re-incubation at high humidity for three additional days, resistant genotypes remained devoid of any disease symptoms (Figure 1c), whereas abundant sporulating mycelium was visible on the cut tuber surface in the susceptible genotypes (Figure 1d). Occasionally, an intermediate phenotype was noted. In such case, the HR-like border was less clear, but no sporulation could be noted on the cut tubers. This phenotype was designated moderately resistant.

The resistances found in tubers of parents (Table 4) were similar to the resistances in foliages (Table 1). RH89-039-16, RH88-025-50, USW5537.3 and 77.2102.37 were susceptible to all three *P. infestans* isolates in tubers as they were in foliage to identical or different isolates (Table 1, data not shown). All genotypes were susceptible to isolate 90128 except 707TG11-1, which contains a novel *R* gene termed *Rpi-abpt* (T.H. Park, submitted). *R3* race-specific resistance was found in tubers of SH83-92-488 that also exists in foliage (Huang et al., 2004). Quantitative differences in resistance to different isolates were also noted. SH83-92-488 and RH90-038-21 tubers were moderately resistant to H30P04 and IPO-0, respectively. RH90-038-21 contains a major QTL for foliage blight resistance (C. Celis, unpublished), which is apparently strong enough to confer tuber resistance to *P. infestans* isolate IPO-0, but too weak for the more complex isolates H30P04 and 90128. 707TG11-1 was fully resistant to IPO-0, but moderately resistant to H30P04 and 90128.

Inheritance of foliage and tuber blight resistance

In the resistance assay with seven parental genotypes, we found that tuber blight resistance coincided with foliage blight resistance. To investigate the inheritance of tuber blight resistance in comparison with foliage blight resistance, 30 genotypes were selected for each mapping population and inoculated with isolate IPO-0 using the wounded tuber assay. All 30 genotypes of the CE population were susceptible in tubers, indicating the absence of any late blight *R* gene. Tuber blight resistance to isolate IPO-0 segregated in the other three

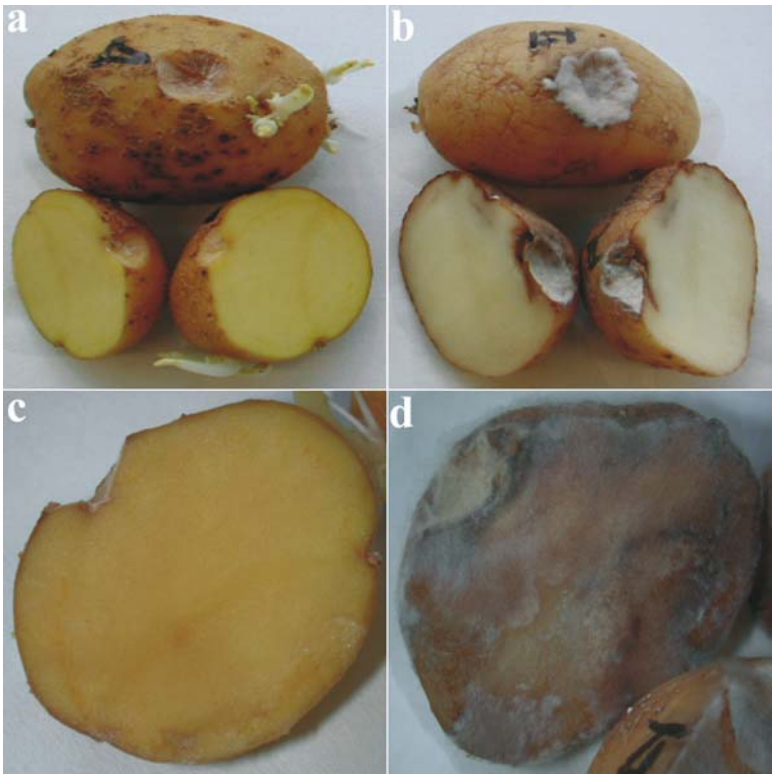

Figure 1. The wounded tuber assay with *P. infestans* isolate IPO-0. Tubers of 707TG11-1 (a, c) and RH89-039-16 (b, d) were cut 5 days after inoculation (a, b) and re-incubated for three additional days (c, d).

Table 4. Tuber late blight resistance data of the parents of the mapping populations (Table 1) to the *P. infestans* isolates IPO-0, H30P04 and 90128

	IPO-0	H30P04	90128
SH83-92-488	R[a]	M	S
RH89-039-16	S	S	S
RH90-038-21	M	S	S
RH88-025-50	S	S	S
707TG11-1	R	M	M
USW5537.3	S	S	S
77.2102.37	S	S	S

[a]Tuber blight resistance is classified into three different classes. R, S and M indicate resistant, susceptible and moderately resistant respectively.

mapping populations. In SHRH and RH94-076, the resistance in tubers correlated with the resistance in foliage. This indicates that *R3* in the SHRH population (Huang et al., 2004) and the QTL in the RH94-076 population (C. Celis, unpublished) are expressed in foliage as well as in tuber. It also would suggest that the QTL of RH94-076 is effective against isolate IPO-0 (race 0) as well as isolate IPO-82001 (race 1.2.4.5.10.11; C. Celis, unpublished). In RH4X-103, tuber and foliage blight resistance were not correlated. Eleven and seven genotypes were resistant and susceptible for both tuber and foliage resistance, respectively, but conflicting results were found in the other 12 genotypes (Table 5).

Localization of tuber resistance in RH4X-103

To further investigate the tuber blight resistance in RH4X-103, the population was expanded to 233

Table 5. Comparison between foliage and tuber blight resistance in 30 genotypes of the RH4X-103 mapping population. Correlation between foliage and tuber resistance was determined by χ^2 test ($\chi^2 = 1.29$; $P < 0.5$)

Foliage\Tuber	Resistant	Susceptible	Total
Resistant	11	4	15
Susceptible	8	7	15
Total	19	11	30

offspring. The resistance of these genotypes was examined by inoculation with the isolates 90128 and IPO-0 using the wounded tuber assay method. All genotypes were susceptible to the isolate 90128. Race-specific resistance was noted to isolate IPO-0, as 79 and 104 genotypes were clearly resistant and clearly susceptible, respectively. The remaining 50 genotypes showing unclear hypersensitive response were excluded from analysis. The resistance data indicates a 1:1 segregation ($\chi^2 = 3.48$, $0.9 < P < 0.95$) for a race-specific *R* gene to *P. infestans*. The segregation of a part of the population is included in Figure 2a.

Based on the results of tuber blight resistance assay with isolate IPO-0, a resistant and a susceptible bulk were composed for molecular marker analysis. 707TG11-1, RH89-039-16, the resistance bulk and the susceptible bulk were screened for BSA (Michelmore et al., 1991), and ten AFLP markers were identified to be linked to the locus for tuber blight resistance (data not shown). Blasting of the sequence of the AFLP markers via the website (http://www.ncbi.nlm.nih.gov/BLAST) showed that EATC/MCGA_332 was identical to the sequence of *S. tuberosum* strain P6/210 clone BAC BA87d17, *S. tuberosum* strain P6/210 clone BAC BA213c14 and *S. demissum* chromosome 5 clone PGEC472P22. A part of the AFLP marker sequence (63 nucleotides) was 82% similar to the sequence of *Lycopersicon pimpinellifolium* Rio Grande 76R *Pto* locus (Chang et al., 2002), which is located on tomato chromosome 5. These data suggest that the resistance gene that is active in tuber is located on chromosome 5.

The tentative location of the *R* gene was further examined with known PCR markers (Table 3). The RFLP marker-derived locus GP179 (Meksem et al., 1995), which is located on chromosome 5, was mapped in the population of 233 genotypes and found to be linked to the tuber blight *R* locus at 8.1 cM genetic distance. Also the race-specific *R1* gene is located near GP179 (Leonards-Schippers et al., 1992). Based on the sequence of *R1*, an *R1* specific marker 76_2s was developed (Table 3; Ballvora et al., 2002) and applied to the 233 genotypes. The 76_2s marker was fully co-segregating with tuber blight resistance locus. In combination with the race-specific resistance data to isolates IPO-0 and 90128, these data indicate that the *R1* or an *R1-like* gene is present in RH4X-103 and active in tubers.

Characterization of the foliage resistance genes in RH4X-103

To identify foliage blight resistance genes in the population RH4X-103, a subset of 52 genotypes and both parents were subjected to detached leaf assays with the *P. infestans* isolates IPO-0 and 90128. A smaller subset of 28 progeny plants was inoculated with the isolates 99018 and H30P04 (Table 2). All isolates showed different segregation patterns in the population, which suggests that at least three *R* genes for foliage resistance are segregating in the population (Figure 2b). The results for resistance to isolate 90128 were adopted from T.H. Park (submitted). In addition, the population of 52 genotypes was analyzed with molecular markers (Table 3). The 76_2s marker (Ballvora et al., 2002) segregated 1:1 (Figure 2c), and exactly matched to the *R1* specific resistance in tuber (Figure 2a). Also the SH23_2 marker for *R3a* race-specific resistance

	Isolate	TG	RH	52 progeny plants																Segregation
a	IPO-0	R	S	R	R	R	R	S	S	S	S	R	R	R	R	S	S	S	S	28 R : 24 S
b	IPO-0	R	S	R	R	R	R	R	R	R	R	R	R	R	R	R	R	S	S	49 R : 3 S
	90128	R	S	R	R	R	R	R	R	R	R	S	S	S	S	S	S	S	S	26 R : 26 S
	99018	R	S	R	nd	R	nd	R	nd	R	nd	R	nd	S	nd	R	nd	S	nd	23 R : 5 S
	H30P04	R	S	R	nd	R	nd	R	nd	R	nd	R	nd	R	nd	S	nd	S	nd	21 R : 7 S
c	Th2	ab	aa	ab	ab	ab	ab	ab	ab	ab	ab	aa	aa	aa	aa	aa	aa	aa	aa	26 ab : 26 aa
	76_2S	ab	aa	ab	ab	ab	ab	aa	aa	aa	aa	ab	ab	ab	ab	aa	aa	aa	aa	28 ab : 24 aa
	SH23_2	ab	aa	ab	ab	aa	aa	ab	ab	aa	aa	ab	ab	aa	aa	ab	ab	aa	aa	33 ab : 15 aa
d	Number of genotypes			4	5	5	2	5	2	1	2	2	4	4	2	6	5	1	2	
	Group			I		II		III		IV		V		VI		VII		VIII		

Figure 2. Graphical genotyping and phenotyping of the parents 707TG11-1 (TG) and RH89-039-16 (RH) and 52 offspring and of RH4X-103. Segregation for resistance to each *P. infestans* isolate and molecular marker is shown. (a): The phenotypic results with isolate IPO-0 in tuber. (b): The phenotypic results with *P. infestans* isolates IPO-0, 90128, 99018 and H30P04 in foliage. (c): The genotypic results detected by the *Rpi-abpt*-specific Th2, the *R1*-specific 76_2S and the *R3*-specific SH23_2 markers (Table 3). (d): Classes determined by phenotypic and genotypic data. The number of genotypes within each group is indicated. R, S, nd, ab and aa indicate resistant, susceptible, not determined, presence and absence of the markers, respectively.

(Huang et al., in press) appeared to segregate in RH4X-103 (Figure 2c). An additional marker Th2 was developed (Table 3, T.H. Park, submitted), which appeared to be 1:1. By combining genotypic and phenotypic data, the 52 genotypes were assigned to eight different groups (Figure 2d). Genotypes that contain any of the three *R* gene-linked markers, i.e. group I–VII, were resistant to isolate IPO-0 in foliage. All genotypes that carry the Th2 marker, i.e. group I–IV, were resistant to all isolates, which is explained by the broad-spectrum resistance of *Rpi-abpt* (T.H. Park, submitted). The genotypes containing only 76_2s or SH23_2, i.e. group VI or VII, show race-specific resistance to isolates 99018, H30P04 and IPO-0, as expected based on virulence data to *R1* and *R3a*. In summary, in the RH4X-103 population, the three *R* genes *Rpi-abpt*, *R1* and *R3a* segregate for foliage resistance, from which only *R1* is functional in tuber.

Discussion

Tuber resistance to *P. infestans* is one of the most important traits in cultivated potatoes. Although it is considered as an essential component for potato breeding, comparatively less efforts are made in breeding for resistance in tuber than in foliage (Świeżyński & Zimnoch-Guzowska, 2001). There is rather limited knowledge on inheritance of tuber blight resistance, but also occurrence of tissue-specific expression of resistance and the difficulty of evaluation complicate the breeding research. To develop a reliable method for tuber blight resistance, seven parental genotypes of four mapping populations of which foliage blight resistances were previously identified were tested using different inoculation methods. The different tuber blight assay methods gave identical results in this genetic material.

The relationship between tuber and foliage blight resistance is not clear and often contradicting. Platt & Tai (1998) and Stewart et al. (1994) found a correlation between tuber and foliage blight resistances, whereas Stewart et al. (1992) and Kirk et al. (2001) did not. *R1*, *R2* and *R3* and some QTL could confer both foliage and tuber blight resistance (Toxopeus, 1961; Roer & Toxopeus, 1961; Stewart & Bradshaw, 2001; Collins et al., 1999; Oberhagemann et al., 1999). However, other genes may be differentially expressed in different tissues or organs. In this study, therefore, we examined the inheritance of tuber blight resistance in four mapping populations and compared the results with foliage blight resistance. The proportion of resistant and susceptible tubers were accepted as a 1:1 ratio in the SHRH, RH94-076 and RH4X-103 populations indicating that the resistance was transmitted as a monogenic trait from the parents to their progenies. Tuber blight resistance inherited independently of the foliage resistance in the RH4X-103 population (Table 5). Tuber blight resistance was conferred by one major gene, which was localized on chromosome 5. This resistance co-segregated with the *R1*-specific marker 76_2s, suggesting that tuber blight resistance in this population was caused by *R1* or *R1-like* as one cultivar containing *S. demissum*-derived fragment was present in the pedigree of the population. In foliage, however, two additional *R* genes were identified to cause foliage-specific resistance. *R3a* (Huang et al., in press) and *Rpi-abpt* (T.H. Park, submitted) were segregating in the population and specifically acting in foliage. However, 707TG11-1 was moderately resistant to isolate 90128 which could be due to the presence of several unknown minor QTLs, which do not have detectable effects on resistance in the progeny after segregation. The moderate resistance to isolate H30P04 could be explained by its high aggressiveness (Table 4). In the SHRH and the RH94-076 populations, tuber blight resistance correlated with the presence of *R3* and a major QTL for foliage blight resistance, respectively.

The *R3* locus in the SHRH population consists of two functionally distinct *R* genes *R3a* and *R3b* that are only 0.4 cM separated from each other (Huang et al., 2004). *R3*-specific resistance occurred in both tuber and foliage in the SHRH population, but the *R3a* gene alone was foliage-specific in the RH4X-103 population. It remains to be determined whether the *R3* specific resistance for tuber blight in the SHRH population is caused by *R3b* or another *R3-like* gene or differences in expression patterns.

In conclusion, we found that the expression of resistance for tuber or foliage late blight depends on the *R* genes. In the RH4X-103 population, *Rpi-abpt* and *R3a* are foliage-specific whereas *R1* or *R1-like* and the QTL from RH94-076 act both in tuber and foliage.

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