

## New Sources of Resistance to Potato Pathogens in old Varieties of the Canary Islands

Nestor Alor<sup>1</sup> · Raquel López-Pardo<sup>1</sup> ·  
Leire Barandalla<sup>1</sup> · Domingo Rios<sup>2</sup> ·  
Enrique Ritter<sup>1</sup> · Jose Ignacio Ruiz deGalarreta<sup>1</sup>



Received: 17 June 2014 / Accepted: 13 April 2015 /  
Published online: 21 May 2015  
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**Abstract** In the Canary Islands, a number of old Andean potato introductions have been maintained by farmers and are cultivated there since the sixteenth century. Genetic resistance is an inexpensive way to control the main pests and diseases of potato and avoids the use of phytochemicals or other costly protective measures. In this study, we have analysed eight *Solanum tuberosum* subsp. *andigena* and *S. tuberosum* subsp. *tuberosum* accessions, representing old potato varieties from Tenerife Island, for their resistance levels to *Phytophthora infestans*, *Globodera rostochiensis*, *Globodera pallida* and *Pectobacterium atrosepticum*. New resistance sources against *P. infestans* in leaves and *P. atrosepticum* were found, as well as partial resistance to both nematode species. The results suggest the potential exploitation of the cultivar Venezolana Negra in breeding programmes in order to improve pest and disease resistance of potato.

**Keywords** *Pectobacterium atrosepticum* · *Phytophthora infestans* · Potato cyst nematodes

### Introduction

The potato (*Solanum tuberosum* L.) is the fourth most important crop in the world after corn, rice and barley (Faostat 2014). This crop represents also a major and basic food crop in many countries and produces a higher amount of energy and protein per hectare

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✉ Jose Ignacio Ruiz deGalarreta  
jiruiz@neiker.net

<sup>1</sup> NEIKER, Instituto Vasco de Investigación y Desarrollo Agrario, Apdo, PO Box 4646, 01080 Vitoria, Spain

<sup>2</sup> Centro de Conservación de la Biodiversidad Agrícola de Tenerife, Cabildo Insular de Tenerife, 38007 Tacoronte, Tenerife, Spain

than any other food crop, including cereals (Singh 2008). Potato was first cultivated 6000 to 10,000 years ago around the Titicaca Lake, Peru (Spooner and Hetterscheid 2004). According to Cook and Cook (1998), the first written references for potatoes were in 1552 who named them “turma de tierra (earth tuber)” and mentioned the local Quetchua name “Papa”. Caspar Bahuin was the first to describe potato in 1596, already 157 years before Carl von Lenné (1753; *Species Plantarum*). However, he used a slightly different name, *S. tuberosum esculentum*.

There were several introductions into Europe around the same time. John Hawkins reported loading potatoes in Venezuela on March 28, 1565. Popular legend has long credited Sir Walter Raleigh as the first bringing the potato to England, but history suggests Sir Francis Drake as a more likely candidate, in 1586, after battling the Spaniards in the Caribbean. According to Ruiz de Gordo (1981), potatoes were sent from Cuzco to the Spanish King Felipe II in 1565, but they could have been introduced even earlier (1562) into the Canary Islands (Ruiz de Galarreta and Ríos 2008).

The first records of cultivated potato outside South America were from Gran Canaria (Canary Islands) in 1567 (Hawkes and Francisco-Ortega 1993; Ríos et al. 2007) and shortly thereafter from mainland Spain in 1573 (Hawkes and Francisco-Ortega 1992; Romans 2005; Ames and Spooner 2008). In 1574, potato appeared in Tenerife Island (Lobo-Cabrera 1988). During the time of the colonies, the Canary Islands were the first entry point into Europe for goods from South America, including novel plant species such as potato. Modern potato cultivars are very different from this original material, but in the Canary Islands, a number of Andean introductions have been maintained and were cultivated since the mid-sixteenth century (Ríos et al. 2007). They were classified for the first time by Zubeldia et al. (1955) into the following species, *S. tuberosum* subsp. *andigena*, *S. tuberosum* subsp. *tuberosum* and *Solanum chaucha*. Rodríguez (2000) made a basic characterization of 14 local cultivars from Tenerife Island: Azucena Blanca, Azucena Negra, Bonita Blanca, Bonita Colorada, Bonita Llagada, Bonita Ojo de Perdiz, Bonita Negra, Colorada, Tormenta, Borralla, Mora, Negra and Andina Blanca y Andina Negra. Ríos (2002) characterized morphologically 52 accessions of Canarian landraces obtaining similar results to those described by Zubeldia et al. (1955).

Based on this study, he argues that 11 of these cultivars have typical characteristics of subsp. *andigena* and two, Mora and Borralla, have features of both subspecies. Barandalla et al. (2006) and Ruiz de Galarreta et al. (2007) analysed with SSR markers the relationship among local cultivars from Tenerife and La Palma islands, respectively. Ruiz de Galarreta et al. (2011) performed also a joint analysis of local cultivars from mainland Spain and from the Canary islands in order to detect potential relationships at the molecular level. All these studies revealed some particularities of certain Canary cultivars which might exist also with respect to disease and pest resistances.

The potato is sensitive to a wide range of pests and diseases, but within landraces, specific resistance against certain pathogens has been found (Ruiz de Galarreta et al. 1998; Ritter et al. 2008). Late blight caused by the oomycete *Phytophthora infestans* is considered the most important potato pathogen worldwide and can destroy a susceptible potato crop within 1 week, especially under favourable climatic conditions. However, under optimal weather conditions, the pathogen may complete several infection cycles a week on a susceptible host, with control failure leading to rapid epidemics and crop loss (Cooke et al. 2012).

After a latent period as short as 3 days (Flier and Turkensteen 1999), new sporangia are formed and spread to infect new plants. The fast and efficient spread, infection and colonization of the host plant gives the potential of destroying all above ground parts of a crop within a week (Andersson 2007).

The infection affects all vegetative parts of the plant including the tubers, requiring frequent fungicide applications for its control. The co-existence of two mating types and sexual reproduction increases the chance of developing resistance to fungicides such as metalaxyl. The majority of varieties grown in Europe and North America are susceptible to late blight (Flier et al. 2003). Several resistance screenings have been performed in *Solanum* wild species (Hawkes 1994). Quantitative resistance does not confer absolute protection, and qualitative or *vertical* resistance is highly race-specific and becomes rapidly ineffective due to changes in the pathogen population (Forbes et al. 2005).

Potato cyst nematodes *Globodera pallida* Stone and *Globodera rostochiensis* Woll. represent also important potato pests (Evans and Trudgill 1992). Initial screenings of tuber-bearing *Solanum* species identified resistance to *G. rostochiensis* in *S. tuberosum* ssp. *andigena* and *Solanum vernei* (Castelli et al. 2003).

Tuber soft rot caused by *Pectobacterium atrosepticum* (syn. *Erwinia carotovora* subsp. *atroseptica* van Hall), generates significant crop losses in seed and ware potato production, both in the field and during storage. Diseased seed tubers are the primary infection source, but spores can survive also in the soil and can be spread by irrigation water (Egúsquiza 2000). Resistance sources are present in several tuber-bearing *Solanum* species (Allefs et al. 1995).

This paper reports on the response of old potato cultivars from Tenerife Island (Spain), in controlled infection experiments with *P. infestans*, *G. rostochiensis*, *G. pallida* and *P. atrosepticum* in order to identify potentially new resistant sources and to extend the present gene pool of exploitable resistances.

## Materials and Methods

### Plant Material

Eight *Solanum* genotypes representing old potato cultivars from Tenerife Island (Spain) were evaluated. The accessions, previously characterized by Ríos (2002) and Ruiz de Galarreta et al. (2011), were obtained from the germplasm collection of the Center for the Conservation of Biodiversity from Tenerife (CCBAT). Three commercial cultivars belonging to the species *S. tuberosum* (Bintje, Desiree and Spunta) were selected as susceptible controls. Table 1 shows the accession code, common name and taxonomic assignment for each accession.

### Resistance Evaluation

#### *P. infestans*

The resistance against *P. infestans* in leaves was evaluated using the method of Vleeshouwers et al. (1999). The MP 324 strain used for inoculations has mating type A1 and a high level of aggressiveness in foliage. It was provided by the Plant Breeding

**Table 1** Local potato cultivars from Tenerife Island and susceptible controls selected for the evaluation of resistances to different pathogens

Code	Variety	Species
NK-127	Bintje <sup>a</sup>	<i>S. tuberosum</i>
NK-276	Desiree <sup>b</sup>	<i>S. tuberosum</i>
NK-069	Spunta <sup>c</sup>	<i>S. tuberosum</i>
NK-383	Bonita Colorada	<i>S. andigena</i>
NK-386	Azucena Negra	<i>S. andigena</i>
NK-390	Terrenta	<i>S. andigena</i>
NK-397	Peluca Rosada	<i>S. tuberosum</i>
NK-401	Bonita Ojo de Perdiz	<i>S. andigena</i>
NK-404	Borralla	<i>S. tuberosum</i>
NK-409	Venezolana Negra	<i>S. tuberosum</i> × <i>S. andigena</i>
NK-415	Moras	<i>S. tuberosum</i>

<sup>a,b,c</sup> Susceptible control varieties used for evaluating resistance against *P. infestans*, *G. pallida*, *G. rostochiensis* and *P. atrosepticum*, respectively

and Acclimatization Institute (IHAR) from Poland and has all virulence genes except R5, R8 and R9. Isolates were first inoculated on tuber slices of the susceptible potato cv. Bintje and incubated in the dark at 18 °C for 5–7 days. When sporulating mycelium was present, small tufts of mycelium were placed in 9-cm Petri dishes containing rye agar medium. Inoculum for infection was prepared by dipping sporulating plates in 4 ml of water, filtering the crude suspension through cheesecloth and adjusting the concentration to  $4.10^4$  sporangia  $\text{ml}^{-1}$ . The experiment was conducted with three replicates per genotype, inoculating five leaflets of each Canarian cultivar and the susceptible control cv. Bintje. The leaflets were collected from each of the two youngest fully expanded leaves of each plant and kept on moist paper in transparent boxes with the abaxial surface upwards. After the discs were inoculated with a 40- $\mu\text{l}$  drop of spore suspension and incubated for 5 days in a climate chamber at 18 °C with an 18-h light period, the estimation of leaf resistance was made according to the percentage of the infected leaflet disc surface, as recorded after 5 days of incubation, when the leaves of the control variety were fully infected. The area under the total disease progress curve (AUDPC) was calculated using the trapezoidal integration method and transformed into the relative area under the disease curve (rAUDPC) (Fry 1978). The AUDPC was calculated as

$$\text{AUDPC} = \sum_{i=1}^n [(x_{i+1} + x_i)/2][t_{i+1} - t_i]$$

where  $x_i$ =proportion tissue affected at the  $i$ th observation,  $t$ =time (days) after inoculation at the  $i$ th observation and  $n$ =total number of observations. Values for AUDPC were normalized by dividing the AUDPC by the total area of the graph (=the number of days from inoculation to the end of the observation period). The

normalized AUDPC is referred to as relative AUDPC. Units for AUDPC are days-proportion, and relative rAUDPC is a percentage value.

Whole-tuber inoculation experiments were performed using tubers from all cultivars and the susceptible control. For this purpose, tubers were dug by hand to minimize wounding, immediately transferred to the laboratory and washed. Five undamaged tubers were inoculated using the same isolate MP324 and were subsequently incubated at 18 °C with an 18-h light period. Tuber resistance against *P. infestans* was determined according to the methods described by Flier et al. (2001). After 2 weeks of storage, tubers were visually examined for the presence of tuber blight symptoms, and the percentage of infected area per tuber was calculated. Diseased tubers were cut longitudinally, and disease severity was scored as described by Flier et al. (2003) for each individual tuber. The following scale was used: 0=no symptoms, 1=<2.5% of cut area with symptoms, 2=2.5–10%, 3=10–25%, 4=25–50% and 5=>50% of cut area with symptoms. Values for AUDPC were also calculated and normalized.

Accessions without infection or with infection not exceeding 10% on any leaf and tuber surface were defined as resistant, whereas accessions with 10 to 20% of infected leaf surface were defined as partially resistant. Genotypes exceeding 20% of infected surface were considered susceptible.

### *G. rostochiensis* and *G. pallida*

For evaluating the resistance against nematodes *G. rostochiensis* (pathotype Ro1,4) and *G. pallida* (pathotype Pa2/3), a bioassay was performed in the greenhouse as a pot test following the methodology described by Ruiz de Galarreta et al. (1998). Five tubers and three replicates with a total of 15 tubers per cultivar were planted individually into pots for the evaluation of *G. rostochiensis* and *G. pallida*, respectively. The infected soil contained 30 cysts per pot of *G. rostochiensis* and *G. pallida* in two sets, separately. The cysts of *G. pallida* Pa 2/3 were collected in 2012 from Bañares (Alava, Basque Country, Spain). For the test on *G. rostochiensis*, the cysts came from infected fields of Urturi (Alava, Basque Country, Spain) and maintained in NEIKER-Tecnalia. Desiree was used as a susceptible control variety in each assay.

Plants were grown at 20 °C for 10 weeks, and the accessions and controls were scored 10 weeks after inoculation. Resistance levels were classified as fully resistant (accessions with an average cyst counts of  $\leq 5$ ), partial resistant (accessions with average cyst counts between 5 and 20) or susceptible (accessions with an average cyst counts of  $\geq 20$  cysts) according to Rousselle-Bourgeois and Mugniery (1995). Resistant genotypes were planted again into pots containing soil with 30 cysts to confirm their resistance.

### *P. atrosepticum*

Resistance levels to the bacteria *P. atrosepticum* were determined as described by Foolad et al. (2002). Tubers were washed thoroughly in running tap water, and the surface was disinfected by dipping in 90% ethanol for 3 min before use. All tests were performed with strain VC7004/CR3 from the NEIKER culture collection. Bacterial suspensions in sterile distilled water were prepared from cultures grown on solid King's B medium at 27 °C for 24 h. The concentrations of the stock suspensions were

calculated from optical density readings of 350 nm and adjusted to  $2 \times 10^8$  cells  $\text{ml}^{-1}$ . The actual number of colony-forming units (CFU) per millilitre of inoculum suspension was determined by plating serial dilutions of each suspension on King's B plates and counting visually the number of colonies formed after 24 h of incubation at 27 °C.

Inoculations were performed according to Lapwood and Gans (1984) with minor modifications. Each tuber was cut longitudinally, and a cylindrical well (5 mm in diameter, 5 mm deep) was extracted from the middle of each half tuber 2 h before inoculation. Half tubers were placed on filter paper in black plastic containers. Six half tubers of each potato genotype were inoculated with 200  $\mu\text{l}$  of suspension and incubated in a chamber for 6 days at 20 °C in constant darkness. The area under the total disease progress curve (AUDPC) was calculated. Genotypes were classified into resistant, partial resistant and susceptible based on the infected surface as described for *P. infestans*. In each batch of inoculations, the susceptible control cultivar Spunta was included.

## Results

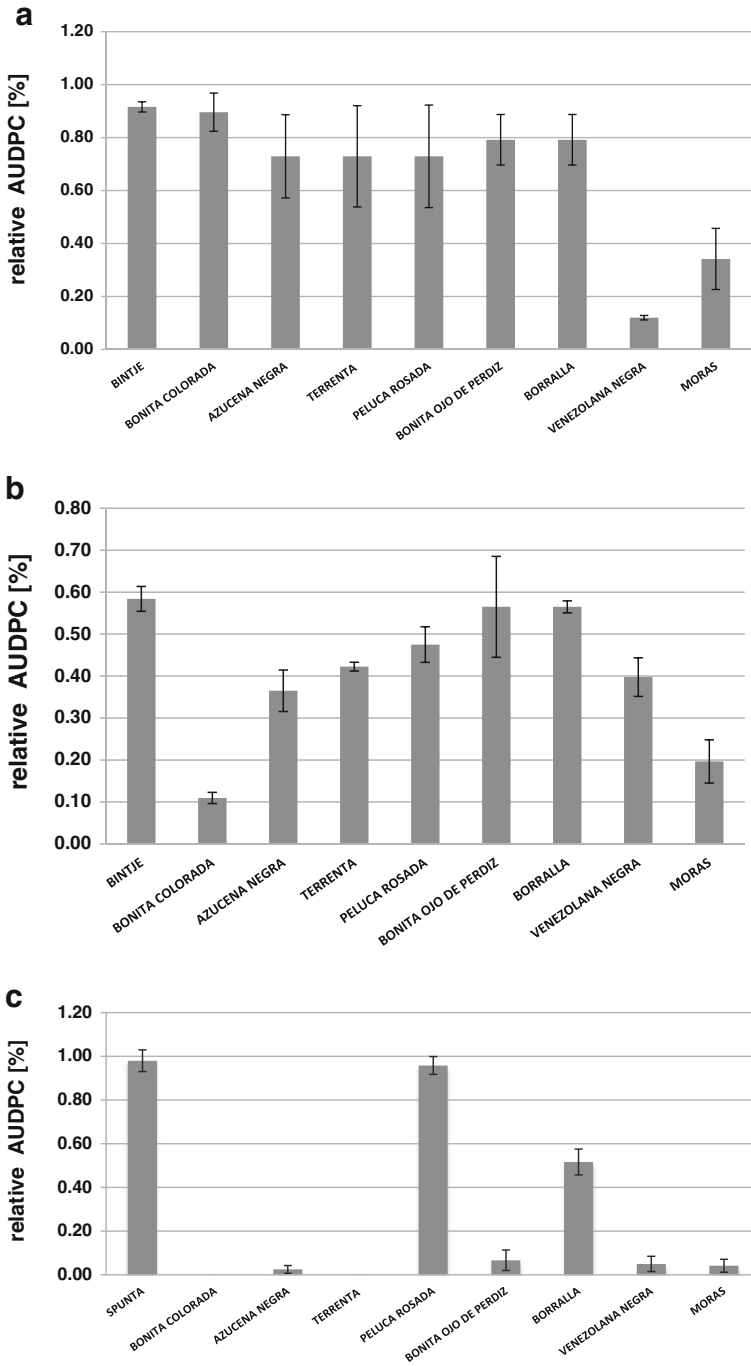
Foliar resistance levels against our late blight isolate varied considerably among the potato cultivars that were evaluated. Venezolana Negra (*S. tuberosum*  $\times$  *S. andigena*) and cv. Moras (*S. tuberosum*) showed partial resistance to the *P. infestans* strain with an rAUDPC mean value of 0.120 and 0.342 (Fig. 1a). In contrast, the susceptible control Bintje had a value of 0.912. All other cultivars showed rAUDPCs comparable with that of cv. Bintje, ranging from 0.729 to 0.896. Moreover, the most resistant cv. Venezolana Negra revealed also the lowest standard deviation of AUDPC values (0.009).

All cultivars were susceptible to tuber inoculations of *P. infestans* with the exception of cv. Bonita Colorada (*S. andigena*) which showed an rAUDPC of 0.110 and was considered as a partial resistant cultivar (Fig. 1b). No relationships between *P. infestans* resistance in tubers and leaves were observed.

With respect to *G. rostochiensis*, all cultivars were susceptible with cyst numbers ranging from 156.3 to 203.1 (Table 2). With respect to *G. pallida* (Pa2/3), partial resistance in cvs. Bonita Ojo de Perdiz (*S. andigena*), Azucena Negra (*S. andigena*) and cv. Venezolana Negra (*S. tuberosum*  $\times$  *S. andigena*) with average cyst counts of  $13.1 \pm 2.3$ ,  $15.3 \pm 1.4$  and  $17.1 \pm 2.5$ , respectively. In contrast, the susceptible control Desiree had an average of  $189.3 \pm 12.1$  cysts. These genotypes were planted again into pots containing soil with 30 cysts, and we confirmed their partial resistance detected.

We found total resistance to *P. atrosepticum* in cv. Bonita Colorada and cv. Terrenta, both *S. andigena* species, showing 0% infection (Fig. 1c). On the other hand, four cultivars Azucena Negra, Bonita Ojo Perdiz, Venezolana Negra and Moras showed partial resistance ranging from 0.025 to 0.067 rAUDPC (Fig. 1c). The susceptible cv. Spunta showed an rAUDPC value of 0.980, similar to that of the susceptible cv. Peluca Rosada with 0.958.

Table 3 summarizes the resistances found in all evaluated cultivars. The multiple resistance of the cv. Venezolana Negra with resistance to *P. infestans* in leaves and partial resistance to *G. pallida* and *P. atrosepticum* are notable.



**Fig. 1** Relative areas under the disease progress curves of an isolate of **a** *Phytophthora infestans* inoculated onto detached leaflets, **b** *Phytophthora infestans* inoculated onto tubers and **c** *Pectobacterium atrosepticum* inoculated on tubers of old Canarian varieties and susceptible controls

**Table 2** Average of final cyst counts existing on the root balls per plant inoculated from *G. pallida* and *G. rostochiensis* in Canarian cultivars and susceptible control

Variety	Species	Mean cyst counts	
		<i>G. pallida</i>	<i>G. rostochiensis</i>
Desiree	<i>S. tuberosum</i>	189.3±12.1	193.2±8.3
Bonita Colorada	<i>S. andigena</i>	201.5±18.4	183.3±11.2
Azucena Negra	<i>S. andigena</i>	15.3±1.4	203.1±7.5
Terrenta	<i>S. andigena</i>	213.2±21.5	183.3±2.6
PelUCA Rosada	<i>S. tuberosum</i>	164.4±14.6	180.1±7.6
Bonita Ojo de Perdiz	<i>S. andigena</i>	13.1±2.3	156.3±14.3
Borralla	<i>S. tuberosum</i>	173.2±12.3	202.2±18.4
Venezolana Negra	<i>S. tuberosum</i> × <i>S. andigena</i>	17.1±2.5	195.3±21.4
Moras	<i>S. tuberosum</i>	178.2±16.4	188.3±17.2

## Discussion

The potato crop is affected by many pests and diseases that cause substantial damages in the field, losses during storage or affects the quality of the tubers. Managing these pathogens requires crop rotations, utilization of pesticides and other practices that are costly to farmers or environmentally unsafe. However, it may be also possible to confer resistance by transferring a naturally found resistance gene to potato cultivars of interest by crossings or somatic hybridizations, if this is possible, or using transgenic approaches.

**Table 3** Observed pathogen resistances in old potato cultivars from Tenerife island

Variety	Species	<i>P. infestans</i> (leaf)	<i>P. infestans</i> (tuber)	<i>G. pallida</i>	<i>G. rostochiensis</i>	<i>P. atrosepticum</i>
Bonita Colorada	<i>S. andigena</i>	S	PR	S	S	R
Azucena Negra	<i>S. andigena</i>	S	S	PR	S	PR
Terrenta	<i>S. andigena</i>	S	S	S	S	R
PelUCA Rosada	<i>S. tuberosum</i>	S	S	S	S	S
Bonita Ojo De Perdiz	<i>S. andigena</i>	S	S	PR	S	PR
Borralla	<i>S. tuberosum</i>	S	S	S	S	S
Venezolana Negra	<i>S. tuberosum</i> × <i>S. andigena</i>	PR	S	PR	S	PR
Moras	<i>S. tuberosum</i>	PR	S	S	S	PR

*R* resistant, *PR* partially resistant, *S* susceptible



On the other hand, native potato species are cultivated under harsh environmental conditions where modern potato cultivars cannot compete. They have been locally selected by the Andean farmers in order to provide their subsistence. Some old introductions of native potato species exist also in Europe. In the Canary Islands, the cvs. Azucena Negra or Peluca Rosada are highly appreciated, among others. Despite its low productivity, the high market prices make it a lucrative crop. Some of these cultivars have been evaluated for their nutritional composition (Rodríguez et al. 2012), but there are no published studies about their resistance levels to the main potato pests and diseases. Ruiz de Galarreta et al. (1998) found resistances against *P. infestans*, in some *Solanum* wild species such as *Solanum bulbocastanum*, *Solanum circaefolium*, *Solanum demissum*, *Solanum phureja*, *Solanum pinnatisectum* and *Solanum stoloniferum*. In the present work, we have found partial foliar resistance to *P. infestans* in the cv. Venezolana Negra and partial tuber resistance in Bonita Colorada. The level of tuber infection was not found to be related to foliar blight resistance, which is in agreement with earlier studies from Wastie (1991).

Gabriel et al. (2008) found a negative correlation between foliar and tuber disease in five diploid potato progenies with segregating resistance levels. Spielman et al. (1992) reported that the sporulation capacity of isolates measured in a growth chamber was closely correlated with the AUDPC measured in a small field experiment. Forbes et al. (2005) found broad geographical stability of quantitative resistance to late blight in a set of potato genotypes from *S. tuberosum* in international trials at several locations. Further studies will be necessary for evaluating field resistance to *P. infestans* in our Canarian cultivars.

Resistance against *G. pallida* Pa2/3 has been reported in specific accessions of *Solanum berthaultii*, *Solanum gourlayi*, *Solanum brevicaulle*, *Solanum multidissectum* and *S. vernei* (Turner 1989; Kreike et al. 1994). Also, Castelli et al. (2003) evaluated the Commonwealth Potato Collection for resistance to *G. pallida* and *G. rostochiensis* and found clones with high levels of resistance. Vallejos (1994) found partial resistance to *G. pallida*, in a native potato variety sipancachi (*S. andigena*). Similar results were obtained in the present work, with cvs. Azucena Negra and Bonita Ojo Perdiz both belonging to *S. andigena*. Also, Estrada (2000) suggested that the maintained sources to improve resistance to *Globodera* sp. should include accessions from *S. vernei*, *Solanum spgazzini* and *S. andigena*.

Since antibiotics are generally not permitted for crop protection purposes, chemical control of bacterial soft rot in potato is not possible. Therefore, genetic resistance is the best method to control this disease. Sources of resistance are present in several tuber-bearing species of *Solanum* (Rousselle-Bourgeois and Priou 1995), which have been exploited in prebreeding and breeding programmes. However, the introgression of the resistance genes into commercial cultivars is difficult because of incompatibility with *S. tuberosum*, complex inheritance and linkage drag of unwanted traits from the resistant parent (Ahmet et al. 2004). Quantitative variation has been observed (Lyon 1989), suggesting that resistance to soft rot is primarily of the polygenic, non-specific type. In our study, we have found resistance in one cv. belonging to *S. andigena* Bonita Colorada. These results agree with those described by Ritter et al. (2008) who also detected resistances in native potatoes from *S. andigena* such as Pulu and Puca Quitish.

In general, the results obtained in our work demonstrate that within the gene pool of *Solanum* still numerous, in part unexploited, resistances are available which could favourably be used for potato breeding by introducing them into new cultivars. However, it will be necessary to know the type of resistance and how they are inherited in each case. Molecular techniques including linkage mapping and QTL analysis would allow to identify markers for qualitative or quantitative resistance genes which could be used in marker-assisted selection.

**Acknowledgements** This work was financed by INIA RTA2013-00006-C03-1, the Cabildo of Tenerife and the Basque Government.

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