Occurrence of the *R1* allele conferring resistance to late blight in potato R-gene differentials and commercial cultivars

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A total of 23 Scottish and 14 Dutch potato R-gene differentials as well as five Austrian, two Dutch and two German commercial potato cultivars were screened for the *R1* allele conferring resistance to *Phytophthora infestans* carrying *Avr1*, via PCR amplification and sequencing. A single 1400 bp fragment with complete sequence identity to the corresponding part of the *R1* allele, was obtained from genomic DNA of all potato R-gene differential clones whose denomination indicates *R1* or a combination of *R1* and other major resistance factors. The *R1* allele was detected, as expected, in all these clones. This fragment also occurred in one Austrian and one German cultivar. Unexpectedly, the same *R1* allele also was detected within all R5, R6 and R9 differentials.

Keywords: international R-gene differential set, *Phytophthora infestans*, *R1* allele

Introduction

The potato-late blight pathogen, *Phytophthora infestans*, forms physiologic races that are able to circumvent resistance determined by specific *R* genes of *Solanum*. Accordingly, the solanaceous hosts of *P. infestans*, including potato, tomato, pepper, pepino dulce and many other species, have evolved multiple *R* genes for race-specific resistance to late blight. Major *R* genes of plants have often been detected in segregating progenies by their highly heritable resistance phenotype. The total number of *R* genes for resistance to late blight in *Solanum* spp. is unknown; they may exceed considerably those represented by the current international set of eleven R-gene differentials (Black *et al.*, 1953; Malcolmson & Black, 1966).

The *R1* gene, characterized by Ballvora *et al.* (2002), confers resistance to strains of *P. infestans* carrying *Avr1* (Van der Lee *et al.*, 2001). *R1* was introduced into the common potato (*S. tuberosum*) from the wild hexaploid, *S. demissum* via cross hybridization and selection for the R1 phenotype. This utilization of potato genetic resources commenced by potato researchers in the 19th century unfortunately has not been fully documented. It is not known whether *R1* was introduced into potato breeding stocks from only one or several different genetic resources. Early accounts (Schick, 1932) refer to a limited number of genetic resources from *S. demissum* and *S.* ×

edinense, its natural hybrid with the cultivated potato that had been used for hybridization experiments by Broili. The German plant pathologist and breeder K.O. Müller described the use of clonal hybrid selections that he labelled 'Ef-Stamm' ('Edinense fraglich'; compare Müller, 1951) referring to their possible taxonomic identity with *S.* × *edinense*. This and other clonal samples, perhaps of a common descent, had been distributed among several potato breeders across the world before 1930.

In 1953, a consortium of potato breeders and pathologists established a set of potato R-gene differentials that would allow for the detection of discriminant avirulence phenotypes (Black *et al.*, 1953). This set comprised clonal selections made individually by W. Black of Scotland, by C. Mastenbroek, the Netherlands, and by W.R. Mills and L.C. Peterson, USA. Other workers at other institutions even had developed individual sets of potato differential stocks maintained as botanical seed (Schick & Schick, 1959). While none of these sets represented all *R* genes and combinations of *R* genes known at that time (by their phenotype), there were several potato clones of possibly diverse origin representing one single factor. This arose as these pioneering late blight researchers maintained differential isolates of *P. infestans* to assay the resistance phenotype of potato segregants containing unknown factors for race-specific resistance. For example, the *P. infestans* isolates breaking R1 resistance were capable of causing disease on the clonal selections namely, 1085(6) (Black's differential), 43154·5 (Mastenbroek), and Essex (Mills and Peterson), all of which attained the status (by their phenotype) of international R1 differentials (Black *et al.*, 1953).

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The international set of differentials (Black *et al.*, 1953) has been maintained clonally and was amended until the late 1960 s (Eide *et al.*, 1959; Black & Malcolmson, 1965; Malcolmson & Black, 1966; Malcolmson, 1969). It comprises clones for the detection of 11 single late blight resistance factors (classified as R1–R11) originating from *S. demissum*.

Although the *R1* gene is overcome by the majority of present-day *P. infestans* populations (Ross 1986; for examples compare Deahl *et al.*, 1991; Andrivon *et al.*, 1994; Drenth *et al.*, 1994; Forbes *et al.*, 1997; Dorrance *et al.*, 1999; Hermansen *et al.*, 2000; Elansky *et al.*, 2001), it has been of interest as a model to plant geneticists. Besides its most obvious role of producing race-specific resistance, it has been suspected to play a role in quantitative field resistance (Darsow *et al.*, 1987; Stewart *et al.*, 2003). Both race-specific and quantitative resistance in the field may, in part, employ the same mechanisms; the basic difference could be the rate and intensity of expression of resistance pathways (Ordoñez *et al.*, 1998; Gebhardt & Valkonen, 2001). The *R1* gene belongs to a large group of structurally related *R1*-like *R* genes and *R* gene analogues whose members appear to be frequent in *Solanum* spp. (Trognitz & Trognitz, 2005).

To assess the power of selectivity of the *R1*-specific PCR primers proposed by Ballvora *et al.* (2002) to tag unequivocally the *R1* allele, these primers have been applied to potato R-gene differential clones and several contemporary and older potato cultivars that are used in breeding. Whether the R1 phenotype of the respective potato R-gene differential clones is reliably associated with the occurrence of the *R1* allele was also determined.

Materials and methods

Plant material

Clones of two potato differential sets (Table 1) were included. The Scottish set of Black's differentials was kindly provided by Dr. H. Stewart, SCRI, Dundee, UK. An incomplete Dutch set has been maintained at the International Potato Centre as described in Trognitz (1998). A copy of this set was provided as stocks *in vitro* by Dr. K. Schüler, Institute of Plant Genetics and Crop Plant Research, External Branch North, Gross Lüsewitz, Germany. In addition, samples of genomic DNA of the Scottish differentials R5, R6, and R9 were kindly provided by Dr. Renata Lebecka, IHAR, Mlochow, Poland). Commercial seed tubers of Austrian, Dutch and German cultivars (Table 1) were obtained from Niederösterreichische Saatbau, Meires, Austria. Plants were maintained pathogen-free *in vitro* and grown in pots in the glasshouse at ARC-sr, Seibersdorf, Austria, according to standard procedures.

Molecular biological procedures

Total DNA was isolated from different plants grown *in vitro* or glasshouse following the instructions of the supplier (DNeasy DNA extraction kit). The *R1*-specific PCR primers 76-2sf2 and 76-2SR identified on *R1* cDNA by Ballvora *et al.* (2002) were applied as indicated by these authors, and ethidium bromide-stained PCR products were visualized on 1%-agarose gels.

For sequencing of DNA fragments, PCR products were cleaned on Sephadex columns; 1 μL of PCR product was mixed with 2 μL BigDye (V 3) reagent (Applied Biosystems), 2 μL buffer, and 0·5 μM *R1*-specific forward or reverse primer. Following the sequence reaction, the cleaned product was mixed with 10 μL HIDI (Applied Biosystems) for processing in an ABI 3100 Genetic Analyser (Applied Biosystems). Forward and reverse sequences were assembled and analysed in Sequencher software (GeneCode).

Detection of plant resistance phenotype

Detached leaflet assays were performed following the procedure of Trognitz (1998). Lateral leaflets were collected from fully expanded top leaves of adult plants. One Petri dish containing four leaflets that had been collected from at least two different clonal plants per genotype represented an experimental unit. A paper towel was folded to fit in the bottom of a Petri dish and wetted to serve as a moisture reservoir. Sporangial inoculum was prepared from infected potato tuber slices (cv. Naglerner Kipfler) and it was applied with a hand-held pump sprayer at a concentration of 20 000 sporangia/mL. The samples were incubated at 18°C for 4–8 days until symptoms were fully developed. Percentage total leaflet area diseased and degree of sporulation were assessed. For all genotypes, tests were repeated on a minimum of two dates. For the inoculations, a 'race 0' isolate of *P. infestans* (provided by W. Flier, Plant Research International, Wageningen, The Netherlands) avirulent on all 11 R-gene differentials but pathogenic on the universal suscept, r0 was used.

Results and discussion

The primers reliably amplified one fragment of the 1400 bp size expected for *R1* (Ballvora *et al.*, 2002; Gebhardt *et al.*, 2004) from 16 R-gene differential clones and two cultivars (Table 1, Fig. 1). The sequences of all fragments proved fully identical with the corresponding part of the *R1* allele at the *R1* locus (accession No. AF447489), regardless of the potato cultivar analysed.

Detached leaflet tests with race 0 gave a resistance reaction on differentials carrying R1–R11 and combinations thereof and susceptibility on the universal suscept. Two of the nine commercial cultivars genotyped were tested with race 0 and of these, Evita was susceptible and this is in accordance with the absence of the *R1* fragment. Linzer Delikatess, also was susceptible in the assays, although it carries the *R1* allele. This suggests that *R1* of Linzer Delikatess either may be suppressed by an unknown intervening genetic element (El-Kharbotli *et al.*, 1996; Ordoñez *et al.*, 1997; Trognitz, 1998), or that an additional unknown, synergistic element required for the function of

Table 1 Potato cultivars and late blight R-gene differentials, tested for presence of the *R1* allele and for resistance to a race 0 isolate of *Phytophthora infestans*

Country of origin	R-gene differential	Clone/cultivar	*R1* fragment	Resistant to race 0
Scotland	Universal susceptible	Craig's Royal	No	No
	R1	Craig's Snow White	Yes	Yes
	R2	1512 c(16)	No	Yes
	R3	Pentland Ace	No	Yes
	R4	1563 c(14)	No	(Yes)[a]
	R5	3053–18	**Yes**[b]	Yes
	R6	XD2–21	**Yes**	Yes
	R7	2182et(7)	No	Yes
	R8	2424a(5)	No	Yes
	R9	2573(2)	**Yes**	Yes
	R10	3681ad(1)	No	Yes
	R11	5008ab(6)	No	Yes
	R1R2	1647b(1)	Yes	Yes
	R1R3	2070(32)	Yes	Yes
	R1R4	1506b(9)	Yes	Yes
	R2R3	1682 c(1)	No	Yes
	R2R4	2070(31)	No	Yes
	R3R4	1488b(1)	No	Yes
	R1R2R3	2070(59)	Yes	Yes
	R1R2R4	2070(69)	Yes	Yes
	R1R3R4	2070(4)	Yes	Yes
	R2R3R4	2070(50)	No	Yes
	R1R2R3R4	2070(54)	Yes	Yes
Netherlands	R1	CEBECO-43154-5, CIP800986	Yes	Yes
	R2	CEBECO-44158-4, CIP800987	No	Yes
	R3	CEBECO-4642-1, CIP800988	No	Yes
	R4	CEBECO-4431-5, CIP800989	No	(Yes)[a]
	R8	Black 2424a(5), CIP800993	No	Yes
	R9	Black 2573, CIP800994	**Yes**	Yes
	R10	Black 3618ad(1), CIP800995	No	Yes
	R11	Black 5008ab(6), CIP800996	No	Yes
	R1R2	CIP800997	Yes	Yes
	R1R3	CIP800998	Yes	Yes
	R2R3	CIP801000	No	Yes
	R3R4	CIP801002	No	Yes
	R1R2R3	CIP801003	Yes	Yes
	R2R3R4	CIP801005	No	Yes
		Arletta (1998)[c]	No	n.d.
		Kuras (1996)	No	n.d.
Austria		Evita (1995)	No	No
		Gabriella (2000)	No	n.d.
		Linzer Delikatess (1975)	Yes	No
		Romina (1989)	No	n.d.
		Rosita (1999)	No	n.d.
Germany		Laura (1998)	Yes	n.d.
		Quarta (1979)	No	n.d.

[a]The race 0 isolate produced small, slowly sporulating lesions on the R4 differentials from different sources indicating that it may possess incomplete avirulence for this resistance factor.
[b]Unexpected phenotype indicated in bold-face, n.d.; not done.
[c]Year of release indicated in parentheses.

R1 is absent in this cultivar. The German cultivar Laura (launched in 1998) also has the *R1* allele; however, its phenotype of resistance to race 0 was not tested. According to varietal assessment results (Anonymous, 2001), the level of susceptibility to foliage blight of Laura (*R1* carrier, second-early maturity) in the field is low–intermediate. For comparison, this level of susceptibility corresponds to a score of 4 on the German 1–9 scale of blight susceptibility (Anonymous, 2003). Laura proved more field-resistant than the other second-early, non-*R1*-carrying cultivars

Figure 1 PCR-amplified *R1* fragment (1400 bp, marked at left) from genomic DNA of potato R-gene differentials and cvs Laura and Linzer Delikatess using *R1*-specific primers. r0, universal susceptible differential (Craig's Royal); R1–R11, Scottish R-gene differentials; La, cv. Laura; LD, cv. Linzer Delikatess. Size standards: centre, Fermentas FastRuler; at right, Invitrogen high DNA mass ladder.
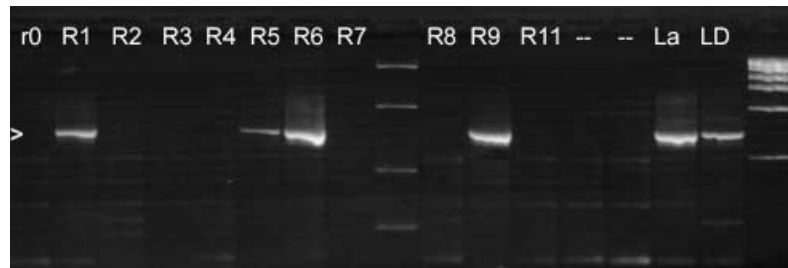
Table 2 Summary of *Phytophthora infestans* avirulence phenotypes on R-gene differentials from published studies on isolates collected between 1983 and 1998

Source	Total isolates	Avirulent on R1	Avirulent on R1 and virulent on R5, R6, R9	Country	Year of collection	Host
Hermansen *et al.*, 2000	374	24	0	Finland, Norway	1990–96	potato
Andrivon *et al.*, 1994	23	1	0	France	1991	potato
Lebreton & Andrivon, 1998	62	1	0	France	1995/96	potato, tomato
Drenth *et al.*, 1994	253	not indicated		Netherlands	1981–91	
Schöber & Turkensteen, 1992	77	12	0	Netherlands	1988	potato
Flier & Turkensteen, 1999	36	7	0	Netherlands	1995	potato
Sujkowski *et al.*, 1996	95	2	0	Poland	1985–91	potato
Elansky *et al.*, 2001	191	5	not indicated	Russia	1997/98	potato, tomato
Abu-El Samen *et al.*, 2003[a]	21	9	1 (on R6)	USA	1994/95	potato
Deahl *et al.*, 1991	10	1	0	USA, Canada	1983–89	potato, tomato
Dorrance *et al.*, 1999	60	4	3 (1 on R5, 1 on R6, 1 on R5+R6)	USA	1996/97	potato, tomato, nightshades
Goodwin *et al.*, 1995	32	6	1 (R5), (R6 not done)	USA, Canada, Mexico	1989–94	potato, tomato
Rivera-Peña, 1990	78	23	9 (5 on R5, R6 not done, 4 on R9)	Mexico	1985/86	wild potatoes
Forbes *et al.*, 1997	108	18	1 (R5)	Ecuador	1993	potato
Oyarzun *et al.*, 1998	60	0	0	Ecuador	1993–95	potato
Oyarzun *et al.*, 1998	60	57	0	Ecuador	1994–96	tomato
Total[b]	1287	170	15			

[a]These authors investigated single-zoospore isolates from two single-lesion isolates; all other authors had single-lesion isolates.
[b]Excluding Drenth *et al.*, 1994.

investigated, Evita and Quarta, which possess an intermediate susceptibility level (score 5). Romina (early) also is intermediately susceptible, whereas the late-maturing cv. Kuras is resistant in the field. Both early-maturing cultivars, Rosita and the silent *R1* carrier Linzer Delikatess display an intermediate-pronounced level of susceptibility in the field (score 6). The first-early cultivar Gabriella has been scored intermediately susceptible and no results are available for Arletta from the same source (Anonymous, 2001).

The experiment reported here confirms that the *R1* gene is distributed across all differentials specific for the R1 factor and for all combinations of R1 with other factors. Therefore, there is a good chance that the R1 phenotype of resistance is expressed by the functional *R1* allele as isolated by Ballvora *et al.* (2002). Gebhardt *et al.* (2004) detected this allele also by its distinctive 1400 bp PCR fragment in several accessions of the Mesoamerican *S. demissum* and in one accession of *S. stoloniferum*.

The occurrence of the *R1* allele in the R5, R6 and R9 differentials was unexpected (Table 1, Fig. 1). Because the phenotype resulting from interaction with the universally avirulent race 0 does not allow discrimination among different R genes, it cannot be assessed whether and to what extent *R1* may contribute to the resistance phenotype displayed by these three R-gene differential clones.

In Table 2, results of 15 studies on avirulence of *P. infestans* isolates collected throughout more than one decade are summarized. Only 170 out of 1287 isolates tested (13%) were avirulent on the R1 differentials and only 15 of these 170 isolates (9%) were virulent on R5, R6, or R9 differential clones. The latter were exclusively reported in studies from the Americas where R-gene differential clones different from those analysed in this study may have been partly used (as an example see Goodwin *et al.*, 1995). However, as the status of *P. infestans* avirulence generally has been assessed by the resistance phenotypes of R-gene differential clones, it is possible that those

multiply-virulent pathotypes may, in part, be artefacts for which inadvertent selection has occurred. This could be verified once additional R-gene differentials of R5, R6, and R9 devoid of *R1* become available. Such additional differentials could easily be obtained by selecting self- and cross-progenies of the existing differentials against R1 using the molecular markers now available (Gebhardt *et al.*, 2004).

Two out of nine commercial potato cultivars tested positive for the presence of *R1* (Table 1) indicating that *R1* still occurs within contemporary European potato breeding stocks although races breaking it down had already appeared in Europe by 1932 (Lehmann, 1937). Selection for this gene was suspended half a century ago when the widespread breakdown of the resistance to several of these R genes was recognized (Ross, 1986). The presence of *R1*, however, is understandable considering the narrow pedigree-breeding schemes widely applied, the long period of generation turnover in potato breeding (Gebhardt *et al.*, 2004), and no directed selection against *S. demissum* R genes. Notwithstanding, there is evidence that defeated R genes still may contribute to an overall increased level of resistance in the field (Darsow *et al.*, 1987; Stewart *et al.*, 2003). Therefore, breeders could be encouraged to use R genes for resistance to late blight particularly when these are easily selected as in the case of the *R1* allele.

Acknowledgements

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