

RESEARCH/INVESTIGACIÓN

AN ASSESSMENT OF POTATO CYST NEMATODE (*GLOBODERA* SPP.) RESEARCH FROM THE ANDEAN REGION OF SOUTH AMERICA. PART 1: OCCURRENCE AND IMPACT

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ABSTRACT

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Potato cyst nematodes (PCN; *Globodera pallida* and *Globodera rostochiensis*) are among the most significant pathogens limiting the production of potato globally. Potato cyst nematodes occur in cooler areas of subtropical and tropical regions and temperate regions throughout the world. Both species have the potential to significantly reduce potato yields. In the South American Andes highlands, potato is a major staple crop and is used mainly for local consumption. Most of the potatoes produced in South America are consumed unprocessed, a principal reason why potatoes remain a staple food for the majority of families. Plant-parasitic nematodes are among the most important phytosanitary pests limiting potato production in these Andean countries. In South America, research has focused on taxonomy and on frequency and severity of PCN, and in calculating damage or yield loss to potato due to PCN. This review reports the distribution of the PCN in the main potato-growing areas of the Andean region of South America, as well as the impact of PCN on regional potato production.

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

RESUMEN

Silvestre, R., L. M. Dandurand, I. A. Zasada, J. Franco and J. C. Kuhl. 2021. Revisión sobre los nemátodos del quiste de la papa (*Globodera* spp.) en la región Andina de América del Sur. Parte 1: Ocurrencia e impacto. *Nematropica* 51:85-105.

Los nemátodos del quiste de la papa (PCN; *Globodera pallida* y *Globodera rostochiensis*) se encuentran entre los patógenos más importantes que limitan la producción del cultivo de papa a nivel mundial. Los nemátodos del quiste de la papa están presentes en áreas más frías de las regiones subtropicales, tropicales y en las regiones templadas del mundo. Ambas especies tienen el potencial de reducir significativamente el rendimiento del cultivo de papa. En los Andes de América del Sur, la papa es un cultivo básico importante y se utiliza principalmente para el consumo local. La mayor parte de la papa producida en América del Sur se consume sin procesar, razón principal por la cual el cultivo de papa sigue siendo un alimento básico para la mayoría de las familias. Los nemátodos fitoparásitos se encuentran entre las plagas fitosanitarias más importantes que limitan la producción del cultivo de papa en estos países

andinos. En América del Sur, investigaciones realizadas se han centrado en la taxonomía, en la frecuencia y severidad de PCN, especialmente en el cálculo del daño o pérdida en el rendimiento del cultivo de papa debido a PCN. Esta revisión reporta la distribución de PCN en las principales áreas productoras de papa de la región Andina de América del Sur, así como el impacto de PCN en la producción regional del cultivo de papa.

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

INTRODUCTION

There are two primary species of potato cyst nematodes (PCN), *Globodera rostochiensis* Wollenweber 1923 and *Globodera pallida* Stone 1973. Both species originated from the Andean region of South America. A third *Globodera* species, *G. ellingtonae* Handoo Carta Skantar Chitwood 2012, was recently described from populations found in Oregon (Handoo *et al.*, 2012). Since this first report in North America, *G. ellingtonae* has also been reported in South America (Lax *et al.*, 2014). Potato cyst nematodes are major pests that affect potato production in Africa, Australia, Canada, Europe, and USA (Minnis *et al.*, 2002; Pylypenko *et al.*, 2005; Hodda and Cook, 2009; Mimee *et al.*, 2015; Dandurand *et al.*, 2019; Mburu *et al.*, 2020) and are capable of reducing potato yields by up to 80% (Brodie and Mai, 1989; Franco *et al.*, 1999a; Contina *et al.*, 2019). *Globodera rostochiensis* is reported in 70 countries and *G. pallida* is reported in 47 countries (Dandurand *et al.*, 2019). In South America, both species have been reported in Argentina, Bolivia, Chile, Colombia, Ecuador, Peru, and Venezuela (EPPO, 2020). It is unclear how *Globodera* speciation and genetic diversification evolved across South America. However, geological events such as the uplift of the Andes allowed for the resurgence of cold adapted biota, potentially an important factor in diversification along the Andes mountain range and in *Globodera* speciation. *Globodera pallida* is better adapted to colder annual mean temperatures, while *G. rostochiensis* is adapted to warmer ecological zones (Evans and Stone, 1977).

The geographic distribution of *G. pallida* lies in Colombia, Ecuador, and Peru to the north of Lake Titicaca, while *G. rostochiensis* is primarily found to the south of this latitude (Evans *et al.*, 1975; Grenier *et al.*, 2010). The center of diversity of *G. pallida* and *G. rostochiensis* is in the Andean region where PCN co-evolved along with their

principal host, potato, and related *Solanum* species, in the highlands of Peru and Bolivia (Evans *et al.*, 1975; Canto and Scurrah, 1977; Franco, 1977; Sosa-Moss, 1987; Subbotin *et al.*, 2019). In the same geographic region, wild *Solanum* species have been identified with resistance to PCN (Hawkes, 1994). Potato cyst nematodes were first reported in Peru in 1952 (Bazán de Segura, 1952), and to our knowledge this is the first report of PCN in South America. Since this date, PCN has been identified throughout the Andean region and the presence of both species with different races has been confirmed and established. Specifically, in the Andean region, *G. pallida* has a wider geographic distribution than *G. rostochiensis* (Franco and González, 2011). The seven countries that are part of this review form the majority of the Andean region in South America. The political organization within each country is as follows: Peru is divided in twenty-five regions, Ecuador is divided in twenty-four provinces, Colombia is divided into thirty-two departments, Bolivia is divided in nine departments, Venezuela is divided in twenty-three states, Argentina is divided in twenty-three provinces, and Chile is divided in sixteen regions.

Plant-parasitic nematodes are a threat to global food security, destroying at least 12% of global food production annually, which is estimated to be more than \$157 billion globally (Hassan *et al.*, 2013). Different agricultural crops are affected by nematode parasitism, reducing the production and quality of crops and causing great economic losses, including to staple crops such as potato. The effect of plant-parasitic nematodes on agriculture is often underestimated as nematodes produce non-specific symptoms that are often confused with water stress, nutritional disorders, soil fertility problems, or with other secondary fungal or bacterial infections (Mesa-Valle *et al.*, 2020). The consequence of nematode invasion depends on the population density in the soil and roots, the susceptibility of the cultivated plant

species, and environmental conditions. The Andean region is the center of origin of potato diversity; therefore, it is also the origin of many potato pathogens, including plant-parasitic nematodes that attack this crop. Root-knot (*Meloidogyne* spp.) and PCN are two of the most important plant-parasitic nematodes on potato when economic impact is considered (Jones *et al.*, 2013). This review is part 1 of 2. Part 1 presents the geographical distribution of infestations of PCN and the economic impact that this group of nematodes causes in the major potato-growing regions of the South American Andes. Part 2 will focus on the search for PCN resistance in the Andean region of South America.

Potato production and impact of PCN in South America

Potato production in the Andean region is the principal economic source for the endemic population. Peru is one of the countries where potato consumption has recently grown significantly, reaching 85 kg/person in 2015 (Devaux *et al.*, 2020). National potato production is highest (87%) in the highlands; mainly in the southern regions of Puno and Cuzco, in the central region in Huanuco and Junin, and in the northern regions in La Libertad and Cajamarca. Fresh potatoes are still a staple food for poor populations in rural Andean areas where there is no adequate infrastructure for storage or processing; almost 90% of potatoes are consumed without processing (Devaux *et al.*, 2010). Potatoes are primarily grown for self-consumption within a subsistence farming system. Subsistence farms are mostly located in remote areas of the Peruvian highlands in adverse agro-climatic zones subject to problems of erosion, drought, frost, pests, and diseases, which tend to lead to low potato yield (Pocco, 2019). One phytosanitary problem of potatoes in the Peruvian Andean region are plant-parasitic nematodes that limit potato yield and are difficult to manage. Potato cyst nematodes and *Nacobbus aberrans* are the most damaging plant-parasitic nematodes to potato crops in the region (Jimenez, 2017).

In Bolivia, 93% of potato production is concentrated in three regions: Puna with 50%, Puna Alta with 25%, and Valleys with 20% (Franco and González, 2011). These regions represent the departments of La Paz, Potosi, Cochabamba, Oruro, and Tarija. The native varieties of *S.*

tuberosum subsp. *andigena* constitute 95% of national potato production. Approximately 70% of production is for fresh consumption, 10% for processing (chuño and tunta), and the remaining 20% is used as seed. Potato is one of the basic food crops in Bolivia and provides work for many families in rural areas of the country. In Bolivia, as in Peru, PCN and *N. aberrans* are the most important plant-parasitic nematodes that affect potato production and seed potato quality (Martinez, 2017). Yield loss due to nematodes (~50%) encourages farmers to plant twice as much land to potatoes than actually needed if nematode control measures were in place. Better nematode control could release land for other crops, such as legumes that offer nutritional improvement for the rural poor. There are two traditional Bolivian crops, lupines or tarwi (*Lupinus mutabilis*) and quinoa (*Chenopodium quinoa*), that could favor the decline of PCN rates when they are included in a rotation since they are non-hosts (Franco *et al.*, 1999b). Currently, bean or barley crops are usually used by farmers in field rotations with potato (Atkinson *et al.*, 2002).

In Colombia, potato is also an important subsistence crop in cold climates where potato is one of the few crops that can be grown successfully. The production areas are distributed among mainly departments whose contributions add up to approximately 89% of the annual national production for either fresh consumption or processing. Around 90% of potato production is concentrated in the departments of Cundinamarca, Boyaca and Nariño and Antioquia, and the remaining 10% is in Cauca, Caldas, Tolima, Valle del Cauca, Huila, Putumayo, Quindio, Santander, and Norte de Santander (Tinjacá and Rodríguez, 2015). As in other countries, PCN are one of the most important pests of the crop with reductions in yield up to 15% or 2 T/ha in crops that do not show above ground symptoms. Within the last 50 years, approximately 40 commercial potato varieties and native potatoes from *S. tuberosum* subsp. *andigena*, *S. tuberosum* subsp. *phureja* and *S. tuberosum* subsp. *chaucha* have been planted in Colombia (Carrión and Rojas, 2013).

In Ecuador, potato is the principal subsistence crop; the vast majority of the crop is produced in the central highland areas of Chimborazo, Tungurahua and Cotopaxi, with 66% produced in the north (Carchi and Imbabura), where 20% of fields grow potato year-round (Devaux *et al.*,

2010). In Ecuador, the ecological niche of PCN is between 2,600 to 3,200 meters above sea level (masl). *Globodera pallida* is the principal nematode species that limits potato production with up to 30% yield losses. The high level of damage due to PCN is primarily due to the continuous planting of potato, and/or short rotation periods (Revelo, 1997a; Mejía and Valverde, 2011). Continuous planting of potato in Ecuador has also favored the increase of *G. pallida* population densities to high levels leading to increased yield losses. In some cases, farmers will unintentionally plant a susceptible native potato after a season of growing an improved, tolerant cultivar, leading to significant yield losses. Farmers may blame yield losses on soil fatigue, poor seed quality, and the use of fertilizers (Andrade, 1997).

Although potatoes are produced widely throughout Chile, the principal regions of commercial production are Coquimbo and Los Lagos, where *G. rostochiensis* is prevalent. These regions produce practically all of the potatoes destined for the main markets. Each area produces its own specialty cultivars for the end market, often defined by consumer preference, climatic conditions, and soil (Inostroza *et al.*, 2017). In Chile, damage caused by PCN can exceed 60% yield losses (Muñoz *et al.*, 2017). Since PCN is a quarantine pest in Chile, seed potatoes cannot be grown for five years after PCN is detected (Brintrup, 2016).

In Venezuela, the principal potato-producing states are Merida, Trujillo, Tachira, Lara, Carabobo, and Aragua. The Venezuela Andean region (Merida, Trujillo and Tachira) produces more than 80% of the potato production in the country (González *et al.*, 2017). Potato is grown at altitudes between 800 and 1,500 masl in the mountainous states of Aragua, Lara, and Carabobo. Potato is also grown at 2,000-4,000 masl in the states of Tachira, Merida, and Trujillo. In Venezuela, 90% of potato production is destined for fresh consumption and is distributed through public and private marketing networks. However, 10% of national potato production is directed for agro-business where it is used by processing companies for the production of French fries and chips, among other uses (Anaya *et al.*, 2005). Studies have showed that *G. rostochiensis* population densities over 5 viable cyst/100 cm³ soil can result in economic damage (Crozzoli, 1989). Similarly, the potato crop was observed to be

severely damaged when the initial nematode population density was over 64 eggs/g soil (Greco and Crozzoli, 1995). The presence of 1 cyst/100 g of soil and more than 120 second-stage juveniles (J2)/100 g soil of *G. rostochiensis* were sufficient to cause crop loss (Añez and Tavira, 1983). The tolerance limit of potato 'Andinita' to *G. rostochiensis* was determined to be 1.5 eggs/100 cm³ in Lara State, where the maximum yield was reduced 73% when the initial population was 256 eggs/cm³ of soil (Jiménez *et al.*, 2000; Jiménez-Pérez *et al.*, 2007). In Venezuela, the use of certified potato seed is limited. The majority of tuber seeds are produced by farmers selecting the best tubers for the market, and the remaining small tubers are used to plant the next season. Importation of certified seed is expensive, and it is difficult for farmers to obtain (Greco and Crozzoli, 1995). Moreover, the potato crop is affected by different critical factors such as price instability, low availability of varieties adapted to local conditions, low availability of quality potato seed, high production costs, and economic losses due to pests and diseases (González *et al.*, 2017).

In Argentina, potatoes that are produced locally are mainly destined for the fresh market, industry, seed production, and export. The percentage of production destined for industrial processing is around 25%. Consequently, the crop provides income for many rural families. Potato is produced in all regions, but the main potato production areas in Argentina are in the provinces of Buenos Aires and Cordoba, which account for around 80% of the production (Haro *et al.*, 2017). In Argentina, potato landraces are grown in the northwestern region (provinces of Jujuy, Catamarca, and Salta), in the high mountain valleys and the Puna and Prepuna phytogeographic areas. In the highlands of northwest Argentina, potatoes are the most important staple food, with different culinary properties as well as agronomic properties (Mondino *et al.*, 2006; Clausen *et al.*, 2010). Published results documenting yield losses due to PCN in Argentina were not found.

Occurrence of PCN in South American potato fields

Potato fields from different areas have been evaluated for the presence of PCN associated with potato roots and in the soil, as well as evaluated for nematode frequency and population density. In

South American countries, PCN are widely distributed in the Andean region.

In 1974, the International Potato Center (CIP; Lima, Peru), initiated a PCN project to collect representative nematode populations in areas where PCN was reported and determine the species and pathotypes present (CIP, 1976; Brodie *et al.*, 2000). Field samples were collected from Peru (Cuzco, Arequipa, Junin, Huanuco, La Libertad, Puno, and Cajamarca), Ecuador, Colombia, Panama, and Mexico. *Globodera pallida* was detected in samples from Peru and Ecuador, while all samples from south of Lake Titicaca in Bolivia contained *G. rostochiensis*, except for one. Results suggested that Lake Titicaca is approximately the dividing line between the two species. *Globodera pallida* and *G. rostochiensis* coexist in the latitude 15°S. To the north of this latitude, the populations were exclusively *G. pallida* and to the south *G. rostochiensis* predominates (CIP, 1975, 1976). While this conclusion was based on the available information at the time, more recent research suggests a significant area of overlap between *G. pallida* and *G. rostochiensis* (Thevenoux *et al.* 2020).

In 1975, the presence and distribution of PCN in four countries from South America was reported (Evans *et al.*, 1975). A total of 26 PCN populations were collected and identified from Colombia, Ecuador, Peru, and Bolivia. *Globodera pallida* was only detected in Colombia, Ecuador, and Peru, while in Bolivia, both *G. pallida* and *G. rostochiensis* were detected. The demarcation line between the areas in which *G. pallida* and *G. rostochiensis* were found was 15.6°S latitude, with one *G. pallida* population at 16.3°S. The results suggested that, at the time, the distribution of the PCN species depended on latitude, different temperature regimes, or day length, as well as the movement of potato tubers. It was concluded that there were a number of possible reasons why the two species of PCN have different distribution and a more thorough survey of PCN distribution in the Andean countries in South America could provide clues about PCN original distribution (Evans *et al.*, 1975). Additionally, Franco (1977) mentioned that based on geographical distribution the demarcation between *G. pallida* and *G. rostochiensis* almost coincides with the political border of Peru and Bolivia where the Altiplano and Lake Titicaca are located (15.6°S).

In Peru, the first report of *G. rostochiensis* was

in 1952 in potato roots from Tarma in the Junin Region (Bazán de Segura, 1952). In 1973, an experiment to evaluate nematicide efficacy was carried out by the Ministry of Agriculture in a potato field in the Junin Region highly infested with *G. rostochiensis* (Gómez, 1973). While these early reports identified *G. rostochiensis*, *G. pallida* is the dominant species in Peru and has been identified in Arequipa, Puno, Cuzco, Junin, Huanuco, La Libertad, Ayacucho, Huancavelica, Apurimac, Piura, and Ancash and Cajamarca Regions (Canto and Scurrah, 1976, 1977; Picard *et al.*, 2004; Picard *et al.*, 2007; Franco and González, 2011; Cadillo, 2019; Subbotin *et al.*, 2019; Thevenoux *et al.*, 2020). Pathotypes commonly identified are Pa4, Pa5, and Pa6 (Franco and González, 1990). While *G. rostochiensis* has been identified primarily in southern Peru. Moreover, *G. rostochiensis* has been detected in localized infestation of potato fields from Cuzco, Ayacucho, Arequipa, and Puno Regions (Canto and Scurrah, 1976, 1977; Delgado de la Flor and Jatala, 1991; Franco and González, 2011; Subbotin *et al.*, 2019; Thevenoux *et al.*, 2020). More recently PCN have been detected in Amazonas Region (Vera and Oliva, 2013; Chávez, 2019).

An extensive project recording incidence (frequency) and density (predetermined scales according to the infestation levels) of PCN and associated losses in potato yield was carried out in Peru and Bolivia (Franco and González, 2011). The information was collected from thesis and diagnostic surveys from each country. The severity of PCN was found to be associated with yield losses when soil infestation was recorded as egg number and/or J2/g soil. Five departments were surveyed in Bolivia (Cochabamba, Potosi, La Paz, Tarija, and Chuquisaca) and the ten regions in Peru (Cajamarca, La Libertad, Junin, Ayacucho, Huancavelica, Huanuco, Apurimac, Arequipa, Cuzco, and Puno). The presence of PCN was reported in all regions of both countries. Sixty-five percent of 3,299 soil samples collected in Peru were infested by PCN with average densities of 317 eggs and J2/g soil. The regions with highest incidence, 78 to 90%, were in the Cuzco, Huanuco, La Libertad, and Huancavelica. The Cajamarca and Ayacucho Regions had areas free of PCN, and incidence ranged between 62 to 69%. High population densities, ranging between 821 to 2,161 eggs and J2/g soil were found in the Junin, Huancavelica, Apurimac, Cuzco, and Puno

Regions. Furthermore, Cuzco, Junin, Huanuco, and La Libertad Regions also recorded the highest losses in potato production. In Bolivia, of the 735 soil samples collected, the incidence level of PCN was 78%. However, low densities were observed in 30% of the samples, medium densities were observed in 26% of the samples, and very high densities were observed in 19% of the samples. Furthermore, the departments having the highest densities were from Cochabamba and La Paz and medium densities observed in La Paz and Potosí. La Paz, Potosí, and Chuquisaca presented the highest losses to potato production due to high infestation levels of PCN. In Peru, the predominate species was *G. pallida*, while *G. rostochiensis* was detected in localized areas in the southern regions of Arequipa and Puno. In contrast, in Bolivia *G. pallida* only slightly exceeded the incidence of *G. rostochiensis*. The departments of Chuquisaca, La Paz, and Cochabamba were the areas most affected by *G. pallida*, while the departments of Tarija and La Paz were most affected by *G. rostochiensis* (Franco and González, 2011; Table 1 and Fig. 1).

In Peru, the province of Luya is one of the main potato-producing areas in the Amazonas Region where the climate is slightly humid and warm without water deficiency (Rodríguez *et al.*, 2010). However, climate, diseases, and pests limit potato production. In this province, 35 potato fields were surveyed to identify plant-parasitic nematodes and determine population frequencies and densities present. The study was conducted by the Phytopathology Laboratory, Universidad Nacional Toribio Rodríguez de Mendoza (Amazonas Region). The study identified 13 genera of plant-parasitic nematodes associated with potato crops. Of the soil and root samples analyzed, 100% and 69%, respectively, contained plant-parasitic nematodes. The genera detected in soil samples with high frequency included *Globodera* in 29% of samples. The highest mean population densities in soil samples were detected for PCN (50 nematodes/100 cm³) and *Helicotylenchus* (26 nematodes/100 cm³). The genera detected in root samples with high frequencies included *Globodera* in 23% of samples. The plant-parasitic nematode diversity detected in Luya potato fields is one aspect to be considered when carrying out phytosanitary measures for potato production in the Amazonas Region (Vera and Oliva, 2013; Table 1 and Fig. 1). Additionally, in the district of Longuita from

province of Luya, PCN was detected in a potato field located at 2,800 masl. Most potato farmers use traditional, low technology cultivation methods. This district has serious problems caused by nematodes, especially PCN, where they are present at high densities and detrimentally effect potato production (Chávez, 2019; Table 1 and Fig. 1).

Paucar (2016) identified nematode species, distribution, and densities in 101 ha of potato fields from four communities in the province of Andahuaylas in the Apurímac Region, Peru. The Apurímac Region is part of the southern potato-producing region where average potato yield is 18 t/ha (MINAGRI, 2017). Potato is the main economic source in these communities due to good agro-climatic conditions and close proximity to local markets. The evaluation was conducted in February 2015, and the samples were obtained from fields with and without potato in which there may or may not have been symptoms of PCN infestation. Additional requirements included that fields must be cultivated for more than 5 years and must be greater than or equal to 1 ha, with 20 sub-samples collected per ha. The study was conducted by the Nematology Laboratory of Plant Health Diagnosis Center SENASA, Lima. It was found that 101 ha were infested with *G. pallida*. Furthermore, *G. pallida* was confirmed to be widely distributed in these communities where potatoes were produced. The range of incidence of *G. pallida* in the potato fields was between 71 and 91%. The highest incidence of *G. pallida* was in the community of Huaraccopata, located at 3,664-3,919 masl (Paucar, 2016; Table 1 and Fig. 1).

A study in the Ayacucho Region, Peru, evaluated native potato fields from six communities in the District of Chungui from province of La Mar in order to identify species, incidence, and population densities of PCN in the fields. The cultivated areas tested were selected based on native potato production. The district of Chungui is located between 800-4,811 masl. Seventy-eight soil samples were collected from different native potato fields from these communities. The samples were collected between April and June 2016. The percentage incidence was for the number of fields affected divided by the number of fields tested and the population densities were considered as eggs plus J2/g of soil, with five density levels from none (0 eggs and J2/g) to very high (>35 eggs and J2/g). The incidence of *G. pallida* in the six communities was 41%, and the

population densities ranged from 0 to 433 eggs plus J2/g soil with the exception of two communities (Chupon and Rumichaca) where 100% of potato fields were free of PCN. One of the reasons PCN might not have been detected in these two communities was attributed to ancestral knowledge. The farmers have a rigorous practice of crop rotation and prolonged use of fallow treatments. Moreover, they alternate their field rotation with legumes such as tarwi and mashua (*Tropaeolum tuberosum*), and the communities conserve and use their own seed that is likely free of nematodes (Aspur, 2017; Table 1 and Fig. 1).

Ñahuis (2017) evaluated the reaction of three potato cultivars, 'Yungay', 'Roja Ayacuchana', and 'Canchan', and three native potatoes, 'Chaulina', 'Tumbay', and 'Peruanita', from the collection at INIA-Ayacucho to PCN. During 1995 and 2000, five PCN populations from infested potato fields were collected from the provinces of Huamanga, Huanta, and La Mar, in the region Ayacucho, and were conserved and analyzed in the Zoology Laboratory from Universidad Nacional San Cristóbal de Huamanga, Ayacucho. These areas are in the agroecological zone considered as middle upper tropical highlands with a temperature between 12° and 18°C. Collected PCN were inoculated on potato tubers under greenhouse conditions. High viability was detected in the PCN populations from Huamanga and La Mar (50 and 47%). Cyst viability of collected PCN was around 50%, and all the potato accessions were susceptible, while potato 'Canchan' and the native potato 'Peruanita' were the most susceptible (Ñahuis, 2017; Table 1 and Fig. 1).

From December 2015 to February 2016, at 4,200 masl in the Puno Region, Peru, 160 soil and root samples from potato fields of seven provinces within the region were evaluated to identify the presence of plant-parasitic nematodes. Eight genera of nematodes including *Globodera* were found. Results showed the presence of plant-parasitic nematode infestation in all the potato fields surveyed in the seven provinces, which are the main potato producing areas of the Puno Region (Flores-Choque *et al.*, 2017; Table 1 and Fig. 1).

In the Huancavelica Region, Peru, 10 fields in four potato areas in the district Paucara from the province of Acobamba were surveyed for *G. pallida*. These areas are located in the highlands at 3,800 masl where the average temperature is 12°C.

Percentage incidence was determined by the number of infected fields divided by the number of fields surveyed. Infestation levels were calculated as the number of J2 and cysts/100 g of soil, using a scale from no nematodes (0 cysts or J2) to high infestation (>70 cysts or J2). Additionally, the infestation level also considered the number of eggs per gram of soil, using a similar scale from no infestation (0 eggs/g) to high infestation (>35 eggs/g). The survey was conducted at the Nematology Laboratory of Santa Ana Experimental Station from INIA-Huancayo. Results showed very high, and low densities of *G. pallida* in the potato fields surveyed, with 140 to 90 cysts/100 g to 32 to 28 J2/100 g (Parejas, 2018; Table 1 and Fig. 1).

In the Province of Sucre, in the Ayacucho Region, Peru, 18 potato fields from eight districts were surveyed to determine the distribution and population densities of PCN. These districts are located between 3,073 – 3,645 masl, and the fields were located on hillsides typical of inter-Andean valleys. The identification of the nematodes was conducted at the Microbiology, Plant Pathology, and Zoology Laboratory from Universidad Nacional de San Cristóbal de Huamanga, Ayacucho. Ninety soil samples were collected between August and September after potato harvest for the 2003-2004 season. Density levels were categorized on a scale from no infestation (0 eggs and J2/g of soil) to very high infestation (>35 eggs and J2/g of soil). *Globodera pallida* was the only species identified. *Globodera pallida* was detected in 28% of the soil samples, and 5% of total soil samples had high population densities. Approximately 69% of potato fields surveyed were found to be free of *G. pallida*. None of the evaluated fields had very high densities. These results suggest that *G. pallida* has limited distributed in the Province of Sucre (Pocco, 2019; Table 1 and Fig. 1).

In Bolivia, *G. pallida* and *G. rostochiensis* have been found, but there are few studies on pathotype diversity. *Globodera rostochiensis* is the predominant species in Bolivia (Franco and González, 2011). The first report of *G. rostochiensis* was in 1955 in the Isla del Sol of Titicaca Lake, Altiplano (Bell and Alandia, 1955). *Globodera rostochiensis* has also been identified in the departments of Cochabamba, La Paz, Potosi, Chuquisaca, and Tarija and, in some cases, in simultaneous infestations with *N. aberrans* (Canto

Table 1. *Globodera* species reported infesting potato crops in countries from South America (G: *Globodera* spp., Gp: *Globodera pallida*, Gr: *Globodera rostochiensis*, and Ge: *Globodera ellingtonae*).

Country	Region/Department	<i>Globodera</i> spp. reported	Reference(s)	No. in map ^z
Venezuela	Lara	Gr	Salinas, 1974; Jiménez <i>et al.</i> , 2000; Crozzoli, 2002; Anaya <i>et al.</i> , 2005; Jiménez-Pérez <i>et al.</i> , 2007; Casanova <i>et al.</i> , 2012	1
	Trujillo	Gr	Salinas, 1974; Crozzoli, 2002; Casanova <i>et al.</i> , 2012	2
	Merida	Gr, Gp	Dao and González, 1971; González and Dao, 1973; Salinas, 1974; Añez and Tavira, 1983; Crozzoli, 2002; Cassanova <i>et al.</i> , 2012; Subbotin <i>et al.</i> , 2019	3
	Tachira	Gr, Gp	Dao and González, 1971; González and Dao, 1973; Salinas, 1974; Crozzoli, 2002; Cassanova <i>et al.</i> , 2012	4
Columbia	Norte de Santander	Gp	Vallejo <i>et al.</i> , 2021	5
	Santander	Gp	Vallejo <i>et al.</i> , 2021	6
	Boyaca	Gp	Carrion and Rojas, 2013; Aguilar <i>et al.</i> , 2014; Carrion <i>et al.</i> , 2014; Rojas <i>et al.</i> , 2014; Vallejo <i>et al.</i> , 2021	7
	Cundinamarca	Gp	Canto and Scurrah, 1977; Carrion and Rojas, 2013; Aguilar <i>et al.</i> , 2014; Carrion <i>et al.</i> , 2014; Rojas <i>et al.</i> , 2014; Vallejo <i>et al.</i> , 2021	8
	Tolima	Gp	Vallejo <i>et al.</i> , 2021	9
	Caldas	Gp	Vallejo <i>et al.</i> , 2021	10
	Antioquia	Gp	Aguilar <i>et al.</i> , 2014; Rojas <i>et al.</i> , 2014; Vallejo <i>et al.</i> , 2021	11
	Cauca	Gp, Gr	Varón <i>et al.</i> , 1972; Nieto <i>et al.</i> , 1983; Vallejo <i>et al.</i> , 2021	12
	Nariño	Gp, Gr	Baeza, 1972; Evans <i>et al.</i> , 1975; Canto and Scurrah, 1976; Canto and Scurrah, 1977; Aguilar <i>et al.</i> , 2014; Rojas <i>et al.</i> , 2014; Vallejo <i>et al.</i> , 2021	13
Ecuador	Carchi	Gp, Gr	Baeza, 1972; Bridge, 1976; Revelo, 1997b; Llumiquinga <i>et al.</i> , 2015; Mejía and Valverde, 2011	14
	Imbabura	Gp	Mejía and Valverde, 2011	15
	Pichincha	Gp	Evans <i>et al.</i> , 1975; Bridge, 1976; Canto and Scurrah, 1976; Canto and Scurrah, 1977; Revelo, 1997a; Mejía and Valverde, 2011	16
	Cotopaxi	Gp	Revelo, 1997a; Mejía and Valverde, 2011	17
	Tungurahua	Gp	Bridge, 1976; Revelo, 1997a; Mejía and Valverde, 2011	18
	Chimborazo	Gp	Bridge, 1976; Revelo, 1997a; Mejía and Valverde, 2011	19
	Bolivar	Gp	Mejía and Valverde, 2011	20
	Cañar	Gp	Revelo, 1997b; Mejía and Valverde, 2011	21

Table 1. Continued.

Country	Region/Department	<i>Globodera</i> spp. reported	Reference(s)	No. in map ^z	
Peru	Piura	Gp	Picard <i>et al.</i> , 2007	22	
	Amazonas	G	Vera and Oliva, 2013; Chávez, 2019	23	
	Cajamarca	Gp	Evans <i>et al.</i> , 1975; Canto and Scurrah, 1976; Canto and Scurrah, 1977; Franco and González, 2011; Picard <i>et al.</i> , 2007	24	
	La Libertad	Gp	Evans <i>et al.</i> , 1975; Canto and Scurrah, 1976; Canto and Scurrah, 1977; Franco and González, 2011; Picard <i>et al.</i> , 2004; Picard <i>et al.</i> , 2007	25	
	Ancash	Gp	Cadillo, 2019; Picard <i>et al.</i> , 2007	26	
	Huanuco	Gp	Evans <i>et al.</i> , 1975; Canto and Scurrah, 1976; Canto and Scurrah, 1977; Franco and González, 2011; Picard <i>et al.</i> , 2007	27	
	Junin	Gp, Gr	Bazán de Segura, 1952; Gómez, 1973; Evans <i>et al.</i> , 1975; Canto and Scurrah, 1976; Canto and Scurrah, 1977; Franco and González, 2011; Picard <i>et al.</i> , 2004; Picard <i>et al.</i> , 2007; Subbotin <i>et al.</i> , 2019	28	
	Huancavelica	Gp	Franco and González, 2011; Parejas, 2018; Picard <i>et al.</i> , 2007.	29	
	Ayacucho	Gp, Gr, G	Franco and González, 2011; Aspuri, 2017; Ñahuis, 2017; Pocco, 2019; Picard <i>et al.</i> , 2007; Subbotin <i>et al.</i> , 2019; Thevenoux <i>et al.</i> , 2020	30	
	Cuzco	Gp, Gr	Evans <i>et al.</i> , 1975; Canto and Scurrah, 1976; Canto and Scurrah, 1977; Delgado de la Flor and Jatala, 1991; Franco and González, 2011; Picard <i>et al.</i> , 2007; Subbotin <i>et al.</i> , 2019; Thevenoux <i>et al.</i> , 2020.	31	
	Apurimac	Gp	Franco and González, 2011; Paucar <i>et al.</i> , 2016; Picard <i>et al.</i> , 2004; Picard <i>et al.</i> , 2007; Thevenoux <i>et al.</i> , 2020	32	
	Arequipa	Gp, Gr	Evans <i>et al.</i> , 1975; Canto and Scurrah, 1976; Canto and Scurrah, 1977; Franco and González, 2011; Picard <i>et al.</i> , 2007; Thevenoux <i>et al.</i> , 2020	33	
	Puno	Gp, Gr, G	Evans <i>et al.</i> , 1975; Canto and Scurrah, 1976; Canto and Scurrah, 1977; Franco and González, 2011; Flore-Choque <i>et al.</i> , 2017; Picard <i>et al.</i> , 2007; Subbotin <i>et al.</i> , 2019; Thevenoux <i>et al.</i> , 2020	34	
	Bolivia	La Paz	Gp, Gr, G	Bell and Alandia, 1955; Evans <i>et al.</i> , 1975; Canto and Scurrah, 1977; Franco and González, 2011; Martinez, 2017; Subbotin <i>et al.</i> , 2019	35
		Cochabamba	Gp, Gr	Evans <i>et al.</i> , 1975; Canto and Scurrah, 1977; Franco and González, 2011; Subbotin <i>et al.</i> , 2019	36
Chuquisaca		Gp, Gr	Franco and González, 2011; Subbotin <i>et al.</i> , 2019	37	
Potosi		G, Gr	Franco and González, 2011; Subbotin <i>et al.</i> , 2019	38	
Tarija		Gp, Gr	Franco and González, 2011	39	

Table 1. Continued.

Country	Region/Department	<i>Globodera</i> spp. reported	Reference(s)	No. in map ^z
Argentina	Jujuy	Gr, G	Moreno, 1956; Brücher, 1961; Lax <i>et al.</i> , 2008	40
	Salta	Gp, Ge, G	Lax <i>et al.</i> , 2005; Lax <i>et al.</i> , 2006; Lax <i>et al.</i> , 2008; Lax <i>et al.</i> , 2014	41
	Catamarca	Gr	Virsoo, 1967	42
Chile	Tarapaca	Gr	Moreno <i>et al.</i> , 1984; Fernandez, 1988	43
	Antofagasta	Gr, Ge	Moreno <i>et al.</i> , 1984; Fernandez, 1988; Subbotin <i>et al.</i> , 2011; Lax <i>et al.</i> , 2014 and Zasada <i>et al.</i> , 2018	44
	Coquimbo	Gr	Guglielmetti and Guíñez, 1982; Fernandez, 1988.	45
	Valparaiso	Gr, Gp	Moreno <i>et al.</i> , 1984; Fernandez, 1988.	46
	Bio-Bio	Gr	Brintrup, 2016	47
	Los Rios	Gr	Moreno-Lehuedé, 2013; Brintrup, 2016	48
	Los Lagos	Gr, Gp	Peña <i>et al.</i> , 2013; Moreno-Lehuedé, 2013; Brintrup, 2016; SAG, 2017	49
	Magallanes y de la Antartica Chilena	Gp	Moreno-Lehuedé and Mansilla, 2005	50

^zSee Figure 1.

and Scurrah, 1977; Franco and González, 2011; Martínez, 2017; Subbotin *et al.*, 2019). Potato cyst nematodes are distributed in most cultivated areas in Bolivia causing severe yield losses and indirect losses due to rejection of seed potatoes from infested fields (Pacajes *et al.*, 2002).

In Bolivia, 32 potato fields of Aypa Yauruta area, province of Pacajes, department of La Paz, were surveyed to identify plant-parasitic nematodes. This area is known for potato and quinoa production. Moreover, this area registers a maximum temperature of 24°C in November, and a minimum of -4°C in June, with an annual mean temperature of 11°C. The survey was conducted by the Phytopathology Laboratory, Universidad Mayor de San Andrés, Bolivia. Eight genera of plant-parasitic nematodes were identified including *Globodera* and *Nacobbus aberrans*. The highest average incidence was *N. aberrans* (36%), while PCN occurred in 10% of samples. However, the average occurrence out of the total nematodes observed were 19% and 7% for *Nacobbus* and PCN, respectively. The authors suggested that the presence of nematodes in infested fields was related to continuous potato cultivation, potato residue, and seed storage time (Martínez, 2017; Table 1 and Fig. 1).

In Colombia, *G. rostochiensis* was reported

for the first time in 1970 in the department of Nariño (Baeza, 1972), and in the following year, *G. rostochiensis* was reported in the department of Cauca (Varón *et al.*, 1972). Since then, *G. pallida* has been identified in soil samples from the departments of Nariño, Magdalena, Cundinamarca, and Cauca (Canto and Scurrah, 1976, 1977; Nieto *et al.*, 1983) and in 2012, in the departments of Boyaca and Cundinamarca, where it had not previously been detected (ICA, 2012; Carrión and Rojas, 2013; Carrión *et al.*, 2014). Additionally, the distribution of PCN has been expanding in different potato-producing areas such as the departments of Antioquia, Caldas, Tolima, Santander, and Norte de Santander (Aguilar *et al.*, 2014; Rojas *et al.*, 2014; Vallejo *et al.*, 2021).

Soil and potato root samples were collected from Departments of Cauca, Valle del Cauca, Caldas, Tolima, Cundinamarca, Boyaca, Santander and Santander del Norte in order to determine the presence of *G. pallida* in these potato-growing areas in Colombia. The survey was conducted during 1979 and 1980. Three-month-old potato plants were carefully removed from the ground to observe the roots in order to determine the presence or absence of cysts. A total of 5,512 soil samples were collected. *Globodera pallida* was detected in the roots of potato plants in the department of



Figure 1. Geographical distribution of *Globodera* species reported in the Andean region of South America.

Cauca; however, mean population densities were considered low (21 cysts/100 cm³). In Cauca, 292 samples had high population densities (average 6 to 47 cysts/200 g of soil) compared with other departments sampled. Furthermore, in the departments of Cundinamarca and Boyaca, only 4% of 3,969 soils samples analyzed contained cysts that were identified as PCN, probably *G. pallida*. A similar situation was found in the departments of Caldas, Tolima, and Valle del Cauca with cysts mostly empty or without eggs and dead J2. In the departments of Santander and Santander del Norte, 100% of 510 soil samples were free of PCN (Nieto *et al.*, 1983; Table 1 and Fig. 1).

Soil and potato root samples were collected from Tausa located in the department of Cundinamarca and from Ventaquemada located in the department of Boyaca, Colombia, in order to identify and delimit PCN infestations. These two potato-producing areas are located at altitudes between 2,630-2,931 masl. Forty potato fields were surveyed, 25 from Tausa, and 15 from Ventaquemada. Density levels were classified using a scale from no infestation (0 cysts/g of soil) to very high infestation (>35 cysts/g of soil). The incidence of *G. pallida* was 68% and 80%, in Tausa and Ventaquemada, respectively. In Tausa, *G. pallida* was detected in 17 out of 25 fields, with a range of 1 to 1,945 cysts/100 g soil, 1 to 778 J2/100 g soil and 273 to 578 eggs and J2/cysts. In Ventaquemada, *G. pallida* was detected in 12 out of 15 fields with a range of 1 to 73 cysts/100 g soil, 1 to 39 J2/100 g soil and 312 to 867 eggs and J2/cysts. Additional laboratory analysis identified *G. pallida* in root samples. It was suggested that high population densities of *G. pallida* in potato fields were related to continuous potato cultivation without crop rotation, infested seed distribution between potato fields, and use of agriculture machines without adequate disinfection. Some potato cultivars grown in this area are considered susceptible to *G. pallida* potentially driving up nematode densities (Carrión and Rojas, 2013; Table 1 and Fig. 1).

To provide information about *Globodera* spp. associated with potato in Colombia, a survey was conducted in the main commercial potato-producing regions from 2013 to 2017. Nine departments were sampled including Cundinamarca, Boyaca, Antioquia, Nariño, Santander, Norte de Santander, Tolima, Caldas, and Cauca, with a total of 589 soil samples

collected and analyzed by the Laboratory of Microbiology at the Corporación Colombiana de Investigación Agropecuaria (AGROSAVIA), Cundinamarca. Potato cyst nematodes were detected in 355 fields (60%) with densities ranging from 1 to 1,327 cysts/100 cm³ of soil. *Globodera pallida* was the predominant species identified in the nine departments with positive samples ranging from 72% in Nariño to 14% of field samples in Caldas. Egg viability ranged from 15 to 80%. Boyaca and Cundinamarca were the departments that had on average higher cyst viability. All nematode populations but one were identified as *G. pallida*. *Globodera rostochiensis* was detected in a field from Cundinamarca, but it was not confirmed. These results demonstrate that *G. pallida* has spread into new regions of Colombia such as Antioquia, Caldas, Tolima, Santander, and Norte de Santander (Vallejo *et al.*, 2021; Table 1 and Fig. 1).

In Ecuador, *G. pallida* is the most prevalent species in potato-growing areas. *Globodera pallida* was first reported in potato and onion fields in the Ecuadorian highlands (Bridge, 1976), as well as in the province of Pichincha (Canto and Scurrah, 1976). Interestingly, Baeza in 1972 reported the presence of *G. rostochiensis* in potato fields from the province of Carchi. *Globodera pallida* is widely distributed in the Ecuadorian Andean region, and there are few potato-growing areas free of this nematode. High levels of infestation have been reported in central and southern regions of Ecuador, in the provinces of Pichincha, Cotopaxi, Tungurahua, and Chimborazo, medium level of infestation in the provinces of Cañar and Bolívar and low levels of infestation have been reported in the northern provinces of Carchi and Imbabura (Revelo, 1997a, 1997b; Mejía and Valverde, 2011).

In 1974 the Instituto Nacional de Investigaciones Agropecuarias initiated a survey to establish the prevalence of nematodes on different crops in Ecuador. Soil and root samples from 25 crops were collected from different places of lowlands and highlands from Ecuador to identify nematodes. Cysts and juveniles collected from potato soil and roots from Tungurahua, Carchi, Pichincha and Chimborazo Provinces were identified as *G. pallida* (Bridge, 1976; Table 1 and Fig. 1).

A study was carried out to characterize PCN morphologically and molecularly in 29 localities from the province of Carchi. *Globodera pallida*

was identified in all the soil samples, and all samples were positives using *Globodera* specific primers. *Globodera pallida* was the only species identified in the areas sampled (Llumiquinga *et al.*, 2015; Table 1 and Fig. 1).

In Chile, *G. rostochiensis* is the most widespread species. *Globodera rostochiensis* was first reported in potato fields from La Ligua in 1973 (Moreno *et al.*, 1984). Moreno *et al.* (1984) reported the occurrence of *G. pallida* and *G. rostochiensis* in soil samples collected from potato-growing areas across Chile. *Globodera rostochiensis* was widely distributed in the northern provinces while *G. pallida* was initially identified in La Ligua in central Chile (province of Petorca, Valparaiso Region). In 1974, *G. rostochiensis* was reported in the province of Elqui (Coquimbo Region), a region of intensive potato cultivation (Guglielmetti and Guiñez, 1982). Moreover, *G. rostochiensis* was reported in other areas from Tarapaca, Antofagasta, Coquimbo and Valparaiso Regions. One of the infested areas, La Serena (Coquimbo region), is a major potato-producing region (Moreno *et al.*, 1984; Fernandez, 1988). During 2000 to 2001, the Servicio Agrícola y Ganadero de Chile (SAG) detected *G. pallida* for first time in native and commercial potato fields of the southernmost area of Chile from Magallanes and Antarctic regions (Moreno-Lehuedé and Mansilla, 2005). In 2012, *G. rostochiensis* was identified in the north, in the province of Arauco, and also detected in the southern regions of Los Rios and Los Lagos, which are the principal seed-producing regions for the country (Moreno-Lehuedé, 2013; Peña *et al.*, 2013; Brintrup, 2016). In 2017, SAG reported new infestations of *G. pallida* and *G. rostochiensis* in potato fields from the Rilán Peninsula (province of Chiloé, Los Lagos Region), where there are around 18,000 potato producers in the region and 50% of them are in Chiloé, where there are many native potatoes cultivars (SAG, 2017). Additionally, a *Globodera* population from Antofagasta, Chile, showed a high degree of molecular similarity with *G. ellingtonae* populations from Salta (Argentina) and Oregon (USA), suggesting that they belong to the same species (Subbotin *et al.*, 2011; Lax *et al.*, 2014; Zasada *et al.*, 2018). Since 2010, the National Potato Health Program of SAG is using molecular identification techniques for *G. pallida* and *G. rostochiensis* to monitor areas free of quarantine pests through the isolation of detected infestation

points. Recently, in northern Chile, (18° and 23° south latitude) a *Globodera* spp. has been detected but could not be identified as *G. pallida*, *G. rostochiensis*, or *G. ellingtonae*, while in southern Chile (53° south latitude) *G. pallida* was identified in small home gardens (Pacheco *et al.*, 2018). When evaluating *Globodera* in Chile, caution should be applied to species identification, especially if the presence of a potentially uncharacterized species is validated.

In Venezuela, both *G. pallida* and *G. rostochiensis* have been observed, but *G. rostochiensis* is the predominant species (Casanova *et al.*, 2012). *Globodera rostochiensis* was first reported in 1970 in potato fields from Estado de Mérida and Táchira (Dao and González, 1971). After this initial report, surveys for *G. rostochiensis* were conducted in potato fields from Mérida, Táchira, Trujillo, Lara, and Carabobo States, however, infestations were only detected in Mérida and Táchira States (González and Dao, 1973). *Globodera rostochiensis* has been detected in potato-producing areas in the highland of the Andes including the states of Lara, Trujillo, and other areas from Mérida and Táchira states (Salinas, 1974; Añez and Tavira, 1983; Greco and Crozzoli, 1995; Jiménez *et al.*, 2000; Crozzoli, 2002; Anaya *et al.*, 2005; Crozzoli and Jiménez-Pérez, 2015; Subbotin *et al.*, 2019). In 2007, *G. rostochiensis* was reported in new areas from Lara state (Jiménez-Pérez *et al.*, 2007). *Globodera pallida* has also been reported in Táchira and Mérida (Matos and Canto-Sáenz, 1993; Cassanova *et al.*, 2012; Crozzoli and Jiménez-Pérez, 2015).

In 1970, in order to determine the presence of *G. rostochiensis* in Venezuela, samples were evaluated from 79 potato farms from Táchira, Mérida, Trujillo, Lara, Carabobo, and Yaracuy states. Around 90% of potato farms were between 1-20 ha. *Globodera rostochiensis* was detected in 52% of potato farms from Táchira and Mérida States. These states have a temperate climate and are between 2,000-3,000 masl. In the other states *G. rostochiensis* was not detected. High average cyst viability per 200 cm³ soil was detected mainly in farms from Mérida and Táchira States and was associated with damage to the potato crop according to visual inspections (Dao and González, 1971; Table 1 and Fig. 1).

In Venezuela, 1,060 samples were collected from Lara State in order to identify plant-parasitic nematodes associated with potato cultivation and to

determinate *G. rostochiensis* pathotypes. Soil and potato root samples were collected from five localities that covered 4,500 ha of cultivation. Eleven species of plant-parasitic nematode and one species not identified from *Aphelenchoides* were detected in the samples. The species with highest frequencies were *G. rostochiensis*, *Meloidogyne incognita*, *Pratylenchus brachyurus*, and *Rotylenchulus reniformis*. However, *G. rostochiensis* was only detected in three localities: Andrés Eloy Blanco, Morán, and Jiménez. The majority of *G. rostochiensis* populations were detected on potato 'Andinita' from Jimenez locality, with an average of 77 eggs/100cm³ soil and 130 J2/10 g of root. In this locality, it was observed that producers often use small tubers as seed for the next crop cycle, which could lead to an increase in nematode densities if the small tubers were contaminated with cysts (Jiménez-Pérez *et al.*, 2007; Table 1 and Fig. 1).

In Venezuela PCN were evaluated in potato fields from Lara, Merida, Tachira, and Tujillo States. The area survey included 16 potato-producing farms (4 per each state) with 20 subsamples collected randomly from each farm. Forty-nine PCN populations were selected for species identification. *Globodera rostochiensis* was identified in 44 samples (90%) and *G. pallida* in only 5 (10%) of the samples. *Globodera pallida* was detected only in samples from Merida state, while *G. rostochiensis* was detected in all the states evaluated. These results confirm the presence of *G. pallida* in Venezuela, although it occurs less frequently than *G. rostochiensis* (Casanova *et al.*, 2012; Table 1 and Fig. 1).

In Argentina, *G. rostochiensis* was first reported in a garlic field in the western part of the country in 1956 (Moreno, 1956). Since then, it has been reported in wild potatoes in the Andean Province of Jujuy (Brücher, 1961), and in potato fields of the western mountainous region, in the province of Catamarca (Virsoo, 1967). However, soil surveys from many different regions showed no evidence of *G. rostochiensis*, suggesting that this species is not widely distributed in Argentina (Del Toro *et al.*, 1994; Doucet and De Doucet, 1997; Mondino *et al.*, 2006). *Globodera pallida* was first detected in the province of Salta infecting roots of two potato cultivars 'Colorada' and 'Ojosa' (Doucet and Lax, 2005; Lax *et al.*, 2005). Furthermore, PCN were detected in others potato varieties from the provinces of Salta and Jujuy (Lax

et al., 2006, 2008). According to reports from the European and Mediterranean Plant Protection Organization (EPPO) in 2020, *G. pallida* is present in Argentina but with few occurrences (EPPO, 2020). In 2011, phylogenetic analysis suggests *G. ellingtonae* was detected in Argentina and Chile (Skantar *et al.*, 2011). Additionally, in 2014, *G. ellingtonae* was identified in potato roots from northern Argentina (Lax *et al.*, 2014). This population collected from the province of Salta was morphologically similar to a *G. ellingtonae* population from Oregon, which was first described in 2011 and 2012 (Handoo *et al.*, 2012; Skantar *et al.*, 2011). Phylogenetic analysis from species and populations of PCN from 23 countries suggested that the southern Andean region could be considered as a center of origin for *G. rostochiensis*, *G. ellingtonae*, *G. tabacum*, and could potentially include uncharacterized species. Moreover, northwest Argentina could be considered the center of origin and diversification for *G. ellingtonae* (Subbotin *et al.*, 2019).

In Argentina in 1993, soil samples were analyzed from 200 ha of the major potato-producing area southeast of Buenos Aires to identify plant-parasitic nematodes. *Globodera rostochiensis* and *G. pallida* were not found in any soil samples. However, *Meloidogyne hapla* and *M. incognita* were the most important nematodes detected parasitizing potatoes, and although they were widespread, potato yield and quality appeared to be unaffected. Additionally, *N. aberrans* was found for the first time parasitizing tuber progeny from certified seed in Tucumán (Chavez and Torres, 1993). During 1992 to 1993, potato, garlic, and onion fields were evaluated from the province of Mendoza to establish the absence of *G. rostochiensis* to allow international export. The annual cultivated area consisted of 4,500 ha and 33% of the area was evaluated. *Globodera rostochiensis* was not identified (Del Toro *et al.*, 1994).

In 2001, a survey was carried out in the Andean valleys of the province of Jujuy, Argentina, in order to investigate the distribution of nematodes in potato fields, as well as identify the genera and abundance of plant-parasitic nematodes. Twenty-six farmer's fields were sampled ranging from 2,300-3,800 masl. At the sites analyzed, 66 genera of nematodes were identified, including *Meloidogyne* (73%), *Pratylenchus* (69%), and *Nacobbus* (61%), which

were widespread throughout the area. *Globodera rostochiensis* was not found from any of sites analyzed, however *G. tabacum* was found at four sites (Mondino *et al.*, 2006).

In Argentina, 65 Andean tuber samples were collected from local markets. These samples correspond to the 2004-2005 crop cycle and were harvested in February and March 2005. Samples consisted of 25 potato cultivars, two varieties of papalisa (*Ullucus tuberosa*) and three oca (*Oxalis tuberosa*). The objective was to evaluate plant-parasitic nematodes from different areas of Argentina (provinces of Jujuy and Salta) and Bolivia (departments of Cochabamba and Tarija). Plant-parasitic nematodes were detected in 57% of the samples analyzed. *Nacobbus aberrans* was the species most frequently found (51%). Globose females with egg masses of *M. incognita* and *M. javanica* were detected in 8% and 9% of potato samples, respectively. Potato cyst nematode cysts were extracted from potato 'Collareja' from the province of Salta. 'Collareja' is one of the most widely grown potato cultivars in northwestern Argentina (Lax *et al.*, 2006). This cultivar has been shown to be highly susceptible to *N. aberrans* (90%), *M. javanica* (40%), and PCN (20%), with some samples found to be simultaneously infected by *N. aberrans* and PCN or *N. aberrans* and *M. javanica* (Lax *et al.*, 2006; Table 1 and Fig. 1).

Similar to the above trial, a total of 60 Andean tuber samples were collected from local markets, agricultural fairs, and grower fields in 27 localities from northwestern Argentina (provinces of Jujuy and Salta) and central southern Bolivia (departments of Cochabamba, Potosi, Santa Cruz and Tarija) to determine the presence of nematodes in the periderm and underlying parenchyma of tubers. These samples corresponded to the 2005-2006 crop cycle, which was harvested in February and March 2006. The samples consisted of 19 cultivars of Andean potato, 2 varieties of papalisa, and 2 varieties of oca. Plant-parasitic nematodes were detected in 60% of the samples. *Nacobbus aberrans* was the species most frequently found (45%), especially in tubers from province of Jujuy. *Meloidogyne incognita* and *M. javanica* were detected in 15% of samples analyzed. Potato cyst nematode cysts were found on the periderm of potato cultivars 'Naviceña' and 'Colorada' from the province of Jujuy. *Pratylenchus* sp. and *Helicotylenchus* sp. were detected in potato tubers from the department of

Cochabamba. Moreover, *N. aberrans* and *Pratylenchus* sp. were found in papalisa samples from Cochabamba. None of the oca samples had plant-parasitic nematodes. Combinations of nematodes were also observed on tubers including *N. aberrans* – *Meloidogyne* sp., *N. aberrans* – *Pratylenchus* sp., *N. aberrans* – PCN, and *Meloidogyne* sp. – PCN (Lax *et al.*, 2008; Table 1 and Fig. 1).

Conclusion

The information presented in this review shows that PCN are widespread across the main potato-growing countries of South America where potato is a principal crop for food security and income generation, especially for small farms. *Globodera pallida* is widely distributed, while *G. rostochiensis* occurs across a more limited area but is still present in many countries (Table 1 and Fig. 1). Historically, PCN distribution in South America was described with *G. pallida* north of Lake Titicaca and *G. rostochiensis* south, the division occurring at 15.6°S (Evans *et al.* 1975; Grenier *et al.*, 2010), while more recent analysis suggests the two species overlap considerably in the larger area surrounding Lake Titicaca (Thevenoux *et al.* 2020). This review clearly shows that currently both species are documented north and south of the historical demarcation line, furthermore a third PCN species, *Globodera ellingtonae*, has been identified (Skantar *et al.*, 2011; Handoo *et al.* 2012; Lax *et al.*, 2014.). The reader should keep in mind that historical and modern distributions of PCN likely reflect human-driven distribution occurring in the intervening years. At the same time, species identification techniques have greatly improved over the years. Moreover, this review provides new information about the status and prevalence of PCN species associated with cultivated potatoes in the main potato-producing Andean region. Considering the presence of PCN species constitutes a threat to potato production, intensive sampling and monitoring of these nematodes should be conducted in order to reduce and prevent spread into new areas, especially in material destined for seed. The information provided here provides a baseline review of PCN in the Andean region onto which new infestations can be added. There is a need to create greater awareness with farmers on the importance of using certified seed, practicing crop rotations and adopting PCN

resistant cultivars, which are crucial steps to reduce PCN population densities. The information provided here could assist in making research decisions related to PCN control or containment.

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