

Solanum* Tuber-bearing Species Resistance Behavior Against *Nacobbus aberrans

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Abstract: *Nacobbus aberrans* is a major pest of the potato crop in the Andean regions of Argentina, Bolivia, and Perú. It is endemic in northwest Argentina and is also found in lowlands. The resistance of eleven Andean potato landraces and three accessions of the wild tuber-bearing species *Solanum acaule*, *S. infundibuliforme*, and *S. megistacrobium* were evaluated against a population of *N. aberrans* from Coctaca, Jujuy province, while *Solanum tuberosum* ssp. *tuberosum* ‘Spunta’, ‘Kennebec’, and ‘Frital INTA’ were evaluated against a population from the southeast of Buenos Aires province. The presence, the number of galls, and the number of individuals were recorded. In addition, a reproduction factor was calculated and races were determined. Results showed that the *N. aberrans* population from Coctaca corresponded to race 2 and the population from the lowlands belonged to the sugar beet group. Landrace Azul, one genotype of *S. megistacrobium*, and two genotypes of *S. acaule* showed resistance towards the race from Coctaca while no infection was recorded in potato cultivars with the *Nacobbus* race from the lowland area.

Key words: Andean potato landrace, *Nacobbus aberrans*, resistance, *Solanum* species, wild tuber-bearing species.

The false root-knot nematode, *Nacobbus aberrans* (Thorne, 1935) Thorne & Allen, 1944, native to North and South America (Inserra et al., 1985), causes damage to potato crops in Andean regions of Argentina, Bolivia, and Peru, destroying up to 90% of the production (Brodie, 1984). In Argentina, *N. aberrans* is widely distributed, being endemic in Andean regions of the northwest such as Jujuy, Tucumán, and Catamarca provinces (Chaves, 1980, 2003), and is also found in lowland areas of the southeast of Buenos Aires province parasitizing tomato (Chaves and Sisler, 1980), but it is unknown whether these populations parasitize potato. It is considered a quarantine plague A1 for Brazil, Paraguay, and Uruguay. Since 1999, the National Institute of Seeds of Argentina (INASE) established nil tolerance for this species in all seed potato categories (Chaves and Torres, 2001). *N. aberrans* also parasitizes numerous weed and other horticultural species (Inserra et al., 1985; <http://nematode.unl.edu/pest27.htm>; Stone and Burrows, 1985).

N. aberrans life cycle comprises the egg, four larval stages (J1, J2, J3, and J4), adult male, immature vermiform female, and saccate adult female. Second stage juveniles (J2) are the infective stage, penetrating host roots where they move intracellularly, feeding for a short while before leaving to re-enter elsewhere. Gall formation is initiated by immature female feeding behavior that re-establishes feeding sites in other roots near the vascular strand to continue development (Clark, 1967). Temperature determines the length of the life cycle, taking 37 to 48 d at 22 to 24°C (Costilla, 1985).

N. aberrans populations have variable behavior, not only in relation to host preferences but also in terms of their aggressiveness (Costilla, 1985; Inserra et al., 1985; Doucet and Di Rienzo, 1991; Baldwin and Cap, 1992; Ibrahim et al., 1997). In nematology the term “race” has been used to identify such variations (Trudgill, 1991). Dropkin (1988) favored a phenotypic basis for race identification and suggested that it could be reliably distinguished in improved standard tests where it would be possible to recognize the nematode reproduction/host plant status by the distinguishing criteria of its host range. Castiblanco et al. (1999) established a classificatory scheme for the identification of five races of *N. aberrans* by considering the presence or absence of nodules on the roots of four differential hosts through differential host preferences. Inserra et al., (1985) distinguish at least three major physiological races: the sugarbeet, the potato, and the pepper nematodes. The Society of Nematologists mentions that based on different host preferences, *N. aberrans* populations can be separated into sugarbeet, potato, and bean groups (<http://nematode.unl.edu/pest27.htm>). In Argentina, Chaves and Torres (2001) were the first to find *N. aberrans* populations on potato in Choele-Choel, Rio Negro, Fighiera, Santa Fé, South and Centre of the country, and estimated that Argentina has at least two groups of this nematode.

The main crop potato (*Solanum tuberosum* L.) is cultivated in the southeast of Buenos Aires province as well as in other parts of Argentina. *Solanum tuberosum* ssp. *andigenum* (Juz & Bukasov) Hawkes (2n = 4x = 48) landraces are widely distributed in the Andes of South America (Hawkes, 1990; Ochoa, 1990) and in are grown in Jujuy, Salta and Catamarca provinces in Argentina, mainly in high mountain valleys and ravines, between the 2000 and 4000 m regions of the Puna and Prepuna phytogeographical areas (Virsoo, 1954a, 1954b; Hawkes and Hjerting 1969; Okada, 1979; Clausen, 1989; Clausen et al., 2005). Closely related are the wild tuber-bearing species (Hawkes, 1990; Spooner and Hijmans, 2001) widely distributed in America. The species *Solanum acaule* Bitter (2n = 4x = 48), *S. infundibuliforme* Philippi

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($2n = 2x = 24$) and *S. megistacrolobum* Bitter ($2n = 2x = 24$) are frequently found in Jujuy as weeds in potato fields or in their vicinity (Clausen et al., 2005). The Andean landraces Huaca Lajra and Tunti Imilla and the wild species *Solanum sparsipilum* have been cited as resistant to *Nacobbus aberrans* (Inserra et al., 1985).

Plants are defined as resistant to nematodes when multiplication does not occur in spite of root invasion by J2. In contrast, susceptible plants allow invasion, nematode development, and multiplication by fertile adult females.

Intraspecific genetic variation in host range and response to specific resistance genes is high, especially for sexually reproducing plant parasitic nematode species (Williamson and Hussey, 1996).

The objective of this work was to evaluate the resistance behavior in Andean potato landraces and in three wild *Solanum* tuber-bearing species present in Jujuy province against a population of *N. aberrans* from Jujuy, as well as the behavior of *S. tuberosum* ssp. *tuberosum* cultivars in response to a population of *N. aberrans* from southeast Buenos Aires Province.

MATERIALS AND METHODS

Nacobbus aberrans inoculum and race determination: A *N. aberrans* population, identified by Chaves et al. (2006), from the locality of Coctaca (3500 m), Jujuy Province, was employed to evaluate Andean potato landraces and wild *Solanum* tuber-bearing species. Naturally infested soil was collected in winter time from a previously cultivated potato field, following a zig-zag pattern and employing a soil core sampling devise, then kept in plastic bags and protected from direct sunlight and overheating. Before planting, the soil was incubated

for a week at 5°C. A *N. aberrans* population from Buenos Aires province (24 m) was employed to evaluate *S. tuberosum* ssp. *tuberosum* cultivars. Naturally infested soil ($\pm 22^\circ\text{C}$) was collected a week before planting from a previously known infested tomato field. Samples were taken from the root zone and employed without temperature treatment. Races were determined following the Castiblanco et al. (1999) classificatory scheme, employing Andean potato landrace Tuni (*S. tuberosum* ssp. *andigenum*), tomato (*Lycopersicon esculentum*), sugarbeet (*Beta vulgaris*), and pepper (*Capsicum frutescens*) as differential hosts. One plant per 0.5-liter plastic pot was planted in soil prepared with one part naturally infested soil, two parts sterile soil, and one part sterile river sand. A completely randomized design was performed with six replicates per host and the evaluation was performed at the end of the cycle before senescence.

Andean potato landraces: Eleven landraces were evaluated: Astilla Rosada, Azul, Blanca, Blanca Redonda, Chacarera, Collareja, Cuarentona, Rosada, Moradita, Tuni and Tuni Blanca (Table 1). One sprouted tuber per 0.5-liter plastic pot was planted in soil prepared for race determination. A completely randomized design was performed with 18 replicates per landrace. Half of the clones were evaluated after 45 d from planting and the rest at the end of the cycle before senescence.

Wild Solanum tuber-bearing species: Three accessions each of *S. acaule* (acl), *S. infundibuliforme* (ifd), and *S. megistacrolobum* (mga) (Table 1) were evaluated. Botanical seeds were treated with gibberellic acid for 24 hr and germinated under 30°C to 20°C temperatures and 8 hr to 16 hr light/darkness intervals. Fifty seedlings per accession were transplanted after the first true pair of leaves appeared in a 4-liter plastic tray with soil

TABLE 1. Andean potato landraces and wild species. Identification and collecting sites (locality/department, coordinates, altitude).

Andean potato landraces	Identification	Locality/Department	Geographic coordinates	Altitude (m)
Astilla Rosada	CIE 1569	La Poma/La Poma	24°32'S/66°11'W	3602
Azul	CIE 1599	Coctaca/Humahuaca	23°08'S/65°17'W	3227
Blanca	CIE 1595	Quebrada de Lipán/Tumbaya	23°39'S/65°34'W	3076
Blanca Redonda	CIE 1571	La Poma/La Poma	24°32'S/66°11'W	3602
Chacarera	CIE 1607	Coctaca/Humahuaca	23°08'S/65°17'W	3216
Collareja	CIE 621	Iruya/Iruya	22°31'S/65°07'W	3100
Cuarentona	CIE 1570	La Poma/La Poma	24°32'S/66°11'W	3602
Moradita	CCS 1330	Rachaite/Cochinoca	22°59'S/66°09'W	3435
Rosada	CCS 1288	Cieneguillas/Santa Catalina	22°07'S/65°52'W	3727
Tuni	CCS 1185	Palca de Aparzo/Humahuaca	23°06'S/65°10'W	3237
Tuni Blanca	CCS 1199	Palca de Aparzo/Humahuaca	23°07'S/65°08'W	3646
Wild species				
<i>S. acaule</i>	CCS 1180	Aparzo/Humahuaca	23°11'S/65°13'W	3893
<i>S. acaule</i>	CCS 1244	Ojo de Agua/Cochinoca	22°59'S/66°00'W	3557
<i>S. acaule</i>	CCS 1254	Abrapampa/Cochinoca	22°37'S/65°49'W	3557
<i>S. infundibuliforme</i>	CCS 1177	Aparzo/Humahuaca	23°11'S/65°13'W	3893
<i>S. infundibuliforme</i>	CCS 1234	Esquinas Blancas/Humahuaca	22°58'S/65°26'W	3496
<i>S. infundibuliforme</i>	CCS 1436	Quebrada de la Soledad/Humahuaca	23°11'S/65°24'W	3413
<i>S. megistacrolobum</i>	Oka 6727	Pucará/Humahuaca	23°12'S/65°17'W	3500
<i>S. megistacrolobum</i>	Oka 7504	Valle Encantado/Chicoana	25°10'S/65°52'W	3450
<i>S. megistacrolobum</i>	CCS 1214	Aparzo/Humahuaca	23°07'S/65°12'W	3836

prepared for race determination and evaluated after 45 d from planting. Landrace Tuni was employed as a susceptible control and genotypes that did not exhibit galls were micro-propagated in active medium (MS) and transplanted in 0.5-liter plastic pots with soil prepared as above, employing one clone per pot. A completely randomized design was performed with 12 replicates per genotype. Half were evaluated after 45 d from planting and the rest at the end of the cycle before senescence.

S. tuberosum ssp. *tuberosum*: Three cultivars were evaluated: Spunta, Kennebec, and Frital INTA. Tomato was included as susceptible control. One sprouted tuber per 0.5-liter plastic pot was planted in soil prepared for race determination and one tomato seed per pot was sown in equivalent conditions. A completely randomized design was performed with six replicates per cultivar and control. The evaluation was performed at the end of the cycle before senescence.

In all cases, plants were grown in a screen-house. The employed containers were placed in plastic bags and embedded in wet sand to prevent soil overheating ($\leq 24^{\circ}\text{C}$) and nematode density and distribution was assured by mixing. Before incorporating the inoculum, nematodes were extracted following the centrifugation method (Jenkins, 1964) and the number of J2/100 cm³ soil was estimated under a stereoscopic microscope.

Data and statistical analysis: Number of galls and fresh root weight were recorded of roots previously washed under running water. Nematodes were extracted according to Coolen and D’Herde (1972) and the number of juveniles and female adults was estimated under a stereoscopic microscope. Variables employed were number of galls, number of galls per fresh root weight, number of individuals per fresh root weight, and reproduction factor ($R = \text{Pf}/\text{Pi}$), which was calculated by dividing the number of juveniles and adult females at the end of the cycle (Pf) by the number of juveniles and adult females after 45 d (Pi). Analysis of variance and means by least significance difference (LSD, 5%) were

performed using PROC MIXED. Otherwise, the PROC GLM of SAS/STAT, Brown & Forsythe Test, Levene Test, and Shapiro-Wilk Test (Kuehl, 2003) were used.

RESULTS

Race determination: The *Nacobbus aberrans* population from Coctaca corresponded to race 2 (Castiblanco et al., 1999) and it parasitized Tuni, tomato, and sugarbeet, but not pepper. The *N. aberrans* population from the southeast of Buenos Aires province did not correspond to any of the established races: It parasitized tomato and sugarbeet but not Tuni or pepper.

Andean potato landraces: The analysis of the variable number of galls showed that Tuni Blanca and Moradita did not differ in their behavior, having the highest values for this variable and differed significantly only from Azul. All of the other landraces did not differ significantly from each other (Table 2).

The analysis of the number of galls per fresh root weight showed no significant differences among the landraces studied (Table 2).

The analysis of the number of individuals per fresh root weight showed that Blanca and Rosada did not differ in their behavior, presenting high values for this variable. Azul had the lowest value but did not differ from Cuarentona, Moradita, or Collareja. The other landraces presented intermediate values (Table 2).

The analysis of the reproduction factor (Pf/Pi) differentiated three groups. The first group included Blanca Redonda, Astilla Rosada and Blanca. The second group consisted of Collareja, Rosada, Cuarentona, Moradita, and Tuni Blanca with intermediate values, and finally Azul with the lowest value for its reproduction factor, which differed from all of the other landraces (Table 2).

Wild Solanum tuber-bearing species: A total of 26 genotypes belonging to the three species studied escaped the initial infection and did not show galls after 45 d.

TABLE 2. Andean potato landraces means for the no. galls, no. galls per fresh root weight, no. individuals per fresh root weight, and reproduction factor (Pf/Pi).

Andean potato landraces	no. galls	no. galls per fresh root weight	no. individuals per fresh root weight	reproduction factor (Pf/Pi)
Tuni Blanca	399.88 a ^a	35.996 a b c e	214.54 b	2.35 b
Moradita	310.00 a b	20.355 a b d	110.48 c	2.55 b
Blanca Redonda	274.67 b c	28.433 a b c d e f	226.83 b	4.98 a
Astilla Rosada	270.71 b c	34.096 a b c e f	248.14 b	4.80 a
Cuarentona	250.33 b c	41.176 a b c f	90.39 c	2.78 b
Rosada	249.57 b c	36.888 a b c e f	316.61 a b	2.80 b
Chacarera	249.56 b c	16.848 a d	157.45 b	3.69 b
Collareja	248.40 b c	33.203 a b c d e f	123.11 c	2.97 b
Tuni	245.25 b c	17.381 a b d	256.91 b	3.29 b
Blanca	208.14 b c	32.107 a b c e f	379.06 a	4.67 a
Azul	165.50 c	21.848 a b d	37.64 c	1.35 c
LSD $\alpha = 5\%$	111.31	11.376	103.04	0.95

^a Same letter express no statistical difference.

Only 12 genotypes were successfully micropropagated and subjected to a second infection cycle. Variability was observed considering the variables registered and significant differences were detected (Table 3).

The analysis of the number of galls showed that genotype 283 (mga) presented the lowest values and differed significantly from all other genotypes, except from 296 (mga). When the number of galls per fresh root weight was considered, the genotypes formed three groups where five genotypes presented low values and differed significantly from the others (285 (acl), 301 (acl), 284 (acl), 286 (acl), and 302 (acl)). Another genotype, 300 (acl), with a low number of galls, did not differ from the second group of genotypes (Table 3).

The analysis of the number of individuals per fresh root weight showed that genotype 284 (acl), with the lowest value for this variable, did not differ from 283 (mga), and 286 (acl), but differed from all other genotypes studied (Table 3).

The analysis of the reproduction factor showed seven genotypes (284 (acl), 286 (acl), 297 (acl), 302 (acl), 296 (mga), 283 (mga), and 278 (ifd)), with low reproduction factor did not differ from each other. Only 284 (acl), with the lowest value for this variable, differed from the rest (Table 3).

S. tuberosum ssp. *tuberosum*: *S. tuberosum* ssp. *tuberosum* 'Spunta', 'Kennebec', and 'Frital INTA' were not parasitized by the population of *Nacobbus aberrans* from Mar y Sierras, but tomato was parasitized, presenting an average of 97 galls and 648 individuals.

DISCUSSION

The incorporation of natural resistance is a major component of nematode management programs. Resistant cultivars have several advantages over other methods of reducing nematode populations. Nematode resistance genes are present in several crop species

and are an important component in many breeding programs (Roberts, 1992), and wild plant species represent the most important source of host plant resistance genes (<http://plpnemweb.ucdavis.edu/nemaplex/Mangmnt/HPResist.htm>). Huaman (1984) mentions that wild *Solanum* tuber-bearing species and primitive cultivated landraces constitute the principal genetic resource for potato. In this context, the purpose of this work was to evaluate the behavior of Andean potato landraces and wild *Solanum* tuber-bearing species against the false root-knot nematode, *Nacobbus aberrans*, for sources of resistance.

As *N. aberrans* populations behave in a variable way, it is necessary to determine the race so as to properly address the results and assure correct and efficient management of this plague (Doucet and Di Rienzo, 1991). The race determinations carried out in this work showed the existence and geographical distribution of two groups in Argentina. Following the three main groups established by The Society of Nematologists (<http://nematode.unl.edu/pest27.htm>), the population from Coctaca, Jujuy corresponds to the potato group which damages potato as well as sugarbeet, but not pepper. Populations of this group do not occur in the USA, but are common in the highland Andean regions of Argentina. The population from the southeast of Buenos Aires belongs to the sugarbeet group mentioned by The Society of Nematologists (<http://nematode.unl.edu/pest27.htm>), which infects sugarbeet but not potato, with populations in Argentina and the USA. None of the two populations employed parasitized pepper and would not correspond to the pepper race cited by Inserra et al., (1985) and reported to be in Argentina. The existence and geographical distribution of the potato and the sugarbeet groups in Argentina confirms the Chaves and Torres (2001) hypothesis of the existence of at least two biotypes, one that parasites potato and another which parasites other vegetable crops.

TABLE 3. Wild *Solanum* tuber-bearing genotypes means for the no. galls, no. galls per fresh root weight, no. individuals per fresh root weight, and reproduction factor (Pf/Pi).

Wild <i>Solanum</i> tuber-bearing genotypes	no. galls	no. galls per fresh root weight	no. individuals per fresh root weight	reproduction factor (Pf/Pi)
278 – ifd CS 1436	156.75 a ^a	11.38 a	12.13 a	6.31 c d
Tuni – control	110.24 b	10.74 a	13.91 a	7.10 b c
299 – acl CCS 1254	84.80 c	7.00 b	11.85 a b	9.78 b
297 – acl CCS 1254	64.20 c	5.59 b	8.99 c d	4.66 d
298 – acl CCS 1254	61.75 c	5.51 b	12.27 a	17.58 a
285 – acl CCS 1244	56.83 c	2.94 c	9.95 b c	8.60 b c
301 – acl CCS 1254	53.33 c	2.91 c	9.64 c	8.48 b c
284 – acl CCS 1244	51.20 c	2.71 c	5.29 e	3.51 d
286 – acl CCS 1244	47.83 c d	2.37 c	7.05 d e	4.44 d
302 – acl CCS 1180	43.40 c d	2.35 c	8.09 c d	4.98 d
300 – acl CCS 1254	43.00 c d	3.65 b c	9.12 c d	10.30 b
296 – mga CCS 1214	25.40 d e	7.71 b	9.71 c	5.60 c d
283 – mga Oka 6727	15.66 e	5.17 b	6.05 d e	5.85 c d
LSD $\alpha = 5\%$	22.82	0.72	2.07	3.27

^a Same letter express no statistical difference.

Evaluations of Andean potato landraces and wild *Solanum* tuber-bearing species' resistance behavior against a population of *N. aberrans* from Coctaca, Jujuy, showed different results depending on the variable employed. Blanca, when evaluated for number of galls, had one of the lowest values, similar to Azul, which had the best behavior, and when analyzed for number of individuals per root weight, had the highest value, in contrast to Azul, showing opposite behavior, a situation that is observed again for the reproduction factor variable. Azul showed the same behavior for the three variables. This indicates that nematode population increased in Blanca but not in Azul, both having a number of galls at the end of the cycle that did not differ significantly. Similar situations are observed for the other studied landraces as well as for wild genotypes.

Variables referring to root weight, and based on multiplication rate turned out to be effective comparisons and thus allowed differentiation of landraces and wild genotypes based on their resistance behavior. Resistance may depend upon the fact that not every plant contains substances necessary for the development and reproduction of a certain nematode species or contains them in an insufficient amount. This resistance is expressed by the failure of females to reach maturity (Giebel, 1982). Souza and Baldwin (1998) hypothesized that migratory females do not feed and that esophageal gland activity is not triggered until a suitable site for induction of syncytia is located and that no reports suggest that migratory females feed or induce cell or tissue alterations before they become sessile. Presence of galls does not necessarily imply that reproduction has occurred because fertilization happens once galls are already formed. This fact would explain low multiplication rates and the presence of high number of galls.

The Andean potato landrace Azul presents promissory resistance behavior against the population of *Nacobbus aberrans* from Coctaca, Jujuy, with the lowest value for three of the four variables studied. Prior evidence of *N. aberrans* resistance in Andean potato landraces have been cited by different authors (Insera et al., 1985; Finetti Sialer, 1990; Ortuño et al., 2003), but none of them address Azul, the specific population of *N. aberrans* from Coctaca, Jujuy. The site of Coctaca is an old pre-Columbian indigenous settlement where potato cultivations have been carried out over many centuries. Evidence for Andean potato domestication includes the use of potatoes as an effigy in pre-Hispanic pottery (Towle, 1961). Also, terracing as a characteristic practice for land utilization in Coctaca is still visible through its ruins. Andean potato diversity is still evident in cradle areas of domestication, maintained as ancestral varieties or landraces by traditional farmers (Brush et al., 1981).

One genotype of *S. megistacrolobum* (Oka 6727:283) and two of *S. acaule* (CCS 1244: 284-286) present promissory resistance behavior against the population of *N. aberrans* from Coctaca, Jujuy. These species are

common weeds found in Andean potato fields or in their surroundings. It is likely that these species may have developed resistance to this pathogen as they persist year after year in these fields due to their ability to reproduce both asexually and by fruit dispersal. Burdon and Jarosz (1989) mention that populations of wild relatives of crop plants can be viewed as representatives of a wide range of naturally co-evolved host-pathogen associations which have developed a variety of ways of ameliorating the worst effects of disease epidemics. Mode (1958) proposed dual systems of balanced polymorphism in pathogens and their hosts as a necessary condition for co-evolution. Pathogens produce selection pressures in their hosts which leads to changes in host resistance and subsequently in pathogen virulence alleles. From the view point of evolution, it seems that plant resistance to pathogens is initially nonspecific. Susceptibility is built up later on and is specific, formed on the one hand during the process of host selection by the pathogen and on the other hand by its adaptation to the host (Giebel, 1982).

The wild *Solanum* tuber-bearing species *S. vernei*, *S. famatinae*, *S. infundibuliforme*, and *S. gourlayi* have been cited by Hawkes, (1958, 1977) to have resistance against *Globodera* spp. Ruiz De Galarreta et al., (1998) present the result of their assessment where some of 98 accessions of wild *Solanum* species also showed resistance to *Globodera pallida*. Williamson and Hussey (1996) mention *S. bulbocastanum* to have resistance to *Meloidogyne chitwoodi*.

There are no previous records of *S. megistacrolobum* as a source of resistance to *N. aberrans* and this is the first time accessions of *S. acaule* from Ojo de Agua - Cochino, Jujuy were evaluated against a population from Coctaca, Jujuy and found to present promissory resistant behavior.

Resistance and susceptibility are arbitrary, relative terms. The plant in a given environment may be susceptible to one but resistant to another pathotype of the same parasite (Giebel, 1982). This would explain landrace Gendarme cited by Ortuño et al., (2003) as resistant to *N. aberrans* but susceptible to a different race of this nematode. The Andean potato landrace and the three wild genotypes with promissory behavior obtained in this work is specific to the population of *Nacobbus aberrans* from Coctaca, Jujuy.

This work helps to clarify the behavior of *S. tuberosum* ssp *tuberosum* cultivars against a population of *Nacobbus aberrans* from the southeast of Buenos Aires province which was known to parasitize tomato. The results allowed us to determine that this population is not a risk for potato production in this region because it corresponds to a group that does not parasitize potato. Trudgill (1991) mentions the existence of an immune host (i.e. no recognition, invasion, or feeding on the host), especially for very polyphagous species, that, rather than lacking specific susceptibility genes, may possess unrecognized resistance genes.

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