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Characterization of the resistance to *Phytophthora infestans* in local potato cultivars in Bolivia

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Abstract This experiment was carried out to investigate whether and how much field resistance to late blight, caused by *Phytophthora infestans*, is present in the local cultivated potato germplasm. In total 36 entries were compared in a field experiment in an area highly conducive to late blight development. Of the 36 cultivars 32 were local cultivars belonging to five *Solanum* species, *S. tuberosum* (1 accession), *S. andigena* (18), *S. juzepczukii* (2), *S. stenotomum* (9) and *S. ajanhuiri* (2). The other four cultivars were derived from breeding programmes, one being the Dutch cultivar Alpha used as a highly susceptible control. The 36 cultivars were planted according to a simple 6×6 lattice design with three replicates. Each replicate was divided in six incomplete blocks each with six cultivars. The disease severity was assessed weekly during 9 weeks starting 48 days after planting. The area under the disease progress curve (AUDPC) was used as a measure of the field resistance. Nine isolates from surrounding potato fields were tested for their virulence to the resistance genes R1–R11 using 22 differential cultivars. The components of the field resistance of 19 of these cultivars were compared in the greenhouse using a local isolate with virulence to all known R-genes, except to R9. The nine isolates represented seven races with a race complexity varying from 7 to 10 virulence factors. All isolates carried virulence against R1, R2, R3, R7, R10 and R11, while virulence against R9 was absent. The AUDPC among the 32 local cultivars ranged from very large, significantly larger than that of 'Alpha' to very small. The AUDPC from *S. stenotomum* accessions ranged from very large to intermediate, those from *S. andigena* accessions from large to very small. Especially among the *S. andigena* accessions interesting levels of field resistance were found. Four components of field resistance were assessed, latency period (LP), lesion size (LS), lesion growth rate (LGR) and relative sporulation area (RSA). All four showed a considerable variation among the cultivars. The LP ranged from 3½ to 6 days. The LS ranged from 225 mm^2 to 20 mm^2. The LGR varied about six-fold, the RSA more than 10-fold. The components tended to vary in association with one another. LP and LGR were well associated with each other and had a significant correlation with the AUDPC.

Keywords Local cultivars · *Phytophthora infestans* · Field resistance · Quantitative

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resistance · Race-specific resistance · Components of resistance · R-genes · *Solanum ajanhuiri* · *S. andigena* · *S. juzepczukii* · *S. stenotomum* · *S. tuberosum* · Virulence

Introduction

The potato, *Solanum tuberosum*, a crop of world wide importance, originated in the Andean regions of South America. Its most important disease, late blight, caused by *Phytophthora infestans*, however did not originate in these regions. It was unintentionally introduced into Europe in the 1840's, causing the Irish famine. From Europe it spread to all potato growing areas. Until the late 1970's all *P. infestans* isolates outside the central highlands of Mexico appeared to belong to one lineage, US-1 of the A1 mating type, indicating a single introduction from central Mexico (Shaw 1987). Even in the central highlands of Peru only A1 mating types of the US-1 lineage were found prior to 1980 (Tooley et al. 1989). However, in the central highlands of Mexico, including the Toluca Valley, many lineages and both mating types, A1 and A2 occur (Shaw 1987; Grünwald et al. 2001**)**. Because of these and other observations it is thought that *P. infestans* originated and co-evolved on native wild tuber bearing *Solanum* species in the central highlands of Mexico (Reddick 1939; Niederhauser 1956; Shaw 1987; Tooley et al. 1989; Grünwald et al. 2001; Shattock 1995). Apparently new introductions from Mexico changed the genetic structure and diversity of *P. infestans* populations dramatically worldwide, replacing the US-1 lineage by new A1 and A2 mating types (Shaw 1987; Grünwald et al. 2001; Shattock 1995). Due to the presence of both mating types the variability of the pathogen has increased considerably, which may increase its aggressiveness and/or virulence (Flier and Turkensteen 1999).

The global interest in resistance to late blight has increased greatly due to the unfavourable side effects of fungicides on the environment and human health (Turkensteen 1993). Resistance in potato to late blight is of two types. A series of major genes (R-genes) each can give a high level of resistance, but the resistance is typical race-specific. Eleven R-genes, derived from *S. demissum* and *S. stoloniferum*, have been identified (Malcolmson and Black 1966; Colon and Budding 1988; Grünwald and Flier 2005) and several were introgressed into *S. tuberosum* cultivars. More recently several other R-genes were reported from *S. berthaultii, S. pinnatisectum, and S. bulbocastanum (*Sanchez et al. 2000; Park et al. 2005; Sliwka 2004; Grünwald and Flier 2005) and suggested in *S. sucrense* and *S. venturii* (Colon et al. 1988). Virulence to each introgressed R-gene appeared very fast and complex races with 9–11 virulences have been found repeatedly (Shattock et al. 1977; Russell 1978; Turkensteen 1993; Andrivon 1994). The pathogen is so versatile that breeding for this type of resistance is futile (Russell 1978).

The second type of resistance is quantitative or field resistance, which is inherited in a polygenic fashion (Toxopeus 1959; Black 1970; Sliwka 2004). This resistance is often considered to be quite durable (Turkensteen 1993; Parlevliet 1993; Colon et al. 1995; Grünwald and Flier 2005). The components of field resistance to *Phytophthora infestans* vary in association with each other, whereby infection frequency shows the least association with the other components (Van der Zaag 1959; Umaerus 1970; Umaerus and Lihnell 1976; Birhman and Singh 1995). Lesion growth rate was found to be a very important component of resistance (Colon et al. 1995).

In the Andean regions of Bolivia tuber bearing potatoes of several *Solanum* species have been a major food crop for ages. Most local cultivars may have been highly susceptible before the late blight pathogen reached this area. This is supported by the observations of Simmonds and Malcolmson (1967) for the 4*n Andigena* potatoes. Since the arrival of the late blight pathogen a selection for quantitative resistance may have taken place.

This research was carried out to investigate the presence of quantitative resistance in local Bolivian potato cultivars.

Materials and methods

The field experiment was carried out in the area of Chullchunq'ani, province Carrasco in the

Eastern range of the Andean mountains at an altitude of 3200 m a.s.l., a site highly conducive for late blight development. The characterization of the isolates collected in the surroundings of the experimental site and the resistance component analysis of the field resistance to *P. infestans* was carried out in the greenhouse and laboratory of the Toralapa research centre of the foundation PROINPA, Bolivia.

Field experiment

The experiment contained 18 cultivars of *S. andigena*, (2× = 48), two cvs of *S. tuberosum*, (2× = 48), two cvs of *S. juzepczukii*, (3× = 36), nine cvs of *S. stenotomum*, (2× = 24), two cvs of *S. ajanhuiri* (2× = 24), two cvs of *tuberosum–andigena* hybrid origin and one cv derived from a complex cross involving four *Solanum* species (*S. tuberosum, S. andigena, S, phureja, S. demissum)*. Of these cultivars 32 were local cultivars, three were locally bred from interspecific crosses and one came from The Netherlands ('Alpha'). The latter was used as a highly susceptible control. The seed potatoes of the local cvs were obtained from the Bolivian Germplasm Bank and were free from viruses. The experiment was planted according to a simple 6×6 lattice design with three replicates. Each replicate was divided in six incomplete blocks each with six cvs.

The growing conditions were similar to those of most farmers in the area. The cultivars were planted in single row plots of five plants with a plant spacing of 0.30 m and a row spacing of 0.70 m, and were fertilized with 80 kg N and 140 kg phosphate per ha just before planting. Late blight developed from natural infection as the potato fields in the surroundings all had late blight. The percentage foliage affected by late blight was assessed every 7 days for 9 weeks starting 48 days after planting when the first symptoms were observed in the susceptible controls. The blight assessments were used to calculate the area under the disease progress curve (AUDPC). Analysis of variance was carried out after angular transformation of the data.

Local isolates

From each of nine potato plots of local farmers with different local cvs within 500 m of the experimental field a sample of leaflets with late blight lesions was collected. Per sample one leaflet with one lesion was taken and four small areas near the margin of the lesion were cut from it. Each piece was placed with the bottom on top of a disinfected tuber slice of 'Alpha' in a Petri dish. After incubation for 3 days at a temperature of 18–22°C and 4 days at 15–18°C, the isolates were transferred to Petri dishes with 10% clarified V8 (MS) medium (Plata 1998). To produce the inoculum, mycelium of the isolates was transferred to potato slices of 'Alpha' in humid chambers and incubated for 10–12 days at 15–18°C.

The virulence pattern of the isolates was tested on the international set of differential cultivars, which carried r, R1, R2, R3, R4, R5, R6, R7, R8, R9, R10, R11, R1R2, R1R3, R1R4, R2R3, R2R4, R3R4, R1R2R3, R1R2R4 R2R3R4 and R1R2R3R4, respectively. Per cultivar and per isolate three Petri dishes were prepared, two to be inoculated with an isolate and one with sterile water. The leaflets taken from the 22 cultivars, grown in the greenhouse, were from the third leaves from the top of the stems. The leaflets were deposited with the bottom upward in turned over Petri dishes plated with water agar, one leaflet per dish. The Petri dishes were placed in a growth chamber with white light and at a temperature of 18–22°C.

In a laminar flow chamber the sporangia were collected in sterile distilled water and the sporangia suspension filtered through a gauze followed by subsequent passages trough a 30 μ and a 10 μ filter. The sporangia were transferred to a cask with sterile distilled water and the concentration adjusted to 60,000 per ml using a haemocytometer followed by incubation at 8–12°C for 2 h to allow the discharge of zoospores. After this the leaflets were inoculated by placing a drop of 20–25 l on both sides of the main leaflet vein. The control consisted of the application of drops of sterile water of the same size and in the same way onto the leaflets.

Infection types (IT) were assessed 5 and 7 days after inoculation. Cultivar/isolate combinations were considered incompatible and indicative for the presence of effective R-genes when the ITs ranged from ''no visible reaction'' to ''flecks with sporadic sporulation'', and compatible and indicative for the absence of effective R-genes when lesions were sporulating more than sporadic.

Components of field resistance

The components of resistance were assessed in the laboratory on detached leaflets as described above for the 22 differential cultivars. Per potato cultivar per isolate five leaflets were used (four to be inoculated and one control). The Petri dishes were placed in a growth chamber with artificial illumination with white light and at a temperature of 18–22°C. The inoculum consisted of sporangia of the most complex race (isolate P3, virulent on the R-genes 1, 2, 3, 4, 5, 6, 7, 8, 10, and 11, Table 2) and was prepared in the same way as described above. The concentration of sporangia used was approx. 20,000 per ml. Leaflets were inoculated as described above. The four replicates were placed in a randomized block design, with the controls randomly distributed over the experimental space. This experiment was done in two series with leaves picked 61 and 75 days after planting the potatoes, respectively.

The components evaluated were:

(1) Latency period (LP) is defined as the period in hours between inoculation and the appearance of the first sporangia. Assessment moments were 84, 96, 108, 120 and 144 h after inoculation from which the LP was interpolated.
(2) Lesion size (LS) in mm^2 as ¼π × length × width of the lesion was measured 108, 120, 144 and 168 h after inoculation.
(3) Lesion growth rate (LGR) was derived from the LS assessments as the average daily increase in area over the observed period.
(4) Relative sporulation area (RSA) was visually assessed as the percentage of the total leaflet area that was sporulating at 168 h.

Results

The resistance to late blight varied greatly among the local potato cultivars, from extremely susceptible, Bol 3739, to highly resistant, Bol 3147 and Bol 2835. Most cultivars showed at least some resistance and a fair number even a considerable level of resistance. Also between *Solanum* species there seem to be differences, *S. stenotomum* being on average considerably more susceptible than *S. andigena*. The AUDPC of the *S. stenotomum* cultivars ranged from 4350 to 1562, while that of the *S. andigena* cultivars ranged from 2836 to 235 (Table 1). Of the *S. tuberosum, S. juzepczukii*, and *S. ajanhuiri* cultivars too few were present to draw any conclusion.

The nine isolates collected in potato fields in the vicinity of the experimental site represented seven races. The number of virulences varied between 7 and 10. Virulence against R9 was absent in all isolates. All isolates carried virulence against R1, R2, R3, R7, R10 and R11 (Table 2).

Of the 19 cultivars compared in the component analysis for their reaction to the most virulent isolate, 17 produced clearly sporulating lesions in both series. The cultivar Bol 1164 produced no visible lesions in one series but showed well sporulating lesions in the other one. Mora papa produced small sporulating lesions in one series and very tiny non-sporulating lesions in the other series. For these two cultivars no component data were collected. All four components, averaged over the series, showed a considerable variation among the cultivars. The latency period (LP) ranged from 3½ days for Bol 2715 and Bol 3819 to 6 days for Bol 2835. The mean LP was 4.4 days. The lesion size (LS) ranged from 225 mm^2 for Bol 225 to 20 mm^2 for Bol 4216 with a mean of 79 mm^2. The lesion growth rate (LGR) differed a factor six between Bol 2699 with the highest growth rate and Bol 4216 with the lowest. The relative sporulation area (RSA) was highest in Bol 2715 (98%) and lowest in Bol 2835 (9%). The components tended to vary in association with one another (Table 3). Especially LP and LGR were well associated with each other and both had a significant correlation with AUDPC, while the other two components did not show a significant correlation with AUDPC.

Table 1 Area under the disease progress curve (AUDPC) of 36 potato cultivars belonging to various *Solanum* species exposed to *Phytophthora infestans*

Entry	Species[a]	AUDPC	
Bol 3739	stn	4350	a[*]
Bol 2836	stn	3669	ab
Bol 2699[b]	stn	3269	bc
Alpha	tbr	3074	bcd
Bol 3130	stn	2975	bcde
Bol 4216[b]	stn	2859	bcde
Bol 1643	adg	2836	bcde
Bol 2715 [b]	adg	2560	cdef
Bol 3395	juz	2545	cdef
Bol 3743	stn	2352	defg
Bol 3856	stn	2264	defgh
Bol 1030	stn	2101	efghi
Yana Runa[b]	adg	1889	fghij
Gendarme	adg	1817	fghijk
82–222-1[b]	(tbr × adg) x adg	1726	fghijk
Bol 3819[b]	adg	1643	ghijkl
Waycha[b]	adg	1637	ghijkl
Bol 1465[b]	juz	1632	ghijkl
82-300-1[b]	complex[c]	1574	ghijkl
Bol 3044[b]	stn	1562	ghijkl
Bol 2695	adg	1483	ghijklm
Sani Imilla	adg	1433	hijklm
Bol 2802[b]	adg	1412	hijklm
Bol 1665[b]	adg	1364	hijklm
Bol 3202	ajh	1198	ijklmn
Mora papa[b]	adg	1033	Jklmno
Bol 3738	tbr	1000	jklmno
Bol 2718[b]	adg	992	jklmno
Bol 3372	ajh	949	klmno
Runa Toralapa [b]	tbr × adg	945	klmno
Bol 2796	adg	785	lmno
Bol 2931[b]	adg	740	lmno
Bol 1164[b]	adg	599	mno
Polonia[b]	adg	384	no
Bol 2835[b]	adg	273	o
Bol 3147	adg	235	o

[a]stn = S. stenotomum, tbr = S. tuberosum, adg = S. andigena, juz = S. juzepczukii, ajh = S. ajanhuiri

[b]Cultivars used in the component analysis

[c]Derived from a complex cross, ([(tbr × adg) × {(phu × dms) × phu}] × (tbr × adg)) × adg

[*]Significantly different according to Tukey's w Procedure at $P = 0.05$ if letters are different

Discussion

The race-specific R-genes are of little use in the protection of potato cultivars to the late blight pathogen. The complexity of the races found in potato fields near the trial field as reported above supports this, especially since effective R-genes are probably absent from the locally grown potato cultivars. Although it is possible that some local cultivars carried R-genes before the arrival of the late blight pathogen, it is very unlikely that the pathogen did not adapt to these R-genes.

Table 2 Virulence against the resistance genes R1 to R11 present in nine isolates of *Phytophthora infestans* collected in the vicinity of the experimental site

Isolate	Virulences
P2	1, 2, 3, 7, 8, 10, 11
P8	1, 2, 3, 4, 7, 10, 11
P4, P7	1, 2, 3, 4, 5, 6, 7, 10, 11
P5	1, 2, 3, 4, 5, 7, 8, 10, 11
P6	1, 2, 3, 5, 6, 7, 8, 10, 11
P9	1, 2, 3, 4, 6, 7, 8, 10, 11
P1, P3	1, 2, 3, 4, 5, 6, 7, 8, 10, 11

Quantitative or field resistance on the other hand is a considerably more durable resistance. Colon et al. (1995) tested 22 cultivars, released between 1900 and 1954 in The Netherlands and known to be free of R-genes, for their level of quantitative resistance in the field to a complex race of *P. infestans*. The quantitative resistance, measured through the AUDPC, correlated closely to the resistance ratings reported in the yearly Dutch Recommended Cultivar Lists from 1929 to 1954. Even after 40 and more years the quantitative resistance was still effective, indicative for its durability. However, due to the presence of both mating types the variability of the pathogen has increased considerably and this may have consequences for the stability and durability of field resistance to this pathogen (Flier et al. 2003). Indeed Carlisle et al. 2002 and Flier et al. observed differential cultivar-isolate interactions

Table 3 Spearman rank correlation coefficients among the area under the disease progress curve (AUDPC), latency period (LP), lesion size (LS), relative growth rate of the lesions (LGR) and relative sporulation area (RSA) of 17 local Bolivian potato cultivars exposed to *Phytophthora infestans*

	AUDPC	LP	LS	LGR
LP	–0.54*	-	-0.37^{ns}	–0.73**
LS	-0.10^{ns}	-0.37^{ns}	-	0.34^{ns}
LGR	0.53*	–0.73**	0.34^{ns}	-
RSA	0.18^{ns}	–0.53*	0.68**	0.61*

*, ** Significant at $P = 0.05$ and $P = 0.01$, respectively

for foliar field resistance. On the other hand Grünwald and Flier (2005) still consider field resistance to be quite durable. Several Mexican cultivars with high levels of field resistance were evaluated for durability of this resistance to late blight based on experimental data recorded between 1960 and 1999. Two of these cultivars (Sangema and Tollocan) were grown on at least 5% of the potato acreage and over long periods of time without an apparent decay in field resistance.

The resistance observed in the local cultivars appeared to be of a quantitative type and varied greatly, from significantly more susceptible than 'Alpha' to high levels of field resistance. The plots were small as only a restricted number of tubers were available. But interplot and even interplant interference does not seem to be of much importance in this pathosystem (Connolly et al. 1995). In this experiment the quantitative resistance may have been slightly underestimated for the resistant accessions and hardly overestimated for the very susceptible ones. The quantitative expression of the resistance is in itself insufficient proof of the absence of effective R-genes. Colon and Budding (1988), Coffey and Rees (1991) and Swiezynski et al. (2000) mentioned that symptoms of field resistance are difficult to separate from those of some R-genes with incomplete resistance ('leaky' R-genes). However, the quantitative resistance observed in the local cultivars, is not due to known leaky R-genes as virulence to the R-genes 1 to 11 was present in the isolates present in the area. And in the greenhouse 19 cultivars, representing the full range of quantitative resistance observed among the local cultivars, were tested with an isolate carrying virulence to all four leaky R-genes. Of these cultivars 17 consistently produced sporulating lesions. Also it is unlikely that in the tested local cultivars unknown effective R-genes, including leaky ones, are present as all reported R-genes have been found in Central American Solanum species, while from *S. andigena* and *S. stenotomum* no R-genes have been reported yet. It is therefore very probable that the quantitative resistance observed in the local cultivars represents true field resistance, a resistance which is presumably much more durable than the R-gene resistance.

Our current knowledge about the pathogen suggests central Mexico as the region of origin of *P. infestans*. This would mean that the cultivated potato evolved as a food crop in South America in the absence of late blight. The late blight pathogen was apparently introduced into South America from Europe or North America as until the late 1970's all *P. infestans* isolates outside the central highlands of Mexico appeared to belong to one lineage, US-1 of the A1 mating type, indicating a single introduction from central Mexico (Shaw 1987; Tooley et al. 1989). So, one would not expect R-gene or field resistance to occur more than incidentally in the local potato cultivars against *P. infestans* in South America. This agrees with the observations of Simmonds and Malcolmson that the 4n *Andigena* potatoes from South America were all very susceptible to late blight like the *Tuberosum* derived cultivars initially grown in Europe. After the late blight introduction in the 1840's in Europe some field resistance to *P. infestans* accumulated through selection in the past 120 years in Europe (Simmonds and Malcolmson 1967). In the data presented here a different pattern was observed. Most of the *S. andigena* cultivars studied had a good to fair level of field resistance to *P. infestans*. Although the local cultivars studied do not represent a random sample, it can be concluded that fair to good levels of resistance are present and apparently not even rare in *S. andigena*. The local cultivars belonging to *S. stenotomum*, *S. juzepczukii* and *S. ajanhuiri* too showed various levels of field resistance. It is quite possible that, due to selection pressure by the pathogen over the past period of many decades field resistance accumulated.

The components of field resistance to *P. infestans* in *S. tuberosum* were found to be associated (Van der Zaag 1959; Umaerus 1970; Umaerus and Lihnell 1976; Birhman and Singh 1995). LGR was found to be an important component of field resistance (Colon et al. 1995). Such an association between components of infection also appears to exist in other tuber bearing *Solanum* species as the components of field resistance studied here concerned 16 accessions from *S. andigena* (12), *S. stenotomum* (3), *S. juzepczukii* (1) and three cultivars bred from interspecific crosses.

Although the local cultivars are classified into several different species it is questionable whether these cultivated *Solanum* species represent true species (Spooner et al. 2005). They concluded that all diploid and tetraploid cultivated landrace populations from the Andean regions form a monophyletic clade, derived from the northern members of the *S. brevicaule* complex. This single Peruvian origin of the cultivated potato is not consistent with a series of species. Spooner et al. (2005) therefore suggest that all cultivated Andean potato populations should be classified as a single species, *S. bukasovii*.

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