Differential histopathological response of pepper (Solanaceae) cultivars to *Nacobbus celatus* (Nematoda) populations

Respuesta histopatológica diferencial de cultivares de pimiento (Solanaceae) a poblaciones de *Nacobbus celatus* (Nematoda)

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Citar este artículo
CABRERA, V. A., M. E. DOUCET & P. LAX. 2024. Differential histopathological response of pepper (Solanaceae) cultivars to *Nacobbus celatus* (Nematoda) populations. *Bol. Soc. Argent. Bot.* 59: 151-159.

DOI: https://doi.org/10.31055/1851.2372.v59.n2.44120

Recibido: 9 Ene 2004
Aceptado: 20 May 2024
Publicado impreso: 30 Jun 2024
Editora: Ana María Gonzalez

ISSN versión impresa 0373-580X
ISSN versión on-line 1851-2372

Summary

Background and aims: The false-root knot nematode (*Nacobbus* spp.) comprises polyphagous species, with pepper (*Capsicum annuum*) being one of the most affected crops. Due to the lack of resistant pepper genotypes, we compared the responses of different commercial cultivars to identify possible plant defence mechanisms against *N. celatus*.

M&M: Nematodes from Río Cuarto (Córdoba Province) and Lisandro Olmos (Buenos Aires Province) were inoculated on pepper cultivars: California Wonder (control), Fyuco INTA, Yatasto, and Fenomeno RZ. Plants were grown under a greenhouse and galls were analysed by histopathological techniques.

Results: The roots of the commercial cultivars showed the typical morpho-anatomical alterations induced by *N. celatus*: gall formation, hyperplasia reactions, development of syncytia in the central cylinder and disorganisation of vascular tissues. Syncytial cells in contact with females of nematodes from Lisandro Olmos showed a defence reaction by Fyuco INTA, whereas feeding sites in Fenomeno RZ did not denote high metabolic activity in nematodes of both origins.

Conclusions: The different responses observed between populations and/or hosts demonstrate the importance of considering nematodes from different geographical origins when testing plant material for tolerance and/or resistance to *N. celatus*. Studies of this nature are necessary since they facilitate a more in-depth understanding of the parasite-plant interaction.

Key words

Capsicum annuum, defence mechanism, false root-knot nematode, histology, syncytium.

Resumen

Introducción y objetivos: El falso nematodo de la agalla (*Nacobbus* spp.) comprende especies polífagas, siendo el pimiento (*Capsicum annuum*) uno de los cultivos más afectados. Debido a la falta de genotipos resistentes del pimiento, comparamos las respuestas de diferentes cultivares comerciales para identificar posibles mecanismos de defensa contra *N. celatus*.

M&M: Nematodos provenientes de Río Cuarto (provincia de Córdoba) y Lisandro Olmos (provincia de Buenos Aires) se inocularon en cultivares de pimiento: California Wonder, Fyuco INTA, Yatasto y Fenomeno RZ. Las plantas se desarrollaron en invernadero y las agallas se analizaron mediante técnicas histopatológicas.

Resultados: Las raíces de los cultivares analizados mostraron las alteraciones morfo-anatómicas típicas inducidas por *N. celatus*: formación de agallas, reacciones de hiperplasia, desarrollo de sincitios en el cilindro central y desorganización de los tejidos vasculares. Las células sincitiales en contacto con hembras de Lisandro Olmos mostraron una reacción de defensa por parte de Fyuco INTA, mientras que los sincitios en Fenomeno RZ denotaron baja actividad metabólica en nematodos de ambas procedencias.

Conclusiones: Las diferencias observadas entre las poblaciones y/o hospedadores demuestran la importancia de considerar nematodos de diferentes orígenes geográficos al analizar material vegetal para determinar su tolerancia y/o resistencia a *N. celatus*. Estudios de esta naturaleza son necesarios ya que facilitan una comprensión más profunda de la interacción parásito-planta.

Palabras clave

Capsicum annuum, histología, falso nematodo de la agalla, mecanismo de defensa, sincitio.

Introduction

The genus *Capsicum* L. belongs to the Solanaceae family and currently includes 43 species; it is native to temperate, subtropical, and tropical regions of the Americas, ranging from the southern United States to central Argentina and Brazil, with the main centre of diversity in the Andes (Barboza *et al*., 2022). This genus comprises a diverse group of sweet and hot peppers, which are consumed by a quarter of the global population (Parvez, 2017). There are five domesticated species, among which *Capsicum annuum* L. stands out for being extensively cultivated worldwide (Barboza *et al*., 2022).

The genus *Nacobbus* Thorne & Allen, 1944 (Phylum Nematoda) is native to the American continent and comprises sedentary endoparasitic species of nematodes with polyphagous habits. Among its wide host range, several species belonging to the Solanaceae family are highlighted, being pepper one of the crops that is severely affected (Lorenzo *et al*., 2001; Manzanilla-López *et al*., 2002; Tordable *et al*., 2010; Lax *et al*., 2016, 2021). The establishment of the immature female on the host root and the development of its feeding site (syncytium) induce the formation of galls (Lax *et al*., 2022). Because of the great damage they cause to agriculture, the *Nacobbus* species are of quarantine importance (EPPO, 2024). These parasites are known as false root-knot nematodes (abbreviation FRKN) because the root symptoms are similar to those produced by the *Meloidogyne* species (root-knot nematodes, abbreviation RKN).

There are no pepper cultivars available that show a certain degree of resistance to *Nacobbus* species (Lax *et al*., 2016; Gómez-Rodríguez *et al*., 2019). For this reason, it is of great importance to evaluate aspects of the parasite-host interaction in different germplasm, even in cases where the nematode succeeds in multiplying, since this may reveal patterns of plant defence against the pathogen. Histology is an efficient resource in infection processes, helping to elucidate penetration and colonisation events, and can reveal structural host defence mechanisms (Bentes & Matsuoka, 2005; Petitot *et al*., 2017; Lopes *et al*., 2020). The reaction to FRKN infection of different commercial and/or experimental pepper lines, some carrying RKN-resistance genes, has been poorly evaluated previously (Lax *et al*., 2006, 2016; Gómez-Rodríguez *et al*., 2019), and, in limited situations, the histopathology of the interaction was considered (Moyetta *et al*., 2007).

Argentina is the main pepper producer in South America, with some 6,000 ha under cultivation and an annual production of approximately 153,000 tonnes (FAO, 2022). In the country, nematode *N. celatus* (ex *N. aberrans*) is an important pest for this crop grown in the field and greenhouses. To identify potential defence mechanisms of the plant reaction, we analysed and compared the response of commercially available cultivars [Fyuco INTA, Yatasto, and Fenomeno RZ (resistant to *Meloidogyne* spp.)], for which the histopathology of the parasite-host interaction is unknown.

Material and Methods

Nematode populations and plant material

Based on its known aggressiveness to pepper, two Argentine populations of *N. celatus* were selected from the localities of Río Cuarto (abbreviation RC, from Córdoba Province) and Lisandro Olmos (abbreviation LO, from La Plata, Buenos Aires Province). Seeds from commercially available cultivars of *C. annuum* were acquired from the market; commercial names: Fyuco INTA, Yatasto, and Fenomeno RZ (35-615). According to the supplier company, the last cultivar has resistance to RKN species: *Meloidogyne incognita*, *M. javanica*, and *M. arenaria*. California Wonder was also used as a positive control due to its known susceptibility to this nematode (Tordable *et al*., 2007).

Pepper seeds were germinated in sterile soil. A completely randomized experimental design was used with eight plants for each cultivar; single four-leaf stage seedlings were transplanted into pots (20 cm long, 4 cm wide) containing sterile soil and sand (3:1). The roots were placed on this substrate, inoculated with 100 second-stage juveniles/1.5 ml of water and covered with the substrate. Plants developed in a greenhouse (temperature 25 ± 2 °C; photoperiod 14 h) and were uprooted 60 days after inoculation. The radical systems were washed to remove soil particles, fixed in FAA (formalin, glacial acetic acid, ethyl alcohol) for 48 h and transferred to 70% ethyl alcohol. From the different treatments, first-order lateral root galls of the four cultivars and fragments (1 cm) of healthy roots were randomly selected. They were dehydrated in an ascending series of ethyl alcohol and embedded in Histowax. Cross-sections of 8-10 µm thick were made with a rotating microtome and adhered with distilled water to clean slides. After 24 h, the inclusion medium was removed with xylol; the slides were stained with the triple stain (hematoxylin-safranin-permanent green) and mounted in distyrene, tricresyl phosphate and xylene (DPX) (Conn *et al*., 1960; Zarlavsky, 2014). Observations and photographs were taken with a Carl Zeiss Axiophot microscope equipped with an AxioCam HRC camera.

Results

Healthy roots of all tested pepper cultivars exhibited a primary structure, with a normal arrangement of the dermal, fundamental, and vascular tissue systems. In cross-section, the epidermis was unistratified and the cortex presented 3-4 layers of parenchyma, with large cells and a thin wall. The endodermis and pericycle were unistratified, with cells smaller than those in the cortex. The metaxylem was located in the centre, and phloem groups alternate with protoxylem poles (Fig. 1A).

All commercial cultivars tested, as well as the positive control, showed galls measuring 2-4 mm along their long axis, induced by the two *N. celatus* populations (Fig. 1B), with development of the feeding site (syncytium) in the central cylinder (Fig. 1C). The syncytial cells had different shapes, mainly isodiametric or elongated. They were hypertrophic (measuring up to 55 µm along their major axis), with dense or fibrillar cytoplasm containing some vacuoles. The walls were cellulosic, thickened (>5 µm thick) and presented some interruptions, allowing the confluence of the cytoplasm in the syncytium. Nuclei and nucleoli were hypertrophic; on some occasions, nuclei (1 to 3 per syncytial cell) exhibited amoeboid contours (Fig. 1D). Xylem cells were observed immersed in the syncytium, resulting in reduction and fragmentation of the conductive tissue. The phloem, and sometimes also the xylem, was displaced towards the periphery due to the presence of the syncytium and the nematode female (Fig. 1E-F).

Differences were observed between populations, especially with higher development of LO feeding sites. For that population, the syncytial cells in contact with the anterior region of the female showed thickened and lignified walls in Fyuco INTA (Fig. 2A). In the same cultivar infected by RC, only well-developed but non-functional syncytia were found (Fig. 2B) and the presence of abundant numbers of juveniles in the cortex was also noted (Fig. 2C). In galls induced by the RC population on the three commercial cultivars, the development of hyperplastic tissue with parenchymatic features in the central cylinder was prominent (Fig. 2C). In Fenomeno RZ, although the feeding sites of both populations were highly developed, the cytological characteristics did not denote great metabolic activity, since they had low density in their cytoplasmic content and were highly vacuolated (Fig. 2D); the most hypertrophic nuclei were observed in the syncytia related to LO. Table 1 summarizes the main differences observed between the nematode populations and/or the tested commercial cultivars.

Discussion and Conclusions

Histopathological studies provide the basis for investigating the molecular mechanisms underlying specific interactions between different pathogen genotypes and a particular host genotype (Toulet *et al*., 2022). Due to the lack of FRKN-resistant pepper genotypes, it is important to investigate the response of available cultivars for possible sources of resistance that can be used as parents for breeding programmes or potential use as rootstocks. In general, the commercial cultivars and the control showed the root typical morpho-anatomical alterations induced by FRKN in different susceptible hosts, including the pepper: gall formation, hyperplasia reactions, development of syncytia in the central cylinder (Moyetta *et al*., 2007; Tordable *et al*., 2007), and disorganisation of vascular tissues (Lax *et al*., 2013; Cabrera *et al*., 2017; Tordable *et al*., 2018). The main characteristics of the syncytial cells also agreed with previous reports for this nematode, including thickened and interrupted cellulose walls, dense and/or vacuolised cytoplasm, as well as hypertrophic nuclei, and nucleoli (Vovlas *et al*., 2007; Tordable *et al*., 2010; Cabrera *et al*., 2017).

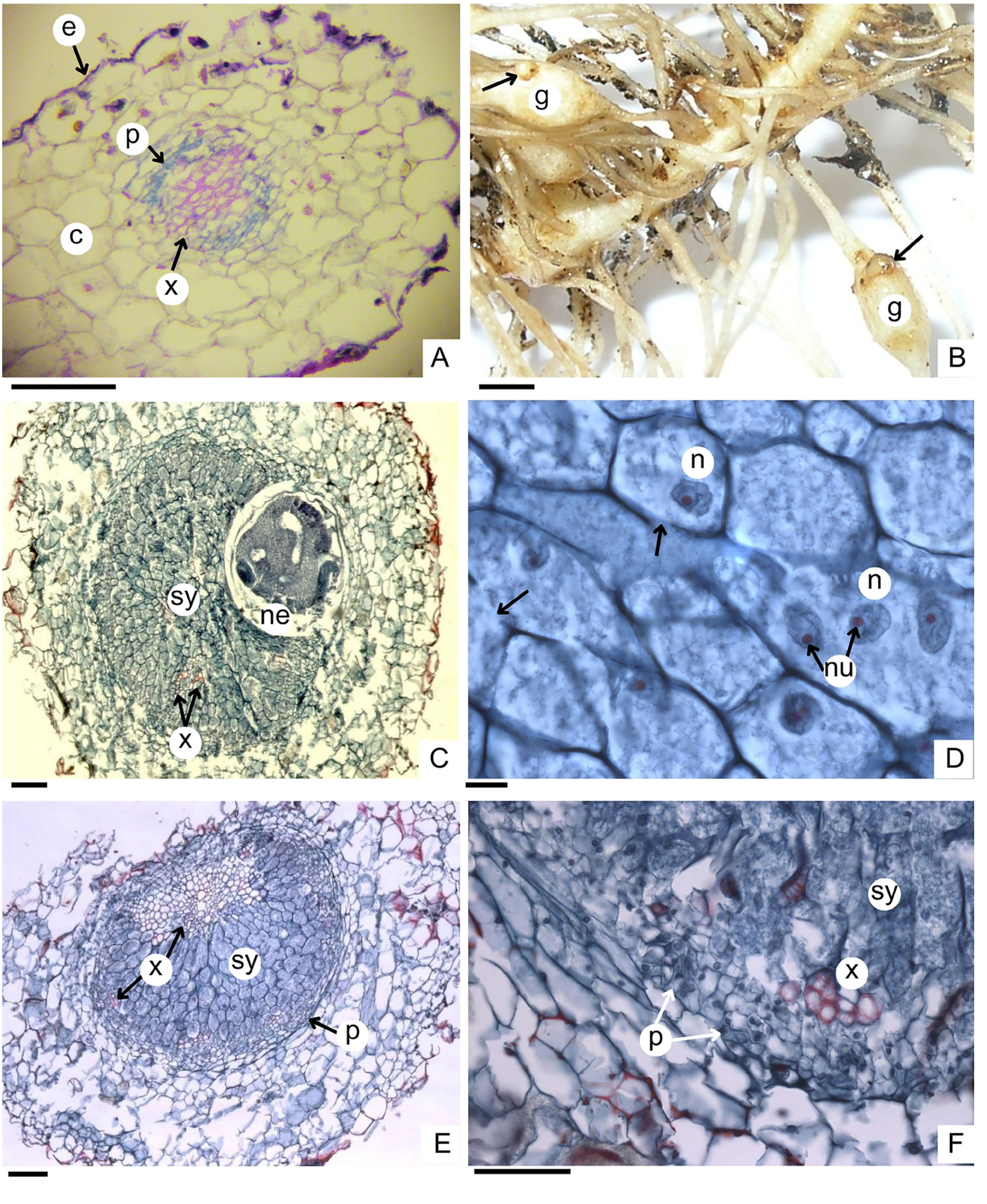

Fig. 1. Histopathological response of pepper, *Capsicum annuum,* cultivars to the nematode *Nacobbus celatus* from Río Cuarto (RC) and Lisandro Olmos (LO) localities. **A**: Healthy root; California Wonder. **B**: Root system with galls, egg masses are marked with arrows; California Wonder-LO. **C**: Gall cross-section containing the female nematode and syncytium; Fyuco INTA-LO. **D**: Detail of the syncytial cells; single arrows indicate interruptions in cell walls; Fyuco INTA-LO. **E**: Xylem reduction and fragmentation; Yatasto-LO. **F**: Phloem displacement and disorganisation; Yatasto-RC. Abbreviations= c: cortex; e: endodermis; g: gall; hy: hyperplastic tissue; n: nucleus; ne: nematode female; nu: nucleolus; p: phloem; sy: syncytium; x: xylem. Scale bars= A: 100 µm; B: 1.5 mm; C: 10 µm; D-F: 100 µm.

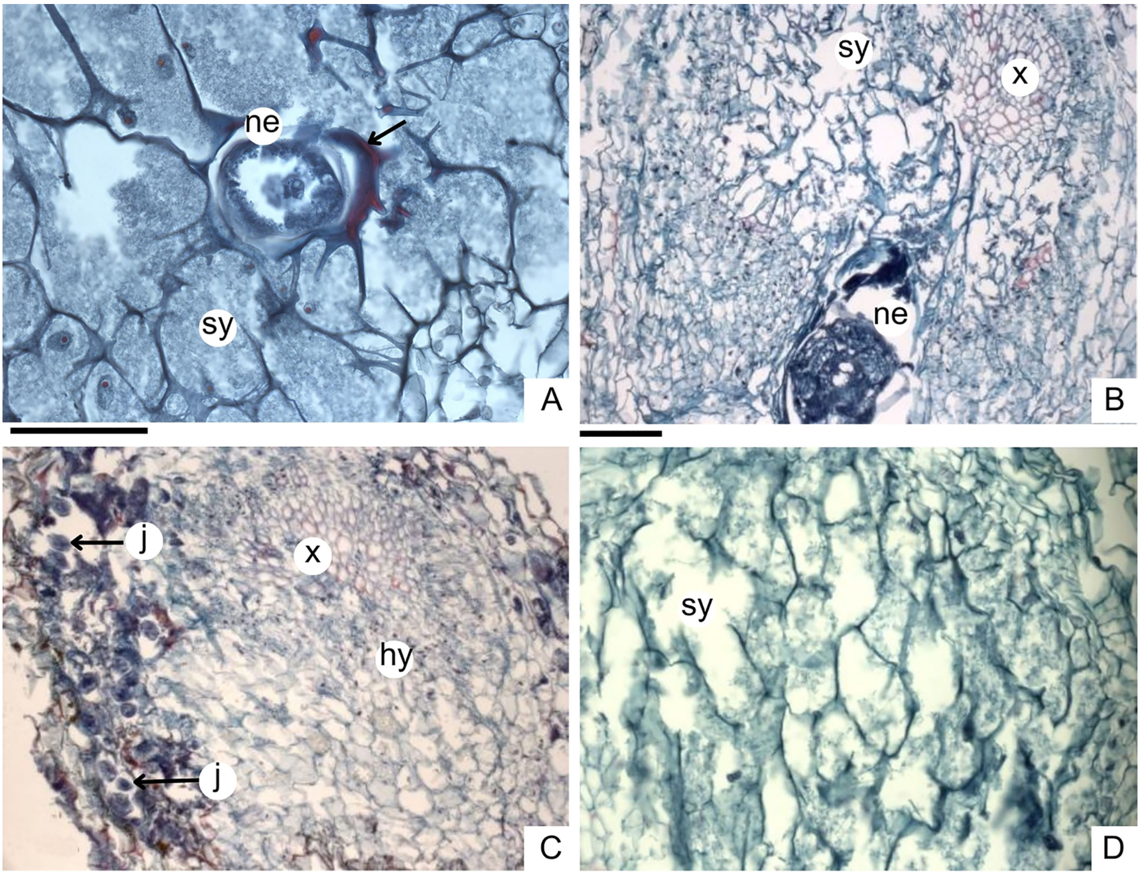

Fig. 2. Histopathological response of pepper, *Capsicum annuum*, cultivars to the nematode *Nacobbus celatus* from Río Cuarto (RC) and Lisandro Olmos (LO) localities. **A**: Syncytial cells with thickened and lignified walls (marked with arrow) around the nematode; Fyuco INTA-LO. **B**: Well-developed but non-functional syncytium; Fyuco INTA-RC. **C**: Nematode juveniles in the gall cortex and hyperplastic tissue; Fyuco INTA-RC. **D**: Syncytium with low metabolic activity; Fenomeno RZ-RC. Abbreviations= hy: hyperplastic tissue; j: juveniles; ne: nematode female; sy: syncytium; x: xylem. Scale bars= A-D: 100 µm.

Table 1. Main histopathological characteristics observed in commercial pepper, *Capsicum annuum*, cultivars parasitised by two *Nacobbus celatus* populations.

Histological response	Nematode population/Pepper cultivar	
	Río Cuarto	**Lisandro Olmos**
Thickened and lignified cell walls associated with females	-	Fyuco INTA
Well developed but non-functional syncytia	Fyuco INTA	-
Juveniles in the cortex	Fyuco INTA	-
Hyperplastic tissue in central cylinder	Fyuco INTA, Yatasto, Fenomeno RZ	-
Syncytia with low metabolic activity	Fenomeno RZ	Fenomeno RZ

The syncytial feeding sites produced by *Nacobbus* species closely resemble those induced by cyst nematodes (abbreviation CN) and differ significantly from the giant cells induced by RKN (Eves-van den Akker *et al.*, 2014). In CN, the flow of solutes from the xylem vessels is a limiting factor for feeding site efficiency; for that reason, contact and connection with the xylem vessels are crucial for their development. The developing syncytia are initially isolated and rely on transport proteins for nutrients but then simplasmically connect to the nutrient-dense phloem (Levin *et al.*, 2020). In FRKN, the initial syncytial cell undergoes local wall dissolution, and its protoplast fuses with those of the neighbouring cells, which are then incorporated into the syncytium (Eves-van den Akker *et al.*, 2014). An unusually high frequency of plasmodesmata between syncytial cells and neighbouring phloem elements was also reported in the *Nacobbus* genus (Jones & Payne, 1977). Our results confirm that the feeding sites induced by *N. celatus* maintain close contact mainly with the xylem but also with the phloem. In addition, it was observed that they incorporate xylem vessels, such as reported in other Solanaceae species parasitised by FRKN, as the tomato (*Solanum lycopersicum* L.) and the potato (*S. tuberosum* L.) (Tordable *et al.*, 2010, 2018). This could support parasite development and/or contribute to maintaining high turgor pressure within the syncytia (Levin *et al.*, 2020).

Although all tested peppers were efficient hosts for both *N. celatus* populations, histopathological studies in some cases revealed differences either between the populations or between cultivars. Fyuco INTA infected with RC showed syncytial cells with cellulose walls surrounding the nematodes. However, this cultivar parasitised by LO showed thickened and lignified syncytial cell walls associated with the anterior region of the females, evidencing a defensive reaction by the plant. Lignification and suberisation are host responses that stop and prevent infection of plant tissues (Lomelí-Rosario *et al.*, 2009). The defence response detected by histopathology for LO is reflected in the lower multiplication rate (Reproduction Factor: abbreviation RF) previously observed, compared to the control (RF Fyuco INTA LO= 20.4; RF California Wonder= 37.9) and the RC population (RF Fyuco INTA LO= 20.4; RF Fyuco INTA RC= 41.5) (Lax *et al.*, 2016). In tomato cultivars marketed, as "nematode resistant" (without specifying the genus and/or species), cell thickening was also observed in the syncytial and parenchyma cell walls surrounding *N. celatus* females, differing from a susceptible cultivar tested (Cabrera *et al.*, 2017). In infections with other plant-parasitic nematode species, secondary thickening of the cell walls surrounding the parasite and egg masses has also been reported as a defence reaction of the plant (Rosso *et al.*, 2004; Hernández-López *et al.*, 2006; Lomelí-Rosario *et al.*, 2009).

Another difference between populations observed at Fyuco INTA was the detection of abundant juveniles in the gall cortex and large, non-functional syncytia in plants parasitised by RC. The presence of non-functional syncytia may indicate a faster invasion and multiplication of individuals from the population on this host; the juveniles found in the gall cortex would correspond to a new re-infection in the roots from the egg masses. This could be explained by the fact that the RC population has a higher degree of aggressiveness, being able to evade or suppress the Fyuco INTA defence response observed at the histopathological level in LO. It would be interesting to conduct further studies to understand the molecular and cellular mechanisms involved in host-specific resistance against different *N. celatus* populations on the same host.

Moyetta *et al.* (2007) evaluated the histopathology of commercial and experimental pepper cultivars with resistance genes against RKN infected by *N. celatus*. However, no morpho-anatomical evidence indicating any degree of tolerance or resistance was found. According to the supplier, Fenomeno RZ carries resistance to RKN. In rice, *Oryza glaberrima* Steud., lines resistant to *M. graminicola* (Petitot *et al.*, 2017) and cowpea, *Vigna unguiculata* (L.) Walp., carrying the *Rk* gene with resistance to RKN (Das *et al.*, 2008), highly vacuolated feeding sites (giant cells) with low cytoplasmic density were observed, indicating low metabolic activity compared to feeding sites of susceptible cultivars. The same characteristics were observed in Fenomeno RZ, which could be attributed to its resistance to RKN. Despite this, it was still able to provide the necessary nutrients for the development of *N. celatus,* as high RF values have previously been observed for both populations multiplied on this cultivar (Lax *et al.*, 2016).

In the present work, the variability in the response of the same population to different pepper cultivars and histopathological differences between populations of FRKN were demonstrated. This highlights the importance of considering nematodes from different geographical origins when screening plant material for tolerance and/or resistance (Lax *et al*., 2006, 2011). Given the limited records of FRKN-resistant germplasm, not only in the pepper but also in the tomato and the potato (Lax *et al*., 2022), the densities of the nematode in the soil are increasing, making its management more complicated. Histopathological studies facilitate a deeper understanding of the nematode-plant interaction, elucidating the behaviour and development of the parasite on the host, as well as differences in plant response to different nematode populations.

Author contributions

PL and VC designed the experience. VC made the figures. All authors participated in the elaboration of the manuscript.

Acknowledgements

We thank Dr. M. del C. Tordable (Universidad Nacional de Río Cuarto) for technical support in the processing of plant material for histological sections. This work was financially supported by the Agencia Nacional de Promoción Científica y Tecnológica (Préstamo BID, PICT 2020 Nº 1342) and the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET, PIP 11220200101685).

Primary research data

The authors declare that they are aware of law no. 26899/2013 and commit to making the primary data available in the repositories of their institutions.

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