

RESEARCH/INVESTIGACIÓN

AN ASSESSMENT OF POTATO CYST NEMATODE (*GLOBODERA* SPP.) RESEARCH FROM THE ANDEAN REGION OF SOUTH AMERICA. PART 2: SEARCH FOR RESISTANCE IN POTATO

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ABSTRACT

Silvestre, R., L. M. Dandurand, I. A. Zasada, J. Franco, and J. Kuhl. Xxxx. An assessment of potato cyst nematode (*Globodera* spp.) research from the Andean region of South America. Part 2: Search for resistance in potato. *Nematropica* 51:106-130.

Potato cyst nematodes (PCN; *Globodera pallida* and *G. rostochiensis*) are among the most significant pathogens limiting the production of potato globally. Since the first PCN detection, research has focused on a diversity of topics, including species identification, geographic distribution, and pathotype characterization. While many have focused on characterizing potato-nematode interactions, identification of resistance has been a challenge, particularly for *G. pallida*. This, in turn, makes it difficult to recommend nematode management strategies. South America is the center of diversity for PCN and includes numerous international institutes and universities conducting PCN resistance research at the regional level. For breeding programs and other users of this information and associated germplasm, a consolidated overview of this research would be beneficial. This review reports on South American research conducted to evaluate potato germplasm response to PCN in the Andean region of South America.

Key words: *Globodera pallida*, *Globodera rostochiensis*, potato cyst nematodes, resistance, potato

RESUMEN

Silvestre, R., L. M. Dandurand, I. A. Zasada, J. Franco and J. Kuhl. Xxxx. Revisión sobre los nemátodos del quiste de la papa (*Globodera* spp.) en la región Andina de América del Sur. Parte 2: Búsqueda de resistencia en el cultivo de papa. *Nematropica* 51:106-130.

Los nemátodos del quiste de la papa (PCN; *Globodera pallida* and *G. rostochiensis*) se encuentran entre los patógenos más importantes que limitan la producción del cultivo de papa a nivel mundial. Desde la primera detección de PCN las investigaciones se han centrado en diferentes temas como la identificación de especies, su distribución geográfica y la caracterización de los patotipos. La mayoría de las investigaciones se han centrado en caracterizar las interacciones papa-nemátodo sin embargo la

identificación de la resistencia ha sido un desafío, particularmente para *G. pallida*. Esto, a su vez, dificulta recomendar estrategias de manejo de nemátodos. América del Sur es el centro de diversidad de PCN e incluye numerosos institutos y universidades nacionales e internacionales que realizan investigaciones sobre la resistencia a PCN a nivel regional. Una visión general de esta información y del germoplasma asociado a estas investigaciones podría ser beneficiosa para los programas de mejoramiento y otros usuarios. Esta revisión reporta investigaciones realizadas para evaluar la respuesta del germoplasma de papa a PCN en la región Andina de América del Sur.

Palabras claves: *Globodera pallida*, *Globodera rostochiensis*, nemátodo del quiste de la papa, resistencia, papa

INTRODUCTION

Potato is the third most important crop for human consumption in the world (Devaux *et al.*, 2020). Potato is a nutritional staple crop that provides food security and generates income (Mburu *et al.*, 2020). The Andean region of South America is the most important center of potato diversity in the world, where more than 4,000 varieties and landraces can be found. Local farmers play an important role in conservation through the cultivation of over 3,000 landraces (Spooner *et al.*, 2014). In South America from 1961-2018, annual potato production increased from 6.4 million tons to 17.4 million tons (FAOSTAT, 2018) with most of this production for human consumption. Potato, a basic staple in the rural Andean highlands, is also widely consumed in urban households in South America (Devaux *et al.*, 2020). However, potato is affected by many plant pathogens, such as potato cyst nematodes (PCN), which are a major production constraint in developing countries and throughout the world (Franco and González, 2011; Coyne *et al.*, 2018; Mburu *et al.*, 2020). Potato cyst nematodes include *Globodera pallida* (the pale cyst nematode) and *G. rostochiensis* (the golden cyst nematode). A review of the occurrence and impact of these nematodes on potato in the Andean region of South America was summarized in Part 1 of this two-part review (Silvestre *et al.*, 2021). Part 1 includes a map that shows PCN locations identified throughout the region. The five countries that are part of this review cover the Andean region in South America. The political organization within each country is as follows: Peru is divided

in 25 regions, Ecuador is divided in 24 provinces, Bolivia is divided in 9 departments, Venezuela is divided in 23 states, and Chile is divided in 16 regions. Argentina and Colombia, which were included in Part 1, are not included in Part 2 because of the absence of PCN resistance evaluations.

Potato plants containing different resistance genes (differential plants) have been used to separate nematode populations that possess different virulence genes affecting their reproduction; these plant-differentiated populations are called pathotypes. Kort *et al.* (1977) proposed a classification scheme identifying five *G. rostochiensis* pathotypes Ro1, Ro2, Ro3, Ro4, and Ro5, and three *G. pallida* pathotypes Pa1, Pa2, and Pa3, based on multiplication rates on a series of differential potato genotypes. *Globodera* pathotypes from the Andean region have more variability than those found in Europe (Plantard *et al.*, 2008). A comparison of European and South American pathotypes was conducted by Canto and Scurrah (1977) resulting in a new naming scheme with four *G. rostochiensis* pathotypes and seven *G. pallida* pathotypes (Table 1). This approach resulted in identification of pathotypes R₁A, R₁B, R₂A, and R₃A for *G. rostochiensis* and P₁A, P₁B, P₂A, P₃A, P₄A, P₅A and P₆A for *G. pallida* (Canto and Scurrah, 1977; Franco and González, 1990). This review will use the South American scheme proposed by Canto and Scurrah (1977). Throughout this review, information on pathotypes are mentioned when available; however, not all sources reported pathotypes used in research trials.

Table 1. Alignment of European and South American pathotypes as reported in Canto and Scurrah (1977) and Franco and Gonzalez (1990). European pathotypes as described in Kort *et al.* 1977.

<i>Globodera rostochiensis</i>							
European	Ro1	Ro4	Ro2	Ro3			
S. American	R ₁ A	R ₁ B	R ₂ A	R ₃ A			
<i>Globodera pallida</i>							
European	Pa1				Pa2	Pa3	
S. American	P ₁ A	P ₁ B	P ₂ A	P ₃ A	P ₄ A	P ₅ A	P ₆ A

Numerous genes conferring resistance to *G. rostochiensis* and *G. pallida* have been characterized over the years, notably from close relatives of potato including *Solanum tuberosum* ssp. *andigena*, *Solanum spigazzinii*, and *Solanum vernei* among others. The dominant gene, *H1*, provides high levels of resistance to *G. rostochiensis* pathotypes R₁A and R₁B (Table 1), and has been widely utilized in breeding programs around the world. Recently, *H1* was shown to provide resistance to *Globodera ellingtonae*, a newly described *Globodera* spp., which reproduces on potato but does not appear to reduce yield (Handoo *et al.*, 2012; Lax *et al.*, 2014; Whitworth *et al.*, 2018; Zasada *et al.*, 2018). The widespread deployment of *H1* in potato cultivars has contributed to the predominance of *G. pallida* in the UK and in many European countries (Minnis *et al.*, 2002) and has led to the emergence of the *G. rostochiensis* R₂A (Ro2) pathotype in New York, USA (Brodie, 1989). Resistance to *G. pallida* is often characterized in quantitative terms and lacks strong dominant resistance genes such as *H1*. Deployment of potato cultivars with *G. pallida* resistance has been limited compared to that of *G. rostochiensis*. The durability of deployed resistance is already in question, with the more complex genetic structure of *G. pallida* populations likely a contributing factor (Niere *et al.*, 2014; Eves-van den Akker *et al.*, 2015; Varypatakis *et al.*, 2019). In addition to the resistance characteristics of a cultivar, tolerance to PCN is also crucial. Tolerant varieties do not suppress buildup of PCN population densities as does cropping with a resistant cultivar; however, yield loss caused by PCN is minimal. Deployment of resistant cultivars that are intolerant to PCN can have significant

adverse effects on potato yield while tolerant but susceptible varieties can facilitate population multiplication. Potato varieties vary in both their resistance and tolerance to PCN, and environmental factors play a key role in the development of these characters.

The search for potato resistance to PCN

This section presents a compilation of reports (from English and Spanish publications) describing the response of potato germplasm to PCN. Potato is economically important throughout South America, and many traits need to be considered when breeding commercial varieties. Nematode resistance is one trait often considered during the breeding process. Effective resistance against PCN has been introduced into European cultivars from potatoes originating in South America (Finlay *et al.*, 1998). This review aims to describe the native and wild potato varieties and breeding material from South America that have been tested for PCN resistance and/or tolerance. When available, a distinction will be made for resistance to *G. pallida* or to *G. rostochiensis*. Information is also included from experiments conducted to identify PCN pathotypes from field collected PCN populations. In some cases, field pathotypes were not identified, in which case an uncharacterized resistance or tolerance is reported.

Definition of resistance and tolerance can vary; however, the general consensus is that the term resistant refers to a potato host that prevents, at least partially, PCN from reproducing, usually observed as cyst or egg numbers. That is, juvenile nematodes can penetrate roots; however female development is inhibited and is independent of

plant yield. The term tolerance is related to the ability of the potato host to grow and remain undamaged during PCN attack, usually evaluated as tuber yield under nematode pressure compared to yield in the absence of PCN (Finlay *et al.*, 1998).

The search for potato resistance to PCN has been pursued in South America since the 1970s. The primary early driver of this search was the International Potato Center (CIP) in Lima, Peru. In the early 1970s, CIP initiated a nematode control strategy with active research on screening and breeding for resistance to PCN and root-knot nematodes (*Meloidogyne* spp.). Records of these efforts were published by CIP from 1974 to 1995. Additionally, other national programs from Ministries of Agriculture and private organizations in South America have also participated in the develop of PCN resistance in potato including the Instituto Nacional de Investigación Agraria (INIA) from Peru, Fundación para la Promoción e Investigación de Productos Andinos (PROINPA) from Bolivia, Instituto Nacional de Investigaciones Agropecuarias (INIAP) from Ecuador, Instituto de Investigaciones Agropecuarias (INIA) from Chile, as well as diverse universities. In this review, these efforts will be organized by country. Breeding clones developed by CIP were evaluated in Peru as well as in other countries; therefore, CIP's effort to identify and select potato clones with resistance to PCN is presented chronologically.

Resistance screening and potato variety development originating in Peru

In the 1970s, the CIP breeding program worked to characterize nematode populations collected from across South America by screening CIP-germplasm for PCN resistance. In 1974, CIP had over 120 PCN populations collected from Peru (Puno, Arequipa, Cuzco, Junin, Huanuco, La Libertad, and Cajamarca Regions), Ecuador, Colombia, Panama, and Mexico. Some of these PCN populations were used to screen CIP germplasm.

In 1974, 50 potato clones were evaluated for yield and reaction to PCN in an infested field in Jauja, Junin Region, Peru. Yields were low for all clones due to the high PCN infestation. From the six clones that had the highest yields, clone

CIP701422 was singled out because reproduction of PCN was slightly decreased under field conditions (CIP, 1975). In 1975, 124 clones from CIP germplasm were tested against PCN populations collected from Cuzco, Huancayo (Junin Region), Otuzco (La Libertad Region), and the Puno Region. Three clones (not listed) were observed to be resistant to three of the four PCN populations, while 18 clones had some resistance to at least one population and eight clones showed some resistance to two populations (CIP, 1976).

In 1976, evaluation of PCN resistance in the CIP germplasm collection was carried out on more than 3,000 clones using three Peruvian populations of *G. pallida* and one of *G. rostochiensis*. Twenty clones were selected because they significantly reduced PCN reproduction. These clones appeared to have single pathotype resistance. From these 20 clones, clone CIP701478 was observed to be resistance to two *G. pallida* populations from Cuzco and Otuzco (CIP, 1977; #1 in Table 2). In 1977, two clones from *S. tuberosum* ssp. *andigena*, CIP702535 and CIP702698, were highly resistant to a *G. pallida* population from Huancayo and somewhat resistant to *G. pallida* populations from Otuzco and Cuzco. These two clones were also observed to be resistant to a *G. rostochiensis* population from Puno. From 1,981 progenies derived from crosses between resistant and susceptible *S. tuberosum* ssp. *andigena* clones, approximately one-third of progeny were resistant to PCN. Of these, 80% of progeny derived from the clone CIP701422 were resistant to a *G. pallida* population from Otuzco and almost 10% of progeny derived from the clone CIP701478 were resistance to both the Otuzco and Cuzco populations (CIP, 1978; #2 in Table 2).

To determine the pathotypes of populations from the Andean region, 56 PCN populations from across South America were collected. Thirty-three populations were from northern Bolivia to southern Colombia and an additional 23 populations were from Lake Titicaca (Peru and Bolivia), and the Junin Region (central Peru). European PCN host differentials and six clones from Germany and USA derived from *S. vernei* (66-1001-2, 66-1003-42, 711-18, 710-6) and *S. spgazzinii* (64-953/4, J 1002-26) were used to evaluate their

Table 2. A list of germplasm evaluated for resistance to potato cyst nematodes in South America.

#	Country of testing	Location tested	<i>Globodera</i> spp ^z	Host	Material tested	Reaction to PCN	Source of material	Reference
1	Peru	Greenhouse - CIP Experimental Station	Gp	Potato clones	CIP701478	Resistant	International Potato Center -Peru	CIP, 1977
2	Peru	Greenhouse - CIP Experimental Station	Gp	Potato clones	CIP702535, CIP702698	Highly resistant	International Potato Center -Peru	CIP, 1978
3	Peru	Greenhouse and Field - CIP Experimental Station	Gp, Gr	Potato clones and cultivar	CIP702535, CIP702698 CIP702626, CIP701323 'Renacimiento'	Highly Resistant Resistant Susceptible	International Potato Center-Peru	CIP, 1981
4	Peru	Field	Gp	Potato breeding clones	CIP279139.5, CIP279142.12, CIP276008.16, CIP280090.10, CIP278096.10	Resistant	International Potato Center-Peru	CIP, 1986
5	Peru	Field- CIP Experimental Station Santa Ana, Huancayo (3280 masl)	Gp	Potato breeding clones	CIP279142.12, clone G83233.12, clone G83117.4, clone G83009.5, clone G83141.12 Clone G83193.3, clone G83251 .23, clone G83009.23 CFK-69.1, 'Revolución'	Resistant Moderately resistant Susceptible	International Potato Center-Peru	CIP, 1987
6	Peru	Field- La Libertad, Junin, Cuzco and Puno Regions	Gp	Potato cultivar	CIP279142.12 ('Maria Huanca')	Resistant	International Potato Center-Peru	Llontop <i>et al.</i> , 1989a
7	Peru	Greenhouse- CIP Experimental Station Santa Ana, Huancayo (3280 masl)	Gp	Potato breeding clones and cultivars	CIP275043.64, CIP275066.83, CIP275131.22, CIP275186.1, CIP275196.12, CIP276031.16, CIP276047.7, CIP278024.8, CIP278037.7, CIP278072.10, CIP278096.10, CIP278107.3, CIP279134.1, CIP280090.10, CIP280236.6 'Libertad', 'Mariva'	Resistant	International Potato Center-Peru	Llontop <i>et al.</i> , 1989b

Table 2. Continued.

#	Country of testing	Location tested	<i>Globodera</i> spp ^z	Host	Material tested	Reaction to PCN	Source of material	Reference
8	Peru	Field from Cuzco, Puno and La Libertad	Gp	Potato clone	CIP279139.5	Resistant	International Potato Center-Peru	CIP, 1991
	Ecuador	Field	Gp	Potato clone	Clone G85043, clone G85044, clone G85101, clone G85244 and CIP720075	Resistant		
9	Peru	Greenhouse and Field	Gp	Advanced clones	CIP377740.2, CIP276724.1, CIP377744.3, CIP380426.1 Clone G87555.2, clone G87382.2, clone G87554.8, clone G87154.10, clone G874344.2	Tolerant Resistant	International Potato Center-Peru	CIP, 1992
	Bolivia	Field	Gp	Potato cultivars	'Sakampayas', 'Wacalajra', 'Palis', 'Sutamari' and 'Chowueluky'	Tolerant		
10	Peru and Bolivia	Greenhouse and Field	G	Potato clones	Clone G87523.8, clone G87540.1, clone G87368.1, clone G87323.4, clone 91-168.2, clone 91-168.5, clone 90-128.21, clone 90-96.8	Resistant	International Potato Center-Peru and PROINPA-Bolivia	CIP, 1995
11	Peru	Greenhouse - CIP Experimental Station Santa Ana, Huancayo (3280 m)	Gp	Potato breeding clones	Clone 381348.7, clone 84.28.58, clone 275186.13 Clone 280240.11, clone 281414.6, clone G-82138.2 Clone 84.122.13, clone 84.122.45 Clone H8.5, clone 14XY.7, clone CUP-199, P3	Resistant Highly Resistant Moderate resistant Susceptible	International Potato Center-Peru	Ortiz <i>et al.</i> , 1997
12	Peru	Experimental Station Santa Ana, Huancayo of INIA and CIP (3280 masl)	Gp	Potato cultivar	'INIA 313- Wankita'	Resistant	Instituto Nacional de Innovación Agraria (INIA-Perú)	Mayer-Scurrah <i>et al.</i> , 2005 and INIA Variety Release technical sheet, 2008

Table 2. Continued.

#	Country of testing	Location tested	<i>Globodera</i> spp ^z	Host	Material tested	Reaction to PCN	Source of material	Reference
13	Peru	Experimental Station Santa Ana, Huancayo of INIA and CIP (3280 masl)	Gp	Potato cultivar	'INIA 309-Serranita' (CIP391691.96)	Tolerant	International Potato Center-Peru	INIA Variety Release technical sheet, 2005
14	Peru	Field-Province of Yunguyo and Puno (3857-3880masl), Laboratory- INIA Experimental Station, Puno	G	Potato cultivars	'Peruanita' 'Imilla negra'	Resistant Susceptible	Instituto Nacional de Innovación Agraria (INIA- Perú)	Jimenez, 2017
15	Peru	Field-Province of Huamanga, Ayacucho (3,379 masl). Laboratory - Plant Genetics and Biotechnology from UNSCH	G	Native potatoes	'Huenco', 'Puca runtus', 'Victor', 'Maco', 'Yanacuhipa runtun', 'P63', 'Alcarraza', 'P62', 'Yuraq millico', 'Ucca huayro', 'Azul ñahui', 'Yuraq suyto', 'P61', 'Leona añil', 'Tambina', 'Yana rosilla', 'Puca ñahui', 'Yutupa runtun', 'P73', 'Capcas', 'Duraznila', 'P65', 'Yuraq chikñas', 'Chiquibonita', 'Soyo caputo', 'Camotillo', 'Limeña', 'Pucavacapa chuñun', 'Amarilla', 'Yuraq sisa', 'P70', 'Royacc halle', 'Ritipa sisan', 'Puca suyto', 'Yana huaña', 'Peruanita', 'Negra', 'Huayro hembra', 'Alleca cambro', 'Huayro', 'Cuchipa acan', 'Ceccorani', 'Runtus', 'Durasnillo 2', 'Muru suyto' and 'Sangre de toro'. 'P67', 'P68', 'Marquina'	Resistant	Universidad Nacional de San Cristóbal de Huamanga (UNSCH)	Alarcón, 2017
16	Peru	Greenhouse - INIA Experimental Station Canaan, Ayacucho (2739 masl)	Gp	Potato breeding clones	Clone 284.14, clone 281.39, clone 282.32, clone 4, clone 217.18, clone 302.34, clone 282.27, clone 3451.1219, clone 302.35 Clone 306.31	Susceptible and tolerant Susceptible and intolerant	Instituto Nacional de Innovación Agraria (INIA- Perú)	Allecahuaman, 2017

Table 2. Continued.

#	Country of testing	Location tested	<i>Globodera</i> spp ^z	Host	Material tested	Reaction to PCN	Source of material	Reference
17	Ecuador	Greenhouse- INIAP Experimental Station Santa Catalina, Pichincha (3058 masl)	Gp	Native potatoes and cultivars	'Milagrosa', 'Conceja Negra', 'Poluya', 'Bolona', 'Chaucha Blanca', 'Unknown', 'Curipamba', 'Leona Blanca', 'Calvache', 'Norte Roja', 'INIAP-Gabriela', 'Carrizo Cotopaxi', 'Uvilla', 'Chaucha Colorada' 'Chaucha Amarilla', 'Violeta', 'Coneja Blanca', 'Rosada', 'Osito', 'Macholulo', 'Yema de Huevo', 'Jubalena', 'Puca Huayco', 'Leona Negra Norte'	Susceptible and tolerant	Instituto Nacional de Investigacion es Agropecuaria (INIAP- Ecuador)	Riera, 2009
18	Ecuador	Greenhouse- INIAP Experimental Station Santa Catalina, Pichincha (3058 masl)	Gp	Native potatoes cultivars and potato clones	'Ratona Lagartija', 'Huagrasinga', 'Tandapapa', 'Roja hacha', 'Corazon lila', 'INIAP-Fripapa', 'INIAP-Natividad', 'Super Chola', 'INIAP-Cecilia', clone 05-24-3, clone 08-20-19 'Uva', 'Sta Rosa Blanca', 'Sta Rosa Amarilla', 'Leona negra norte', 'Cuchiisma', 'INIAP-Pan', 'INIAP- Suprema', clone 98-2-6, clone 05-28-3, clone 06-92-1	Resistant and tolerant	Instituto Nacional de Investigacion es Agropecuaria (INIAP- Ecuador)	Meja and Valverde, 2011
19	Ecuador	N/A	Gp	Potato cultivars	'Super Chola', 'INIAP-Fripapa', 'INIAP- Gabriela' 'INIAP-Cecilia'	Tolerant Susceptible	Instituto Nacional de Investigacion es Agropecuaria (INIAP- Ecuador)	Mastrocola <i>et al.</i> , 2016

Table 2. Continued.

#	Country of testing	Location tested	<i>Globodera</i> spp ^z	Host	Material tested	Reaction to PCN	Source of material	Reference
20	Ecuador	Greenhouse- INIAP Experimental Station Santa Catalina, Pichincha (3058 masl)	Gp	Potato breeding clones and cultivars	'INIAP-Puca Shungo', clone 07-32-01, clone 10-10-97 'INIAP-Gabriela', 'INIAP-Fripapa', 'Superchola', 'INIAP-Estela', 'INIAP- Esperanza', 'INIAP-Libertad', 'INIAP- Victoria', 'INIAP-Yana Shungo', 'Uvilla', 'INIAP-Natividad', 'Leona Negra', clone 07-40-1, clone 98-2-6, clone 97-25-3, clone 07-28-2, clone 07- 24-18, clone 97-46-8, clone 07-32-15	Susceptible and intolerant Susceptible and tolerant	Instituto Nacional de Investigacion es Agropecuaria (INIAP- Ecuador)	Castillo <i>et al.</i> , 2017
21	Ecuador	Greenhouse- INIAP Experimental Station Santa Catalina, Pichincha (3058 masl)	Gp	Potato breeding clones and cultivars	'Leona Negra', 'INIAP-Natividad', 'INIAP-Libertad', 'INIAP-Josefina', clone 08-01-06, clone 07-31-11, clone 09-01-35, clone 08-02-07, clone 09-01- 32, clone 09-01-31, clone 09-01-29, clone 07-05-06, clone 07-32-15, clone 08-09-03, clone 11-9-91, clone 07-32-01	Susceptible and Tolerant	Instituto Nacional de Investigacion es Agropecuaria (INIAP- Ecuador)	Llumiquina and Rivadeneira, 2018
22	Ecuador	Greenhouse- INIAP Experimental Station Santa Catalina, Pichincha (3058 masl)	Gp	Potato breeding clones and cultivar	Clone 09-1-29, clone 09-1-1, clone 09-1-32, clone 08-1-6, clone 08-2- 7, clone 07-32-1, clone 07-31-11, clone 07-32-15, 'Leona Negra' Clone 09-1-35, clone 08-9-3, clone 07-5-6	Susceptible and tolerant Susceptible	Instituto Nacional de Investigacion es Agropecuaria (INIAP- Ecuador)	Castillo <i>et al.</i> , 2019
23	Chile	Field - La Serena, Region Coquimbo and Experimental Station La Platina (INIA)	Gr	Potato clones	'Cardinal', clone 47, clone 22, clone 28, clone 36, clone 68, clone 31, clone 32, clone 43, clone 65, clone 16, clone 93, clone 54, clone 92 'Ultimus', clone 75, clone 19, clone 30, clone 25, clone 81, clone 64, clone 45,	Resistant Susceptible	Instituto de Investigacion es Agropecuaria (INIA- Chile)	Guglielmetti and Guíñez, 1982

Table 2. Continued.

#	Country of testing	Location tested	<i>Globodera</i> spp ^z	Host	Material tested	Reaction to PCN	Source of material	Reference
24	Chile	Fields - Osorno, Llanquihue, Temuco and La Platina	Gr	Cultivar	'Yagana-INIA'	Resistant	Instituto de Investigaciones Agropecuarias (INIA-Chile)	Kalazich <i>et al.</i> , 1982
25	Chile	Field - La Serena, Region Coquimbo and Laboratory - Experimental Station La Platina, Santiago (INIA)	Gr	Potato cultivars and advanced clones	Clone 2703, clone 82177, 'Altena', 'Hertha', clone 38, clone 318, clone 2164, 'Atlantic', 'Cardinal', 'Remehue 5', 'Remehue 9', 'Wauseon', 'Yagana' Clone 82188-1, 'Clavela', clone 72215-15, 'Ultimus', 'Mirka', clone 82341 b-5, 'Désirée', clone 78220-1, 'Remehue 8', clone 8195-4, clone 82186-1, clone 82140-2, clone 82319-1, clone 812, clone LT-2, clone 81105-2, 'Spartan 93', 'Bracka', 'Romano', clone 828, clone Br-6315, clone BL-22	Resistant	Instituto de Investigaciones Agropecuarias (INIA-Chile)	Fernandez, 1988
26	Chile	Fields - Osorno, Carahue, Cañete, Santiago, Curavi and La Serena	Gr	Potato cultivar	'Karu-INIA'	Resistant	Instituto de Investigaciones Agropecuarias (INIA-Chile)	Kalazich <i>et al.</i> , 2004
27	Chile	Greenhouse- Universidad de la Serena	Gr	Potato breeding clones and dihaploids	Clone 92-4578-8 XIVP-121 (P5), clone 92-4595-14 XIVP-121 (P1), clone 421-CON-921-X-IVP-121 P1, clone 90-3898-6, clone 92-4616-9, clone 84-5875-X 14X VATO (OP)74, clone 280-CON-755, clone 254-CON-902, clone 304-VA-1135	Resistant	Universidad Austral de Chile	Milla and Krausz, 2004

Table 2. Continued.

#	Country of testing	Location tested	<i>Globodera</i> spp. ^z	Host	Material tested	Reaction to PCN	Source of material	Reference
27	Cont.				Clone 92-4578-2 XIVP-121 (P-23), clone 92-4578-2 XIVP-121 (P-16), clone 92-4578-2 XIVP-121 (P-1), clone 92-4578-2 XIVP-121 (P-3), clone 92-4578-19 XIVP-121 (P-3), clone 92-4578-2 XIVP-121 (P11), clone 92-4578-3 XIVP-121 (P1), clone 92-4578-13 XIVP-121 (P4), clone 92-4594-8 XIVP-121 (P1), clone 92-4595-14 XIVP-121 (P2), clone 92-4576-8 XIVP-121 (P-2), clone 92-4576-8 XIVP-121 (P-1), clone 421-CON-921 XIV-121 P1, clone 182-VA-1601 XIVP-121 (P1), clone 89-3425-4, clone 89-3236-4, clone 86-1570-2, clone 86-1987-3, clone 88-2994, clone 88-2908, clone 85-1500-3, clone 85-1478-1, clone 85-1463-1, clone 84-5875-14X AUTO-(OP) 61, clone 86 FUEGUINA-88, clone 277-CON-913, clone 592-CON-1329, clone 284-CON-815, clone 372-CON-1090, clone 597-CON-1336, clone 87-CON-1152	Partially resistant		
28	Chile	Greenhouse - Estación Experimental Austral	Gr	Potato breeding clones and cultivars	Clone 547-UA-1053, clone 464-UA-1360, clone 244-CON-1266, clone 97-UA-1296, clone 236-UA-1031, clone 362-CON-1052, clone 93-COCHRANE-2, clone NG-156, 'Yagana-INIA', 'Cardinal-INIA', Clone 596-CON-1335, clone NG-140, clone 592-CON-1329, clone 541-UA-1042, clone 458-CON-963	Resistant	Universidad Austral de Chile	Brintrup, 2016
						Partially resistant		

Table 2. Continued.

#	Country of testing	Location tested	<i>Globodera</i> spp ^z	Host	Material tested	Reaction to PCN	Source of material	Reference
28	Cont.				Clone 92-4594-14 XIVP-121 (P5), clone 381-VA-1091 XIVP-121 P1, clone 85-1335-1, clone 86-1692-3, clone 370-CON-790, clone 69-CON-898, clone 278-VA-1146, clone 42-VA-1258, clone 178-VA-1238A, 'Cardinal-INIA'	Moderately susceptible		
29	Bolivia	Field- Province of Ingavi, Department of La Paz (3798 masl)	G	Potato breeding clones and cultivar	Clone 390159.4, clone G84381.9, clone G85472.20	Partially resistant	International Potato Center - Peru	Pacajes <i>et al.</i> , 2002
30	Venezuela	Greenhouse -Lara State (1400 masl)	Gr	Potato breeding clones and cultivar	'Sani Imilla' CIP393558.44, CIP392636.9, CIP393073.15 CIP393465.38, CIP392634.21 CIP393134.10, CIP393193.16, CIP393565.1, CIP392639.17, CIP393180.32, CIP393073.29, CIP392636.50, CIP392634.13, CIP392639.42, CIP393180.11, 'Andinita'	Susceptible Moderately resistant Resistant Susceptible	International Potato Center- Peru	Anaya <i>et al.</i> , 2005

^zG, *Globodera* species; Gp, *G. pallida*; Gr, *G. rostochiensis*

potential as differentials for these populations (Canto and Scurrah, 1977). *Solanum tuberosum* ssp. *tuberosum* cultivar 'Woudster' and *S. tuberosum* ssp. *andigena* 'Renacimiento' were used as susceptible control plants. The PCN differential plants were susceptible to most of the Andean PCN populations. 'Renacimiento', 'Amaryl' (with the *H1* gene), and 'Woudster' were found to be the most susceptible. *Globodera pallida* was identified in 80% of the populations. The area with the greatest nematode variability was the highlands around Lake Titicaca, while limited variability was found in central Peru (*G. pallida* pathotype P₂A, P₄A, and P₅A), southern Colombia (*G. pallida* pathotype P₂A) and Ecuador (*G. pallida* pathotype P₂A and P₄A). *Globodera rostochiensis* pathotype R₁A, R₂A, and R₃A and *G. pallida* pathotype P₁B, P₄A, P₅A were identified in highlands around Lake Titicaca between Peru and Bolivia. Twenty-four PCN populations from central Peru, southern Ecuador and Colombia did not reproduce on *S. vernei* hybrid clone (VTⁿ)2 62.33.3. In general, the highest reproduction rates were found in northern Peru populations. However, these populations appeared to be the least variable since all clones were susceptible. At the time, the authors applied British and Dutch pathotype identification systems; however, both systems had significant limitations detecting pathotype variation, leading to the development of a new South American system. The new scheme for Andean populations classified *G. pallida*: P₁A, P₁B, P₂A, P₃A, P₄A, P₅A and *G. rostochiensis*: R₁A, R₁B, R₂A, R₃A (Canto and Scurrah, 1977).

In 1978, CIP screened 2,395 clones from various sources for resistance to four populations of *Globodera* spp. from Huancayo, Cuzco, Puno, and Otuzco. This research used the Canto and Scurrah (1977) pathotype scheme. From these, 860 clones were resistant to one or more PCN populations. This work identified two clones of *Solanum juzepczukii*, CIP702626 and CIP701323, with resistance to PCN populations from Huancayo, Cuzco and Puno. Moreover, of the clones tested, clones from the Netherlands were also resistant to a population from Huancayo. Previously characterized root-knot nematode resistant clones of *Solanum sparsipilum* and

Solanum chacoense had broad resistance to *Globodera* populations, while none of the clones that included introgressions of *Solanum sanctae-rosae*, *S. chacoense*, *Solanum multidissectum*, and *S. vernei* from Cornell were resistant to all four PCN populations. In 1978, CIP maintained 252 PCN populations collected from Bolivia (35), Colombia (11), Ecuador (16), Peru (112), and 78 populations obtained from 23 other countries. More than 60% of pathotypes identified in the Andean region were *G. pallida* pathotypes P₄A and P₅A. Moreover, *G. pallida* pathotype P₁B, P₂A, and P₃A and *G. rostochiensis* R₁A, R₁B, R₂A, and R₃A were also identified. The *S. tuberosum* ssp. *andigena* clones CIP702535 and CIP702698 were highly resistant to P₄A and P₅A, and were used as parents of crosses made in 1978. Additionally, 52 potato locations between 3,000 and 4,500 masl were surveyed in Peru and Bolivia. Ten of 24 locations in north and central Peru were infested with *G. pallida*, while *G. rostochiensis* was identified in one location. Six of 28 locations in Bolivia were infected with *G. pallida*, while *G. rostochiensis* was found at three locations (CIP, 1979).

In 1979, *S. tuberosum* ssp. *andigena* clones CIP702535 and CIP702698, previously shown to be resistant to pathotypes P₄A and P₅A, were tested against 33 PCN populations from Colombia, Ecuador, Peru, and Bolivia. Clone CIP702535 was resistant to 30 of these PCN populations while clone CIP702698 was resistant to 16 PCN populations (CIP, 1980). Resistance to *G. pallida* pathotype P₄A and P₅A in these CIP clones were evaluated using the susceptible potato 'Renacimiento' as a control. Thirty cysts consisting of approximately 3,870 eggs were inoculated in pots containing tubers of these clones. An average of 1.4 cysts (182 eggs), 4.6 cysts (597 eggs), and 232.6 cysts (30,164 eggs) were recovered from CIP702535, CIP702698, and 'Renacimiento', respectively. Additionally, CIP tested 2,042 clones from seven sources (Cornell, Wisconsin, USDA, The Netherlands, Germany, Mexico, and CIP) to *G. pallida* pathotype P₄A from Huancayo and P₅A from Otuzco. Of those tested, 487 clones were resistant to P₄A and 345 to P₅A (CIP, 1981; #3 in Table 2).

In 1976, 44 South American (Colombia, Peru, Ecuador, and Bolivia) and 9 European (Iceland, United Kingdom, Italy, and Spain) PCN populations were tested on potato cultivars with resistant genes *H1*, *H2*, or *H3*: 'Maris Piper' with the *H1* (resistant to *G. rostochiensis* pathotype Ro1 and Ro4), clone P55/7 with *H2* (resistant to *G. pallida* pathotype P₁A), and the hybrid E45/65 with *H3* (resistant to *G. pallida* pathotype P₃A); the susceptible *S. tuberosum* ssp. *tuberosum* 'Arran Banner' was used as a control. On 'Maris Piper' (*H1*), reproduction of one *G. pallida* population was reduced to only 10% compared to the control 'Arran Banner'. Reproduction by two *G. pallida* populations was reduced to less than 10% on clone P55/7 (*H2* gene) compared to the control. Reproduction of three *G. pallida* populations was decreased to less than 10% compared to the control on hybrid E45/65 (*H3* gene). E45/65 was resistant to all European *G. pallida* and *G. rostochiensis* populations evaluated, except for one *G. rostochiensis* population from United Kingdom. Resistance observed for this population was partial, suggesting either the populations were mixed or that *H3* is not a single major gene. In conclusion, most of the South American populations were able to multiply on plants containing resistance genes *H1*, *H2* or *H3*, whereas all the European populations were controlled by one or two genes (Franco and Evans, 1978).

In 1984, 10,000 progenies with resistance to *G. pallida* pathotypes P₄A and P₅A generated during the 1983 breeding cycle were field tested. From 94 families, clones CIP266090.10 and CIP280240.11 were found to produce excellent progeny in terms of tuber shape and yield. A total of 257 families were evaluated for *G. pallida* resistance from the 1984 breeding cycle. Progeny from 84 families were resistant to both P₄A and P₅A, while progeny from 21 families and 66 families were resistant to P₄A and P₅A, respectively. Since *G. pallida* pathotype P₅A was present only in the Andean region of northern Peru, 20 PCN populations from the three main potato-growing areas of northern Peru in La Libertad Region (Otuzco, Huamachuco and Santiago de Chuco) were collected. The populations were confirmed to be *G. pallida* pathotype P₅A. These

populations were evaluated on CIP potato clones CIP280090.10 and CIP280236.10 and on European differential clones. The two CIP clones were included to confirm the genetic variability within the P₅A pathotype. The 20 PCN populations showed greater variability among them when the multiplication rate on CIP clones was compared with that on European differential clones. This variability was interpreted as the presence of modifying genes for aggressiveness. The *G. pallida* population from Huamachuco was the most aggressive (Aggressiveness Index (AI): 82-88%) followed by Santiago de Chuco (AI: 35-41%) and Otuzco (AI: 12-24%). Aggressiveness Index (%) is the number of susceptible clones divided by the total clones evaluated (Llontop *et al.*, 1989a). The Aggressiveness Index is dependent on the selected clones and is only applicable for this experiment. Additional clones were field tested for *G. pallida* resistance in the northern central and southern highlands of Peru. Of these clones, 70% were resistant to P₄A in central Peru and P₅A in northern Peru while 85% were resistant to P₄A in southern Peru (CIP, 1985).

In 1985, CIP potato accessions with resistance to *G. pallida* were provided to national programs across the Andean region to evaluate against local PCN populations. Of this group, 295 potato clones were evaluated in Ecuador by INIAP. Of these clones, 39 were resistant to *G. pallida* in Ecuador, however only 6 clones had good yield and tuber characteristic. In Peru, the national potato program evaluated 37 clones for resistance to *G. pallida* and agronomic characteristics; three clones, CIP279139.5, CIP279142.12 and CIP276008.16, were confirmed with good levels of *G. pallida* resistance and acceptable agronomic characteristics. Moreover, a new set of standard potato host differentials, resistant clones CIP278096.10 and CIP280090.10, were included to determinate *G. pallida* pathotypes P₄A and P₅A (CIP, 1986; #4 in Table 2).

In 1986, 43 potato clones selected from crosses performed in 1983 by the CIP breeding program were evaluated by a Peruvian national program for resistance to *G. pallida* pathotypes P₄A and P₅A and adaptation to the climate of the north and central highlands of Peru. Ten clones

showed better yield than ‘Revolución’ (control) and resistance in field trials in the Junin Region. Of these, clone CIP279142.12 was selected due to high levels of resistance to *G. pallida* pathotype P_{5A} and moderate resistance to pathotype P_{4A}. Moreover, after five years of trials, the Peruvian potato national program released the clone CIP279142.12, named ‘Maria Huanca’, which performed especially well. Moreover, during four years of trials ‘Maria Huanca’ was shown to be tolerant to late blight (*Phytophthora infestans*) and outperformed in yield (43 t/ha) compared to local Peruvian varieties such as ‘Yungay (19 t/ha) (CIP, 1987; #5 in Table 2).

Since 1980, CIP has sent clonal material to Peruvian potato national programs to evaluate performance and resistance to PCN with the objective of selecting resistant varieties. In 1987, the outstanding clone CIP279142.12, ‘Maria Huanca’ was the first variety released with resistance to *G. pallida* P_{4A} and P_{5A} in Peru and Latin America. ‘Maria Huanca’ was the result of crossing the female parent, CIP276012.24, with resistance to *G. pallida* P_{5A} derived from *S. tuberosum* ssp. *andigena*, and the male progenitor, AM66-246, with resistance to *G. pallida* P_{4A} derived from a hybrid of *S. tuberosum* ssp. *tuberosum* x *S. vernei*. Furthermore, ‘Maria Huanca’ is tolerant to late blight and smut (*Tecaphora solani*), immune to Potato virus X, hypersensitive to Potato virus Y, and resistant to races 1 and 2 of wart *Synchytrium endobioticum*. However, it is sensitive to powdery scab (*Spongospora subterranean*), rhizoctonia (*Rhizotocnia solani*), powdery mildew (*Erysiphe cichoracearum*) and phoma leaf spot (*Phoma andigena*). ‘Maria Huanca’ was tested in four Peruvian regions, La Libertad (north), Junin (center), Cuzco (south) and Puno (south). ‘Maria Huanca’ was observed to be susceptible in fields from La Libertad, where a new *G. pallida* pathotype P_{6A} was identified that was virulent on clones with P_{5A} resistance. While ‘Maria Huanca’ was resistant to both P_{4A} and P_{5A} pathotypes in laboratory and greenhouse evaluations, since 1982 in field tests ‘Maria Huanca’ was considered resistant and moderately resistant to P_{5A} and P_{4A}, respectively (Llontop *et al.*, 1989b; #6 in Table 2).

Fourteen CIP potato clones selected with resistance to *G. pallida* pathotype P_{5A} (Otuzco population) and some with resistance to P_{4A} (Huancayo population) were evaluated to determine the virulence and aggressiveness of 20 *G. pallida* populations collected in the provinces of Otuzco, Sanchez Carrion, and Santiago de Chuco from La Libertad Region (2600-3500 masl). Controls included CIP278096.10 (resistant to *G. pallida* pathotype P_{4A} and susceptible to *G. pallida* pathotype P_{5A}), the susceptible cultivars ‘Liberteña’ and ‘Mariva’ and one *G. pallida* population pathotype P_{4A} from Huancayo, Junin Region. The reproduction factor (RF), which is defined as the final population/initial population (Pf/Pi), was used to determine if clones were resistant or susceptible. A clone was considered resistant when $RF \leq 1$, and susceptible when $RF > 1$. Ten clones were found to reduce the RF and were considered resistant or moderately resistant to *G. pallida* pathotype P_{5A} (RF 0.25 to 3.19) when compared to the susceptible controls ‘Liberteña’ and ‘Mariva’ (RF 36.47 and 39.40, respectively). These results also confirmed the *G. pallida* pathotype P_{6A} was a new pathotype, since it overcame both P_{5A} and P_{4A} resistance, RF of 1.16 to 20.62. More than half the populations collected were identified as P_{6A}. Three unique clones, CIP275066.83 (Pf/Pi = 0.59), CIP280090.10 (Pf/Pi = 0.25), and CIP275043.64 (Pf/Pi = 0.54), were resistant to all P_{5A} populations. The clones CIP280090.10 and CIP280236.6 were highly resistant to *G. pallida* pathotypes P_{4A} and P_{5A} and showed lower multiplication rates to P_{6A} compared to the other clones evaluated. CIP278096.10, was confirmed to be resistant to *G. pallida* pathotype P_{4A} (RF 0.46); however it was highly susceptibility to pathotype P_{5A} (RF = 14.9) and to P_{6A} (RF = 17.7). Overall, the more virulent populations were found to be more aggressive. P_{6A} populations were found to be the most aggressive reaching an AI = 100% in one *G. pallida* population from Otuzco and AI = 93% in the rest of the *G. pallida* populations (Llontop *et al.*, 1989a; #7 in Table 2).

Levels of resistance to *G. pallida* P_{6A} were further evaluated by Franco and González (1990). Susceptible cultivar ‘Désirée’, ‘Maria Huanca’ (partially resistant to P_{4A} and resistant to P_{5A}) and

the clone CIP280090.10 (resistant to P₄A and P₅A), were incorporated into a standard set of differential plants for identification of *G. pallida* pathotypes. Hybrids and selfed progeny of *G. pallida* populations were obtained by crossing populations collected from pieces of tubers grown in petri dishes containing water agar. Crosses between pathotypes *G. pallida* P₄A, P₅A, and P₆A were conducted, including all possible combinations, to detect the presence of maternal or cytoplasmic type inheritance. Second-stage juveniles (J2) were inoculated on the three potato clones. Results confirmed partial resistance of 'Maria Huanca' to pathotypes P₄A and resistance to P₅A and full resistance of CIP280090.10 to both pathotypes. However, both were susceptible to pathotype P₆A, demonstrating the ability of this pathotype to overcome resistance sources to pathotypes P₄A and P₅A. No maternal inheritance was observed among P₄A, P₅A, and P₆A populations. Pathotype P₆A was the most virulent and aggressive pathotype evaluated (Franco and González, 1990).

In 1987, 12 PCN populations were collected from 11 provinces in the Cuzco Region and evaluated on differential clones to identify pathotypes of *G. pallida* and *G. rostochiensis*. Collection sites included the major potato-producing areas in the region. These experiments were conducted in greenhouses from CIP-Lima. *Globodra pallida* pathotype P₄A population from Huancayo, one *G. pallida* pathotype P₅A population from La Libertad as nematode controls. Differential clones, CIP278096.10 (resistant to P₄A) and CIP280090.10 (resistant to P₄A and P₅A) as potato controls and 'Désirée' as susceptible control were evaluated. Clones were considered resistant if Pf/Pi was ≤ 1 and susceptible if Pf/Pi was > 1 . Potato 'Désirée' and differential clone P 55/7 were susceptible to all PCN populations. Clone KTT 60.21.19 was susceptible to the majority of PCN populations except for two populations identified as P₂B. Clone GLKS 58.164.42 was susceptible to all PCN populations. The differential clone 62.33.3 (*S. vernei*) was more resistant to pathotype P₄A than the clone CIP278096.10. Clone CIP280090.10 was effective at reducing reproduction of eight PCN populations. However, four PCN populations had a Pf/Pi > 1 on

CIP280090.10 resulting in pathotype P₆A to be identified in this region. One PCN population was a mix of *G. pallida* and *G. rostochiensis*, identified as P₂B and R₂B, respectively (Delgado de la Flor and Jatala, 1991).

The CIP breeding program evaluated 150 advanced clones in infested fields from Huancayo for PCN resistance. Sixty-three selected clones were then evaluated in fields from La Libertad, Cuzco, and Puno Regions. The clones G86056.8 (2.86 kg/plant) and G86147.9 (2.70 kg/plant) had the highest yields compared with 'Maria Huanca' (1.94 kg/plant) and 'Tomas Condemayta' (1.54 kg/plant), and were partially resistant to *G. pallida* pathotypes P₄A and P₅A. Five advanced clones were sent to the Ecuadorian national program for evaluation, and all were shown to have *G. pallida* resistance and yielded well, with CIP279023.3 having the highest yield. Additionally, studies of *G. pallida* and late blight resistance were carried out in Huancayo where 60 clones resistant to *G. pallida* and late blight were selected. Of these, 21 clones were resistant to *G. pallida* pathotype P₅A but were susceptible to pathotype P₄A, 17 clones were resistant to *G. pallida* pathotype P₄A but were susceptible to pathotype P₅A, and 22 clones were resistant to both *G. pallida* pathotypes P₄A and P₅A (CIP, 1990).

Field and greenhouse evaluations were conducted on CIP germplasm for resistance to *G. pallida* in Peru, Ecuador, and Bolivia. Seventeen CIP clones were tested in Ecuador, with all being resistant to *G. pallida*. Five advanced potato breeding clones (G85043, G85044, G85101, G85244 and CIP720075) were shown to be more resistant to *G. pallida* than two local Ecuadorian potatoes 'Gabriela' and 'Maria'. In CIP-Peru, a total of 18,000 seedlings from 198 families were screened against *G. pallida* pathotypes P₄A, P₅A, and P₆A under greenhouse conditions. Fifty-two percent were resistant to pathotype P₄A, 39% to P₅A, and 50% to P₆A. These clones were used as part of CIP breeding program for resistance to the three *G. pallida* pathotypes P₄A, P₅A, and P₆A. Moreover, 48 selected clones were found to be resistant to *G. pallida* under greenhouse conditions; of these clones, 90% were resistant to pathotypes P₄A and P₅A. An additional 180 clones

were selected for resistance to *G. pallida* pathotypes P₄A and P₅A in Huancayo; of these, 112 were shown to be resistant to both pathotypes in greenhouse evaluations. Evaluations concluded that the advance clone CIP279139.5, with resistances to *G. pallida* and late blight, was economically advantageous compared to traditional Peruvian cultivars (CIP, 1991; #8 in Table 2).

In 1992, the 198 potato families tested under greenhouse conditions against *G. pallida* pathotypes P₄A, P₅A, and P₆A reported on in 1991 were evaluated in PCN infested Peruvian fields. After field evaluations, the advanced potato breeding clones CIP377740.2, CIP276724.1, CIP377744.3, and CIP380426.1 were selected for tolerance to *G. pallida*. Greenhouse evaluations were conducted in Huancayo on 372 potato clones and in Puno on 44 clones selecting for resistance to *G. pallida* pathotypes P₄A, P₅A, and P₆A. Of these, clones G87555.2, G87381.2, G87554.8, G87154.10, and G874344.2 were resistant to *G. pallida*. Part of this study included integrated pest management trials conducted in Cajamarca, where susceptible, resistant, and tolerant potato cultivars were rotated with non-host crops (wheat, barley, lupine, ulluco, faba beans, peas, oats, quinoa and maize), with other cultural and biological control methods. In all trials where potato was rotated with a non-host, a reduction of 40-90% in PCN population densities was observed. In Bolivia, 52 potato clones were evaluated, of which 13 clones had no cysts associated with their roots. Furthermore, potatoes 'Sakampayas', 'Wacalajra', 'Palis', 'Sutamari', and 'Choweluky' were tolerant to *G. pallida* (CIP, 1992; #9 in Table 2).

During 1993 and 1994, 400 genotypes from crosses made in 1992 were evaluated for *G. pallida* resistance under greenhouse conditions. Of these, 36% were resistant to P₄A, 26.5% to P₅A, 9.3% to P₆A, and 2.8% (~11 clones) were resistant to all three *G. pallida* pathotypes. Of these, evaluation of 77 genotypes was repeated, and 45 of these genotypes inhibited female development. Of these 45 genotypes, 19 were selected for agronomic characteristics including high yields compared with 'Maria Huanca'. Another group of 85 potato clones were field tested; 73% of these were

resistant to *G. pallida*, 10 of these clones were selected for high yield, of which seven were tolerant to *G. pallida*. In addition, studies were conducted in Bolivia in fields with *G. pallida* and *G. rostochiensis*. Clones were selected from PROINPA and CIP breeding programs with resistance to mixed populations of *Globodera* and some with resistance to *Nacobbus aberrans*. Of them, seven of the selected clones (G87523.8, G87540.1, G87368.1, G87323.4, 91-168.5, 90-128.21, and 90-96.8) were used in further PCN management trials in farmers' fields (CIP, 1995; #10 in Table 2).

Potato clones were used in a study to transfer *G. pallida* resistance from diploid tuber-bearing *Solanum* species to the tetraploid gene pool using a 4x-2x breeding approach. Specifically, resistance to *G. pallida* from *S. vernei*, *S. sparsipilum*, and haploids of *S. tuberosum* ssp. *andigena* was introgressed into conventional tetraploid clones using first division restitution (FDR), 2n gametes. Tetraploids clones with different level of resistance to *G. pallida* pathotypes P₄A (Huancayo population) and P₅A (Otuzco population) were selected as female parents. They were crossed to three diploid clones with 2n pollen and three tetraploids. A total of 35 tetraploids families were obtained to be analyzed. Additionally, five diploid clones were used to produce six diploid families. A few of the families showed resistance to both *G. pallida* pathotypes P₄A and P₅A. All diploid families were resistant to *G. pallida* pathotype P₅A while only 33% of them were resistant to *G. pallida* pathotype P₄A. Moreover, the highest frequencies of resistant progeny were observed in families derived from crossing a susceptible tetraploid female with a resistant tetraploid male. The best diploid male parent with *G. pallida* resistance was CIP381348.7, derived from a tetraploid clone with *G. pallida* resistance genes from *S. sparsipilum*. All progeny from this clone were resistant to *G. pallida* pathotype P₄A and 83% of progenies were resistant to *G. pallida* pathotype P₅A. Two diploid clones, 84.28.58 and 84.122.45, were derived from tetraploids with resistance to *G. pallida* from *S. vernei* and *S. tuberosum* ssp. *andigena*, respectively. Sixty-seven percent of the progeny from 84.28.58 were resistant to P₄A and 50% were

resistant to P₅A. Forty percent of progeny from 84.122.45 were resistant to P₄A and 75% were resistant to P₅A. Clone G82138.2 was selected as the best tetraploid female parent for *G. pallida* resistance. All progeny from this clone were resistant to both *G. pallida* pathotypes P₄A and P₅A (Ortiz *et al.*, 1997; #11 in Table 2).

In 2002 the INIA-Peru reported the release of INIA-313 'Wankita', whose main attributes were high levels of resistance to *G. pallida* pathotypes P₄A, P₅A, and P₆A and good tuber yield. It is a clone whose female parent is the clone G84415.3 and the male parent is 'Maria Huanca'; both parents are resistant to *G. pallida*. It is believed that resistance comes from the wild potato relative, *S. vernei*. 'Wankita' was field tested in the district of Quilcas – Huancayo, Junin Region, where *G. pallida* pathotype P₄A is present. On 'Wankita', *G. pallida* had a Pf/Pi of 0.18, while susceptible 'Yungay', 'Canchán', 'Revolución', and 'Peruanita' had Pf/Pi's of greater than 15.3. Moreover, the tuber yield of 'Wankita' was 26.2 t/ha compared with yields ranging from 0.4 to 18.5 t/ha for 'Yungay', 'Canchán', 'Revolución', and 'Peruanita' (Mayer-Scurrah and Chumbiauca, 2005; INIA, 2008; #12 in Table 2). Another variety release by INIA-Peru was INIA-309 'Serranita' in 2005. It is resistant to late blight and tolerant but susceptible to *G. pallida*. 'Serranita' has excellent culinary quality, with good flavor (INIA, 2005; #13 in Table 2).

Two potato cultivars, 'Imilla Negra' and 'Peruanita', were evaluated in the Puno Region. Soil samples were collected from fields located in the districts of Yunguyo (3,857 masl) and Capachica (3,880 masl). The genera identified were *Nacobbus*, *Pratylenchus*, *Helicotylenchus*, and *Globodera*. In the district of Capacachi the average *Globodera* population densities at the time of sampling were 70 cysts/100 g soil for 'Imilla Negra' and 59 cysts/100 g soil for 'Peruanita', while in the district of Yunguyo average populations densities were 95 cysts/100 g soil for 'Imilla Negra' and 78 cysts/100 g soil for 'Peruanita'. *Globodera* and *Nacobbus* population densities were higher on the native 'Imilla Negra', unlike the improved 'Peruanita', which showed better resistance to *Globodera* and *Nacobbus*.

Yield loss caused by *G. pallida* was 43% for 'Imilla Negra' compared to 21% for 'Peruanita' (Jimenez, 2017; #14 in Table 2).

More recently from December 2013 to July 2015, 49 native potato accessions from the Universidad Nacional de San Cristobal de Huamanga, Ayacucho Region, were evaluated for resistance and tolerance to *Globodera* spp. Field samples were collected from Ayacucho, Apurimac and Junin Regions to identify *Globodera* spp. using species-specific primers. Results identified *G. pallida* in field samples from Ayacucho and Junin Regions and *G. pallida* and *G. rostochiensis* in field samples from Apurimac Region. Of the 49 native accessions, 6% were tolerant and 94% were resistant (Pf/Pi = 0.02 to 0.44) to *Globodera* spp. (Alarcón, 2017; #15 in Table 2).

Commercial potatoes 'Yungay', 'Canchán', and 'Roja Ayacuchana' and native potatoes 'Peruanita', 'Chaulina', and 'Tumbay' were evaluated against *Globodera* populations collected in 1995 and 2000. In 1995, three *Globodera* populations were collected from province of Huamanga and in 2000 two populations were collected from the provinces of Huanta and La Mar. These populations were maintained in the Zoology Laboratory of Universidad Nacional San Cristobal de Huamanga. All potatoes were inoculated under greenhouse conditions. All the potato varieties were susceptible to *Globodera* spp. (Ñahuis, 2017).

In 2016, 10 clones of *S. tuberosum* from the INIA-Peru Experimental Station in Canaan were evaluated for *G. pallida* resistance and agronomic response under greenhouse conditions in the Ayacucho Region. The resistant potato 'Maria Huanca' and the tolerant potato 'Yungay' were used as controls. The *G. pallida* used in this study was a mixture collected from infested potato fields in the community of Allpachaca, Ayacucho Region. Pathotype(s) were not reported. The 10 clones were selected for their productivity, culinary and disease resistance characteristics. Reproduction of *G. pallida* on these clones was between 240 to 3,510 cysts per plant at the end of the experiment and all were considered susceptible. Tuber yield decreased on average by 5.6% on the inoculated clones compared to the uninoculated

clones. Nine potato clones were tolerant to *G. pallida* while one clone was intolerant (Allcchahaman, 2017; #16 in Table 2).

Resistance screening and potato variety development in Ecuador

Twenty-four Ecuadorian native potatoes selected by the Programa Nacional de Raíces y Tubérculos (PNRT), INIAP, were evaluated for resistance and tolerance to *G. pallida* in the province of Pichincha. The *G. pallida* population was collected from a potato field in the province of Tungurahua; pathotype(s) were not reported. Thirteen native potatoes were determined to be susceptible and tolerant to *G. pallida*, as well as the control potato 'INIAP-Gabriela'. The other 11 varieties were susceptible and intolerant. The potato yield of intolerant varieties was considerably reduced by *G. pallida*. The native potato 'Leona Negra Norte' was the most intolerant with an average of yield of 0.2 kg/plant and yield loss of 46% compared to uninoculated plants. The native potato 'Milagrosa' was susceptible and tolerant, with the highest average yield of 0.4 kg/plant. Moreover, the native potatoes 'Milagrosa', 'Coneja Negra', 'Bolona', and 'Poluya' were selected from the susceptible and tolerant group due to somewhat lower *G. pallida* reproduction. It was suggested that these four native potatoes should be used in Ecuadorian breeding programs (Riera, 2009; #17 in Table 2).

In Ecuador, native potatoes, commercial varieties, and breeding clones were evaluated for their response (resistance and tolerance) to *G. pallida*. The *G. pallida* population used for inoculations was collected from the province of Tungurahua. Twenty-four potato accessions were selected from PNRT-INIAP. Forty-six percent of the evaluated potato accessions were resistant and tolerant, 41% were susceptible and tolerant, and 13% were resistant and intolerant. The native potatoes that were resistant and tolerant to *G. pallida* were 'Ratona-Lagartija', 'Huagrasinga', 'Tandapapa', 'Roja Acha', and 'Corazon Lila'. The commercial varieties that were resistant and tolerant to *G. pallida* were 'INIAP-Fripapa', 'INIAP-Natividad', 'Super Chola', and 'INIAP-

Cecilia' (Mejía and Valverde, 2011; #18 in Table 2).

In 2016, the "Catalog of potato varieties from Ecuador" by FAO-INIAP published the main agronomic quality characteristics and morphological description of many potato varieties cultivated in Ecuador. The catalog described the improved varieties 'Super Chola', 'INIAP-Fripapa', 'INIAP-Gabriela' as tolerant and 'INIAP-Cecilia' as susceptible to *G. pallida* (Mastrocola *et al.*, 2016; #19 in Table 2).

Eleven improved varieties and nine promising clones from the INIAP potato collection were evaluated for resistance and tolerance to *G. pallida* in order to select parental clones for the development of new varieties. Potato 'Leona Negra' was used as a susceptible control. Evaluations were carried out in greenhouses at the Experimental Station Santa Catalina, INIAP. All but three accessions were found to be tolerant to *G. pallida*, with inoculated potato yields similar to uninoculated treatments. Results identified 85% of the material to be susceptible and tolerant to *G. pallida*. The smallest Pf/Pi (2.7) was identified for the variety 'INIAP-Gabriela'. Potato 'Leona Negra' was confirmed to be susceptible and tolerant (Castillo *et al.*, 2017; #20 in Table 2).

Four improved varieties and 12 promising clones from PNRT-INIAP were evaluated to determine resistance and tolerance to *G. pallida* under greenhouse conditions. The *G. pallida* population was collected from potato fields at the Santa Catalina Station, INIAP. All of the potato varieties and promising clones were susceptible to *G. pallida*. Moreover, the four improved varieties and 11 of the promising clones were tolerant to *G. pallida*. The improved variety 'INIAP-Josefina' and the clone 07-32-15 were considered to be more tolerant to *G. pallida* than the others (Llumiquinga and Rivadeneira, 2018; #21 in Table 2).

Recently, 11 potato clones from PNRT-INIAP were evaluated for resistance and tolerance to *G. pallida* under greenhouse conditions. The *G. pallida* population was collected from a potato field at the Santa Catalina Station, INIAP. Potato 'Leona Negra' and eight of the clones evaluated were considered susceptible and tolerant to *G. pallida* (Castillo, *et al.*, 2019; #22 in Table 2).

Resistance screening and potato variety development in Chile

In 1974, the Minister of Agriculture from Chile identified potato fields severely infested with *G. rostochiensis* in the province of Elqui, Coquimbo Region. The *G. rostochiensis* pathotype was identified as R₁A. Thirty potato clones were evaluated in 1978 and 13 clones in 1979 in fields in La Serena. Potato 'Ultimus' was used as the susceptible control and 'Cardinal' as the resistant control. The majority of clones did not produce cysts and were considered resistant. One possible explanation was that resistant clones carried the *H1* gene from hybridizations with *S. tuberosum* ssp. *andigena* (Guglielmetti and Guíñez, 1982; #23 in Table 2).

The Instituto de Investigaciones Agropecuarias in Chile (INIA-Chile) reported that potato 'Yagana-INIA' was resistant to *G. rostochiensis* as well as potato leafroll virus (PLRV), and moderately resistance to *P. infestans* and *Streptomyces scabies*. 'Yagana-INIA' is considered a high-yielding variety with very good culinary characteristics (Kalazich, 1982; #24 in Table 2).

Use of resistant potatoes to control *G. rostochiensis* is a major objective of the Potato Program of INIA-Chile. Advanced potato breeding clones have been evaluated in fields with high infestations of *G. rostochiensis* in La Serena. Potato cultivars and advanced potato breeding clones, 38 in total, were evaluated in the laboratory and in the field to determine resistance to *G. rostochiensis*. Of the 38 accessions evaluated under laboratory or field conditions, 22 accessions were susceptible to *G. rostochiensis*, and 16 accessions were resistant to *G. rostochiensis*. These results showed a significant correlation between laboratory and field evaluations. It was concluded that germplasm could be screened in the laboratory and material identified as resistant sent to the field (Fernandez, 1988; #25 in Table 2).

In 1989 the Potato Breeding Program of INIA-Chile developed 'Karua-INIA'. This cultivar is high yielding and is well adapted to the majority of potato-growing areas in Chile. 'Karua-INIA'

parental clones include the Chilean potato 'Yagana-INIA', released in 1983 with resistance *G. rostochiensis* and PLRV, and the cultivar 'Fanfare', of Dutch origin. 'Karua-INIA' is resistant to *G. rostochiensis* pathotypes R₁A and R₂A, with high levels of resistance to PLRV, extremely resistance to Potato virus X (PVX) and resistance to dry rot (*Fusarium* sp.). It was developed for the fresh potato market and has excellent flavor and texture when boiled (Kalazich *et al.*, 2004; #26 in Table 2).

Forty-nine potato clones and diploid potatoes from the Chilean Potato Genebank at the Universidad Austral de Chile were evaluated to detect resistant accessions to *G. rostochiensis*. The resistant potato 'Cardinal' was used as a resistant control. The accessions were evaluated under greenhouse conditions from November 1998 to February 1999. Inoculum was collected from infected soils from four fields in the Province of Elqui: Las Rojas, Pan de Azucar, Vegas Norte, and Altovalsol. Eighteen percent of accessions were considered resistant, 62% partially resistant, and 20% moderately susceptible to *G. rostochiensis*. In this study, 'Cardinal' was moderately susceptible to *G. rostochiensis*. It was suggested that this was caused by increased virulence of *G. rostochiensis* from the Elqui area, or possibly the presence of an unknown pathotype in the inoculum (Milla and Krausz, 2004; #27 in Table 2).

Twenty potato accessions from the Potato Genebank at the Universidad Austral de Chile were evaluated for their *in vivo* response to *G. rostochiensis*. Eleven potato accessions with the Gro1-4 resistance gene, eight accessions with the *H1* resistance gene and one accession with both resistance genes were selected. Potato 'Désirée' was used as a susceptible control and 'Yagana' and 'Cardinal' as resistant controls. The *G. rostochiensis* population was collected from an infested potato field in the Los Lagos Region and the *G. rostochiensis* pathotype was determined to be R₁A. Potatoes 'Cardinal' and 'Yagana,' were both resistant. Of the accessions evaluated, 40% were resistant, 25% partially resistant, 25% moderately susceptible, and 10% susceptible to *G. rostochiensis*. The one accession with both resistance genes was susceptible. Four accessions

had *G. rostochiensis* cysts that did not contain eggs; these accessions will be used in future breeding efforts (Brintrup, 2016; #28 in Table 2).

Two hundred and seventy-one potato accessions from the collection of the Potato Genebank at the Universidad Austral de Chile were evaluated for resistance genes to PCN, potato virus X and potato virus Y. Linked molecular markers were used to detect resistance genes to *G. pallida* and *G. rostochiensis*. The HC and Gro1-4 molecular markers were used to identify the GpaVvrn_QTL and Gro1-4 resistance genes to *G. pallida* and *G. rostochiensis*, respectively (Asano *et al.*, 2012; Dalton *et al.*, 2013). Of the 271 accessions analyzed, 99 accessions amplified the HC marker, and 54 accessions were positive for the Gro1-4 marker. Two accessions (280-CON-755 and 254-CON-902) described in previous research by Milla and Krausz (2004) as resistant *G. rostochiensis* amplified the Gro1-4 marker in this study (López *et al.*, 2015).

Resistance screening and potato variety development in Bolivia

A one-year study was conducted in the central highlands of Bolivia to evaluate three potato clones suspected to have partial resistance to *G. pallida*. The study included susceptible potato ‘Sani Imilla’, bean, and barley as well as cultural practices to control *Globodera* spp. The potato clones G84381.9, CIP390159.4, and G85472.20 were from CIP-Peru. In 1995, the experiment was conducted in fields infested with both *G. pallida* and *G. rostochiensis* in the Province of Ingavi, La Paz, pathotype(s) were not reported. The multiplication rate of *Globodera* was 30% higher on the clone CIP390154.4, 13% higher on G84381.9, and similar on the clone G85472.20, compared to ‘Sani Imilla’. Since no reduction of *Globodera* densities was observed the authors speculated *G. rostochiensis* was not affected by the partial resistance to *G. pallida*. The clone G390159.4 was considered to have the best yield of all the clones, while all three had lower yields than ‘Sani Imilla’. The authors suggest that the impact of PCN on the three potato cultivars may not only reflect the incidence of nematodes but also the agronomic characteristics inherent in each clone. (Pacajes *et al.*, 2002; #29 in Table 2).

Resistance screening and potato variety development in Venezuela

In Venezuela, 15 advanced potato breeding clones from CIP-Peru were evaluated in a greenhouse study for possible resistance to *G. rostochiensis*. The *G. rostochiensis* pathotype R₂A was collected from an infested potato field in the community of Jimenez, Lara State. Two clones, CIP393465.38 and CIP392634.21, were found to be resistant to *G. rostochiensis*. However, CIP393465.38 was also considered intolerant to *G. rostochiensis*. CIP393465.38 was the result of crossing ‘Serrana INTA’ (pedigree includes wild species *S. demissum*, *S. vernei*, and *S. spegazzinii*) with the clone CIP387170.9 (derived from tetraploids potato *S. tuberosum* ssp. *andigena*, *S. tuberosum* and wild species susceptible to *G. rostochiensis*) (Anaya *et al.*, 2005; #30 in Table 2).

Conclusions

Studies described in this review made considerable efforts to identify new sources of potato with PCN resistance and tolerance and to also speed the incorporation of these sources into cultivated germplasm. For the Andean region where PCN is endemic, only a few named cultivars have been released with PCN resistance. In Peru ‘Maria Huanca’ and ‘Wankita’ were released with *G. pallida* resistance, as well as ‘Serranita’ with tolerance to *G. pallida*. In Ecuador three cultivars with *G. pallida* resistance were released, ‘Supe Chola’, ‘Fripapa’, and ‘Gabriela’. Three cultivars have been released in Chile with resistance to *G. rostochiensis*. In some cases, resistance originated from known sources such as *S. vernei* and *S. tuberosum* ssp. *andigena*, while other sources remain unknown. This review provides breeding programs an extensive list of germplasm for developing new PCN resistant varieties. It is important for any breeding program to work with multiple sources of resistance to maximize durability. Furthermore, the extensive diversity of *Globodera* populations throughout South America means that numerous sources of resistance will be needed, either in one variety or in multiple varieties. As pointed out in Part 1, better characterization of PCN diversity will improve the selection of resistant varieties. Close study of

resistance genes and their modes of action may help diversify resistance sources. This review also documents potato germplasm from various genebanks and other entities evaluated for PCN resistance and tolerance, and, in some cases, inheritance. Potato cyst nematode resistant and tolerant germplasm from the Andean region described in this review are, for the most part, available for breeding programs to develop new potato varieties. Potato germplasm of the Andean region is a valuable source of genetic diversity which must be conserved, evaluated, and used in potato breeding programs in order to provide new varieties to farmers who depend on this crop for their sustainability and to reduce or avoid the use of highly toxic nematicides.

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