

Response of roots of different plants to the presence of the false root-knot nematode *Nacobbus aberrans*

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Summary. *Nacobbus aberrans* is native to the American continent and produces severe damage to several crops. The response of roots of potato (*Solanum tuberosum*), tomato (*S. lycopersicum*) and weed quinoa (*Chenopodium album*) inoculated with nematodes from the localities Coronel Baigorria (CB) and Río Cuarto (RC) (province of Córdoba, Argentina) was evaluated. Quantitative parameters (number of galls and Gall Index) and qualitative parameters (histological studies that evaluate alterations in root tissues) were determined. The populations differed in their capacity to invade roots. Neither was able to infect potato; the most efficient hosts for CB and RC were quinoa and tomato, respectively. At the histological level, potato did not show symptoms of nematode attack. Hyperplastic tissue in the central cylinder with transformed cells forming syncytia along vascular cells was present in galls of tomato and quinoa. While each population showed preference for a single plant, the histological analyses did not reveal differences between the alterations induced by a single population on the two infested plants, but they did reveal between-population differences in the response of tissues of tomato and weed quinoa to the parasite attack.

Key words: Argentina, false root-knot nematode, histology, plant-parasite relationships, potato, tomato, weed quinoa.

The false root-knot nematode *Nacobbus aberrans* is native to the American continent (Sher, 1970); up to the present the species has been recorded in Argentina, Bolivia, Chile, Ecuador, Mexico, Peru and USA (Manzanilla-López *et al.*, 2002). It is a quarantine organism and is subject to strict pest regulations in various parts of the world (OEPP/EPPO, 1984). In Argentina, the species distribution has expanded significantly since it was first detected in 1977 (Costilla *et al.*, 1977), affecting several horticultural crops, both in the field and in glasshouse conditions (Doucet & Lax, 2005).

Nacobbus aberrans is an endoparasite of roots that induces galls in the tissues of infested plants. It has been cited as a parasite of about 84 plant species belonging to 18 families (Manzanilla-López *et al.*, 2002). Some of its populations exhibit a wide host range (Inserra *et al.*, 1985; Costilla, 1990; Doucet & Lax, 2005).

The nematode induces a number of cellular and histological alterations on infected roots, causing the formation of galls where the parasite feeding site (syncytium) develops. Several histopathological studies have been conducted in different crops, such as potato (*Solanum tuberosum*) (Finetti Sialer, 1990), sugarbeet (*Beta vulgaris*) (Inserra *et al.*, 1983, 1984), tomato (*S. lycopersicum*) (Doucet *et al.*, 1997; Lorenzo *et al.*, 2001; Vovlas *et al.*, 2007), pepper (*Capsicum annuum*) (Lorenzo *et al.*, 2001), eggplant (*S. melongena*) (Doucet *et al.*, 1997) and weeds (Doucet & Ponce de León, 1985; Ponce de León & Doucet, 1989; Tovar *et al.*, 1990; Doucet *et al.*, 1994, 1997, 2005). Evaluations to compare possible differences in the alterations induced by the same population among different plants (Moyetta *et al.*, 2007; Tordable *et al.*, 2007) or between populations on a single host (Tordable *et al.*, 2007) are scarce.

The aim of this work was to analyse the plant-nematode relationship in roots of three plant species inoculated with second-stage juveniles of two Argentine *N. aberrans* populations.

MATERIAL AND METHODS

Nematode populations and plant material.

Nacobbus aberrans populations were obtained from two localities of the department of Río Cuarto (province of Córdoba, Argentina) that are 33 km apart: Coronel Baigorria (CB) and Río Cuarto (RC). CB nematodes were obtained from the weed quinoa (*Chenopodium album*) where it occurs naturally; RC nematodes were extracted from infested pepper roots from a glasshouse in the locality of origin. To obtain the inocula, roots of infested plants were gently washed to remove adhering soil particles. Nematode egg masses present in the galls were extracted under a stereoscopic microscope and placed in Petri dishes with distilled water at room temperature to favour egg hatching. Mobile second-stage juveniles (J2) were recovered with a micropipette and concentrated in a test tube.

Seeds of tomato cv. Platense and weed quinoa were germinated in trays with sterile soil. Seedlings at four-leaf stage were placed individually in plastic containers with 50 g of soil and vermiculite (1:1). Roots were arranged horizontally on this substrate and 100 J2 1.5 ml⁻¹ of water were inoculated with a micropipette. Another 50 g of that substrate was then added to cover the roots. Potato cv. Spunta was obtained by *in vitro* multiplication of plants originated from meristem culture (Roca & Mroginski, 1993). Plants were planted in pots containing sterile soil and vermiculite (1:2) and maintained at 21°C for 15 days to favour development of the root system. After that period, they were transplanted to plastic pots containing 150

g soil and vermiculite (1:1) and the same number of J2 were inoculated following the procedure mentioned above. Six replications per plant were performed. The experiment was conducted at a mean temperature of 21 ± 3°C and a 14-h photoperiod. After 90 days of inoculation, plants were extracted and roots were washed free of adhering mineral particles.

Estimation of Gall Index and statistical analysis. The number of galls (NG) induced by the nematode was counted by observing the roots of each plant under a stereoscopic microscope. Gall Index (GI) was estimated based on a 0 to 5 scale proposed for *Meloidogyne* spp., where: 0 = no galls, 1 = 1-2 galls, 2 = 3-10 galls, 3 = 11-30 galls, 4 = 31-100 galls, and 5 = more than 100 galls per root (Hartman & Sasser, 1985). Data of NG and GI were transformed into log₁₀ (x+1) and subjected to an analysis of variance ($P \leq 0.05$).

Histological studies. Healthy (without galls) and infected (with galls) roots were cut into small segments of about 5 mm in length and fixed in FAA. Then they were dehydrated in a series of ethyl alcohol and xylene baths and embedded in histowax. Serial transverse and longitudinal sections 8 to 10 µm thick were obtained with a rotary microtome. Sections were stained with triple staining (hematoxylin-safranin-fast green) and mounted in Depex (Johansen, 1940; O'Brien & McCully, 1981). Photographs of the exomorphological characteristics were taken with a Canon digital camera mounted on a stereoscopic microscope (SV6 Carl Zeiss). Micrographs were obtained with an AxioPhot Carl Zeiss microscope equipped with an AxioCam HRC camera and AxioVision 4.3 digital image analysis software.

Table 1. Mean value of the number of galls and Gall Index of two *Nacobbus aberrans* populations from Córdoba, Argentina, on three plant species (six replications).

Plant species	Common name	Number of Galls		Gall Index	
		CB	RC	CB	RC
<i>Chenopodium album</i>	Weed quinoa	7.7	0.7	2.2	0.5
<i>Solanum lycopersicum</i>	Tomato cv. Platense	3.0	6.5	1.2	2.0
<i>S. tuberosum</i>	Potato cv. Spunta	0.0	0.0	0.0	0.0

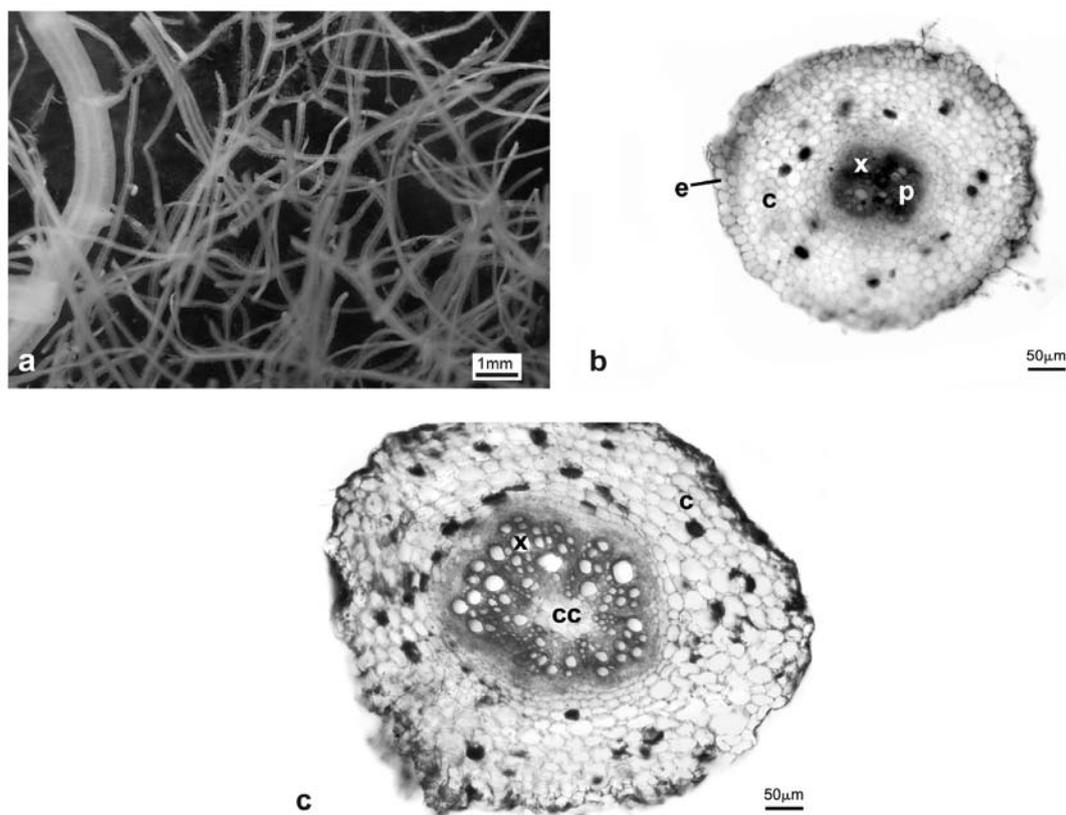


Fig. 1. Histopathology of potato (*Solanum tuberosum*) roots cv. Spunta inoculated with second-stage juveniles of *Nacobbus aberrans* from Coronel Baigorria and Río Cuarto (Córdoba, Argentina). a) External view of lateral roots; b, c) Transverse section of roots; b) Root with incipient secondary growth; c) Root with important development of secondary growth. Abbreviations. c: cortex; cc: central cylinder; e: epidermis; p: phloem; x: xylem.

RESULTS

The analysis of variance of the quantitative parameters (NG and GI) did not show significant differences between nematode populations for a single plant or between plant species for a single population ($P \leq 0.05$). Neither nematode population infested the potato cultivar (GI=0); weed quinoa was the most efficient host for CB population (GI=2.2), whereas tomato was the most efficient host for RC population (GI=2) (Table 1).

Potato. The potato plants did not show external symptoms of attack by either nematode population (Figure 1a). The two typical root zones, cortex and central cylinder, were assessed by means of the histological analysis performed in different root sectors both with primary and secondary growth. Both root zones were organised and composed of non-transformed tissues (Figure 1 b, c); no feeding sites or evidence of the nematode presence was observed.

Tomato. Tomato was infested by the two populations; gall formation was observed in main

and lateral roots (Figure 2, a). At gall level, the histological analysis showed the presence of hyperplastic tissue occupying part of the central cylinder. Cells of this tissue appeared transformed, forming syncytia, which were also composed of parenchymatic cells of vascular tissues. In the central root zone, *N. aberrans* females closely associated with feeding sites were also observed.

CB population. Galls containing between one and three mature females were observed. The hyperplastic tissue and syncytia were distributed in the central zone, producing tissue disorganisation, displacement, and fragmentation (Figure 2, b). Feeding sites developed adjacent to the vascular tissues, whose cells could be either incorporated into the sites or become crushed and broken (Figure 2 c). Feeding sites were composed of numerous cells (more than 30 as observed in a transverse section), of variable shape and different degrees of hypertrophy related to cell differentiation. Poorly-differentiated cells were approximately 26 µm, measured along the long axis and had dense, barely

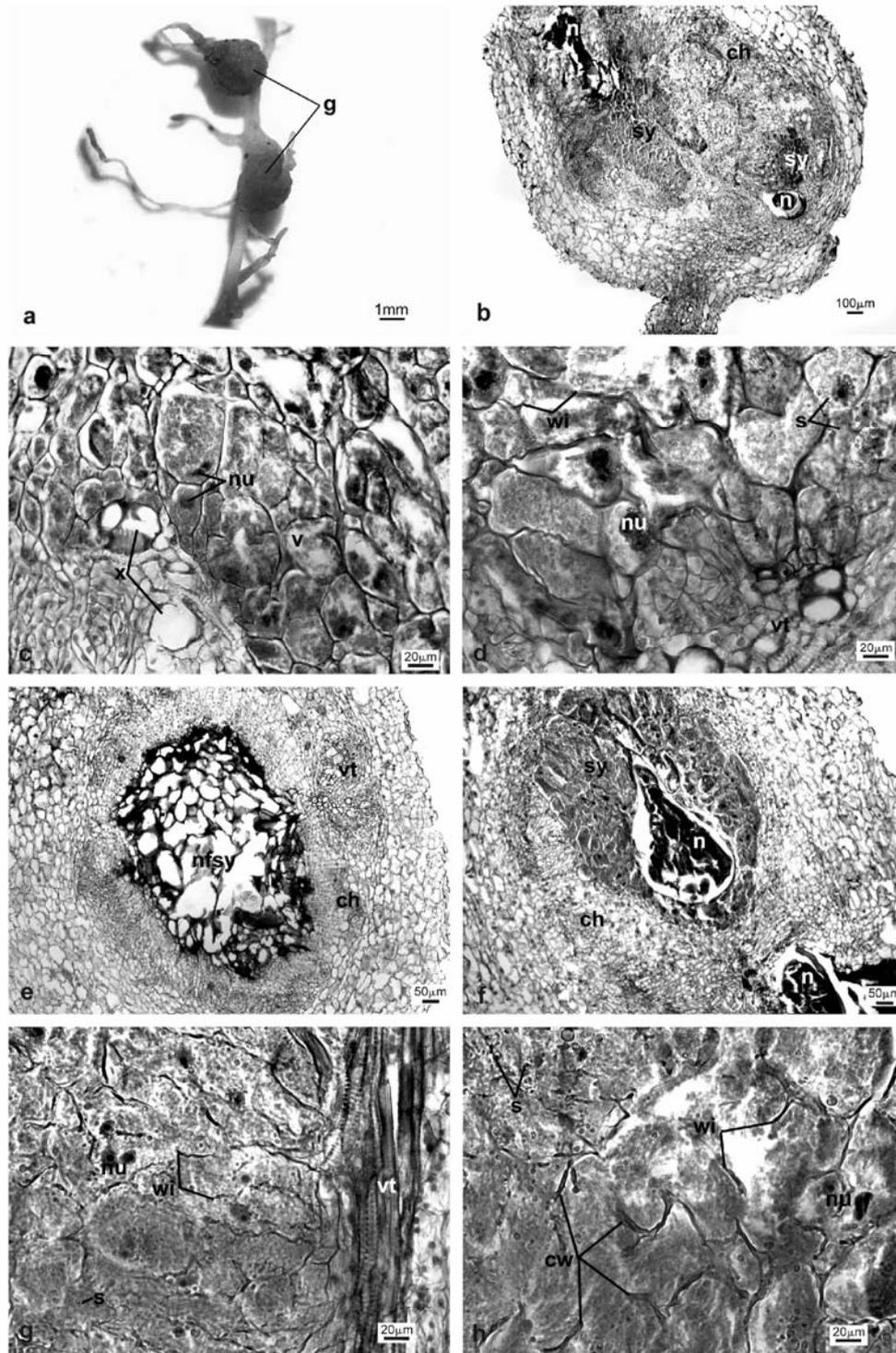


Fig. 2. Anatomical changes induced by *Nacobbus aberrans* populations from Coronel Baigorria (CB) and Río Cuarto (RC) (Córdoba, Argentina) on tomato (*Solanum lycopersicum*) roots cv. Platense. CB Population, a) External view of galls; b) Transverse section of gall with hyperplastic tissue, functional syncytia and nematodes; c) Close view of a sector with crushed and broken xylem cells; d) Close view of a sector showing syncytial features; e) Non-functional syncytium. RC Population, f) Gall with hyperplastic tissue, functional syncytium and nematodes; g, h) Detail of different sectors showing syncytial features. Abbreviations. ch: cellular hyperplasia; cw: cell wall; g: gall; n: nematode; nu: nucleous; nfsy: non-functional syncytium; s: starch; sy: syncytium; v: vacuole; vt: vascular tissues; wi: wall interruption; x: xylem.

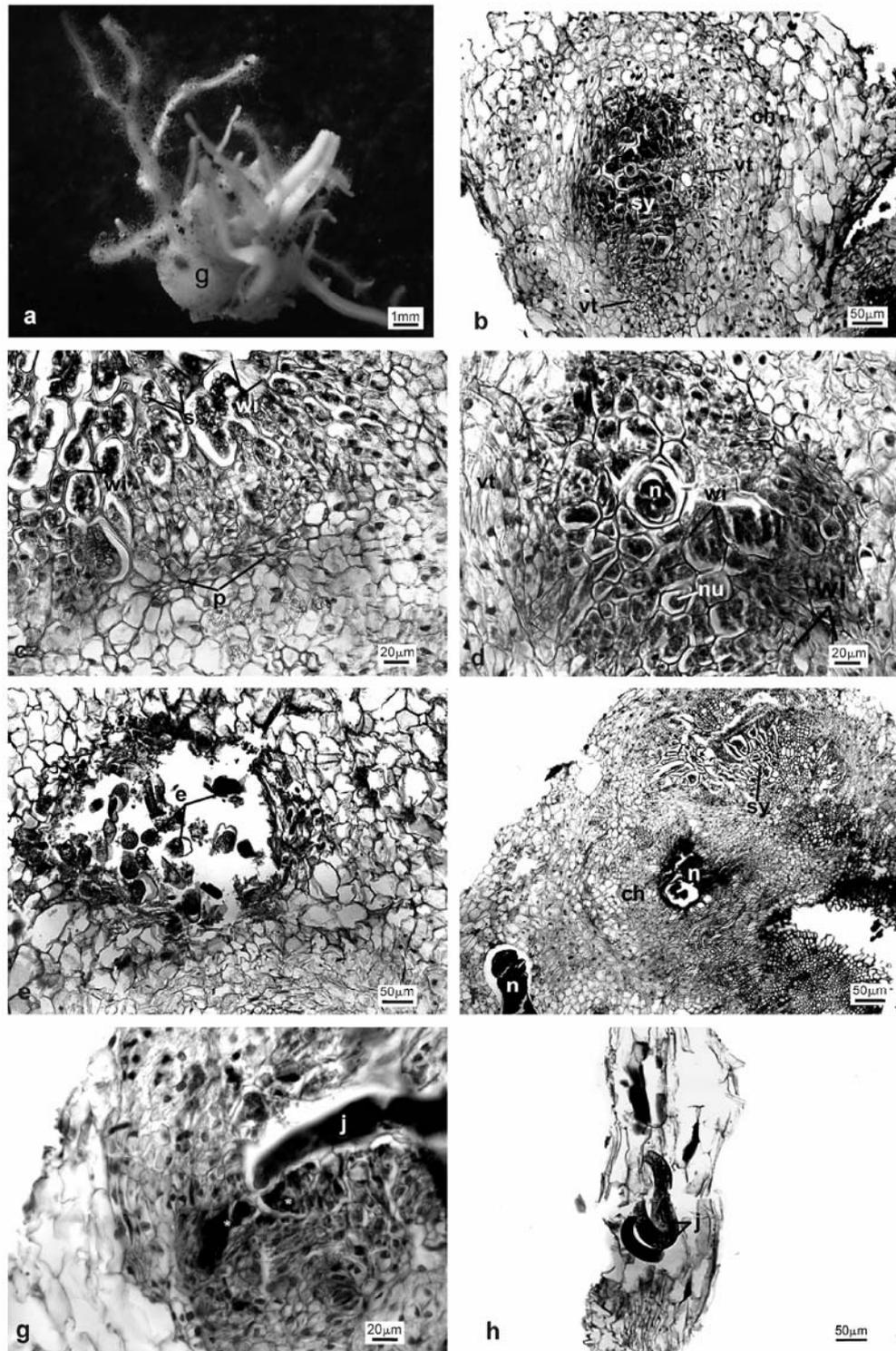


Fig. 3. Anatomical changes induced by *Nacobbus aberrans* populations from Coronel Baigorria (CB) and Río Cuarto (Córdoba, Argentina) on weed quinoa (*Chenopodium album*) roots. CB population, a) External view of galls; b) Transverse section of gall with hyperplastic tissue and functional syncytium; c, d) Close view of a sector showing syncytial features; e) Sector of gall with an egg mass. RC Population, f) Gall with hyperplastic tissue, functional syncytia and nematodes; g) Nematode juvenile stage in a gall and some syncytial cells in differentiation process (asterisk); h) Nematode juvenile stage in lateral root of gall. Abbreviations. ch: cellular hyperplasia; e: eggs; g: gall; j: juvenile; n: nematode; nu: nucleous; p: phloem; s: starch; sy: syncytium; vt: vascular tissues; wi: wall interruption.

vacuolated cytoplasm, some of them with starch grains. The largely-differentiated cells reached 45 μm along the long axis and exhibited a gradual regression of cytoplasm, which was separated from the cell walls and acquired a fibrillar texture (Figure 2 d). In all the cells observed, nuclei were hypertrophied, spherical or lobulated in shape, and contained prominent nucleoli. Cell walls were thin (approximately 2 to 3 μm), cellulosic, and partially fragmented, allowing neighbouring cytoplasm to join. Cells that originated the syncytium, which in some sectors were in contact with the body of females, were crushed and broken by the increasing nematode volume. Walls were thickened (approximately 6 μm) only in these cases. Non-functional syncytia composed of empty cells with somewhat thickened walls were also observed (Figure 2 e). Mature females with their egg masses were found associated with these syncytia.

RC population. Galls with two mature females on them were usually observed (Figure 2 f). During development, feeding sites also occupied the central zone of galls and syncytial characteristics were similar to those described in tomato attacked by the CB population. Cell walls in these syncytia, however, were thicker (approximately 6 μm), maintained their cellulosic nature, and were notably fragmented in wide sectors, which hindered individualisation of the most transformed cells (Figure 2 g, h).

Weed quinoa. Populations attacked quinoa, galls being detected both in main and lateral roots (Figure 3 a).

CB population. Galls with a female in the central zone associated with the feeding site were observed. The main effects of syncytia formation were displacement and separation of vascular tissues (Figure 3, b). As a consequence, some sections revealed that syncytium development caused a withdrawal of the phloem towards the periphery of the area, losing connection with the xylem in these sectors (Figure 3 c). During their formation, syncytia incorporated xylem cells, causing a reduction of this tissue enhanced by the interruption of the vascular cambium. Cells that originated the syncytium were slightly hypertrophied (15 μm in diameter) and maintained their shape and individuality because the walls, of cellulosic nature, exhibited partial interruptions or dissolutions in a few sectors. Syncytial cytoplasm was very dense, with scarce vacuolisation and starch, and had the particular feature of detaching from the cell walls in large sectors (Figure 3 c, d). Non-functional syncytia were composed of empty cells with thick walls, reaching approximately 9 μm in some sectors; mature females with their egg masses embedded in

the gall tissues were observed associated with those non-functional syncytia (Figure 3 e).

RC population. Galls with marked proliferation of lateral roots were observed. Although these galls held established mature females and syncytia similar to those observed associated with the CB population (Figure 3 f), the presence of juvenile stages in different gall sectors was remarkable. Some syncytial cells with thick (approximately 6 to 7 μm) and lignified walls were observed closely associated with the anterior portion of nematode juvenile stages (Figure 3 g). Juveniles inside the lateral roots were also observed (Figure 3 h).

DISCUSSION

Although the two *N. aberrans* populations considered were at a relatively short distance, they showed different behaviour towards the same plant and a clear preference for a given host. Furthermore, the invading capacity of each population also differed between the three plant species. This can be considered as an indicator of the physiological variability of different populations of the nematode, suggesting the existence of races/groups within the species (Inserra *et al.*, 1985; Costilla, 1990; Manzanilla-López *et al.*, 2002).

The histological and cytological features of syncytia in infested tomato and weed quinoa are, in general, consistent with features already mentioned for other Argentine *N. aberrans* populations parasitising the same plants (Doucet & Ponce de León, 1985; Doucet *et al.*, 1997; Lorenzo *et al.*, 2001; Vovlas *et al.*, 2007). Similar situations were reported for other hosts (Inserra *et al.*, 1983, 1984; Moyetta *et al.*, 2007). In the present analysis, the galls of both hosts exhibited an important amount of hyperplastic tissue in the central cylinder zone, which may be a defence feature (Suárez, 2007). This feature was not recorded in tomato infected by an *N. aberrans* population from the locality of Oliva (province of Córdoba, Argentina) (Lorenzo *et al.*, 2001). Regarding the location of syncytia, both in tomato and quinoa they occupied only the central zone of galls, whereas in previous research conducted on the same hosts, syncytia were detected in cortex and central cylinder (Doucet & Ponce de León, 1985; Doucet *et al.*, 1997; Lorenzo *et al.*, 2001).

In syncytia induced in weed quinoa no cell specialisation features ('wall ingrowths') were observed in the walls adjacent to the xylem, as previously observed in the same host (Doucet *et al.*, 1997). In this work, the scarce amount of starch in syncytial cells was also noticeable, a feature that does not agree with previous observations in this host, in which cells full of starch were found (Doucet *et al.*,

2005). The presence of this carbohydrate is one of the characteristics that distinguish *N. aberrans*-induced feeding sites and might indicate an intense metabolic activity of syncytial cells (Sousa, 2001). The presence of starch-rich amyloplasts in syncytia is among the earliest events in feeding-site formation; these nutrient reserves would be used by the nematode during the reproductive stage (Schuster *et al.*, 1964). Therefore, while syncytia observed in this work remain functional, they may be already composed of fully differentiated and more mature cells.

Although each population showed preference for a single host (tomato in RC and quinoa in CB), at the histological level no differences between alterations induced by a single population on both host plants were observed. However, each host reacted differently to the attack of each population. Tomato roots inoculated with CB juveniles were characterised by the presence of: galls harbouring a larger number of females, central cylinders with greater reduction of vascular tissues, accompanied by conductive elements of the xylem that were broken or had an atypical arrangement, and hypertrophied cells of the vascular cambium with dense cytoplasm and secondary vacuoles being part of the syncytia. This group of features would indicate that the CB population would be more aggressive on tomato than the RC population. This assumption is not consistent with GI values, since the attack of the CB population on tomato was less aggressive. Although these nematodes would be less capable of invading tomato roots, the few individuals that would succeed in penetrating the roots would produce more damage in the tissues, at the histological level, than the other population.

Quinoa roots parasitised by RC individuals were characterised by the presence of juvenile stages in different gall sectors, as well as a pronounced proliferation of lateral roots with the presence of nematodes. This would indicate that the plant is not an efficient host for that nematode population. Once inside the roots, some juveniles might not have continued to develop their life cycle, which accounts for the low GI values recorded. These differences in aggressiveness to a plant observed between populations agree with results recently obtained for CB and RC on pepper cv. California Wonder and sugarbeet cv. Detroit (Tordable *et al.*, 2007). In that work, while both plants were susceptible, RC nematodes were more aggressive in tissues of both hosts.

None of the *N. aberrans* populations was able to invade tissues of the potato cultivar Spunta. However, *S. tuberosum* is an efficient host of other

N. aberrans populations in Argentina, mainly in the provinces of Catamarca and Tucumán (Costilla *et al.*, 1977; Costilla, 1985) and in the northwest of the country it is closely associated with numerous varieties of Andean potato (*S. tuberosum* subsp. *andigenum*) (Lax *et al.*, 2006, 2008). Within the species *N. aberrans*, some groups of populations have been proposed, depending on the plants they are able to infest: *i*) bean (populations that attack beans and pepper but not potato or sugarbeet); *ii*) sugarbeet (populations infecting sugarbeet, pepper, and tomato but not potato); and *iii*) potato (populations that damage potato, sugarbeet, and tomato but not pepper) (Manzanilla-López *et al.*, 2002). The fact that the populations evaluated are capable of infesting pepper and sugarbeet (Tordable *et al.*, 2007), along with the present results, suggests that RC and CB populations would belong to the so called 'sugarbeet group'.

Intraspecific variation in *N. aberrans* affects crop rotation planning, such as the selection of sources of resistance for breeding (Manzanilla-López *et al.*, 2002). Knowing the response of crops to different nematode populations is very important for selecting suitable management strategies. In Argentina, quinoa is a widely distributed weed of great importance for crops both in the field and in the glasshouse. Therefore, in studies of this type it is important to include weeds, since many of them may be excellent reservoirs for the nematode in the absence of a crop (Doucet & Lax, 2005).

The evaluation of the response of 41 species of cultivated and non-cultivated plants to nine populations of *N. aberrans* from different geographical origin showed that roots of some plants that were efficient hosts had an asymptomatic reaction (Castiblanco *et al.*, 1999). However, different stages of the nematode life cycle (females, males and eggs), which are indicators of the normal development of the parasite in the plant, were found inside the tissues. Histological studies are useful to analyse situations like the present one, in which no external symptoms are apparent in the root tissues attacked by the nematode. At the same time, possible differences in the reaction of a single host to different nematode populations can be detected with such studies.

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M. del Carmen Tordable, P. Lax, M. Edmundo Doucet, P. Bima, D. Ramos, L. Vargas. Реакция корней различных растений на поражение нематодами *Nacobbus aberrans*.

Резюме. Нематоды *Nacobbus aberrans* происходят из Южной Америки и причиняют существенный вред различным культурам. Изучена реакция корней картофеля (*Solanum tuberosum*), томатов (*S. lycopersicum*) и чилийской мари (*Chenopodium album*) на инокуляцию нематодами, выделенными в Coronel Baigorria (CB) и Río Cuarto (RC) (обе точки в провинции Córdoba в Аргентине). Определяли количественные (число галлов и индекс галлообразования) и качественные параметры (результаты гистологического исследования тканей корней растений). Две изученные популяции различались по способности поражать корни растений. Ни одна из популяций нематод не была способна поражать картофель, так что наиболее подходящим растением-хозяином для них были томаты и мари. На гистологическом уровне не были выявлены признаки поражения на картофеле. Разрастание ткани в центральном цилиндре корня с трансформацией нормальных клеток в синцитий была выявлена в галлах на томатах и мари. Каждая из изученных популяций наковбусов показала предпочтение одного из видов растений. Гистологическое исследование не выявило различий в строении измененной ткани у двух восприимчивых растений, однако были отмечены различия в характере реакции растений на поражение нематодами из двух разных популяций паразитических нематод.
