

## REVIEW ARTICLE

# An emergent plant-parasitic nematode in Brazil: *Aphelenchoides besseyi*. Current status and research perspectives

Victor Hugo Moura de Souza<sup>1</sup>  | Sophia Moracchioli Philadelphi<sup>2</sup> | Rafael Galbieri<sup>3</sup> | Unnati Sonawala<sup>1</sup> | Sebastian Eves-van den Akker<sup>1</sup>

<sup>1</sup>Crop Science Centre, University of Cambridge, Cambridge, UK

<sup>2</sup>Department of Plant Pathology and Nematology, Escola Superior de Agricultura 'Luiz de Queiroz' (ESALQ/USP), Piracicaba, Brazil

<sup>3</sup>Instituto Mato-grossense do Algodão (IMAm), Department of Plant Pathology, Primavera do Leste, Mato Grosso, Brazil

## Correspondence

Victor Hugo Moura de Souza, Crop Science Centre, University of Cambridge, Cambridge, UK.  
Email: [vhm24@cam.ac.uk](mailto:vhm24@cam.ac.uk)

## Funding information

Biotechnology and Biological Sciences Research Council, Grant/Award Number: BB/S006397/1, BB/R011311/1 and BB/X006352/1; Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Number: 2020-2080; HORIZON EUROPE Marie Skłodowska-Curie Actions, Grant/Award Number: 101025218; Leverhulme Centre for Integrative Research on Agriculture and Health, Grant/Award Number: RPG-2023-001; UKRI Frontier, Grant/Award Number: EP/X024008/1

## Abstract

*Aphelenchoides besseyi* is an emerging and yet overlooked plant parasite of many economically important crops, including cotton, soybean and common bean. It presents an economic risk to these crops in several countries, notably in Brazil. Although first reported infecting strawberries in the United States as early as 1942, it was only identified to be the causal agent of green stem and foliar retention (GSFR) disease in Brazil in 2017. Currently, there are no chemical nematicides registered in Brazil against *A. besseyi*, and no known sources of genetic resistance. Here, we review the biology of *A. besseyi*, its spread across Brazil, its relevance to the country's current and future agriculture and the limited control measures. We describe control measures that have been successfully used to manage infestations of other plant-parasitic nematodes and could potentially be extended to use in the control of *A. besseyi*. We also review and discuss potential future control measures, such as RNA interference and genome editing, for the development of crops with enhanced resistance to *A. besseyi*.

## KEYWORDS

*Aphelenchoides* syndrome, emerging pathogen, foliar nematode, *glycine max*, management

## 1 | INTRODUCTION

Plant-parasitic nematodes (PPNs) are a major constraint to world agriculture. More than 4100 species of PPNS have been described and are responsible for the decrease in yield and production of a variety of crops, including grains, fruits, vegetables and oil seeds (Decraemer & Geraert, 2006; Jones et al., 2013; Nicol et al., 2011). In Brazil, the most economically important species of PPNS are the root-knot nematodes (*Meloidogyne* spp.), soybean cyst nematode (*Heterodera glycines*)

and the lesion nematodes (notably *Pratylenchus brachyurus* and *P. zaeae*). Due to their importance to several major and minor crops of the country (e.g., soybean, *Glycine max*) and cotton (*Gossypium hirsutum*), in 2015 they were listed among the main pests in Brazilian agriculture by the Ministry of Agriculture, Cattle and Supplying (Brazilian Ministry of Agriculture, 2015). However, another nematode has remained unrecognized across soybean and cotton fields of Brazil and now represents an emerging threat to producers across this country, and by extension the region at large: the foliar nematode *Aphelenchoides besseyi*.

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs](https://creativecommons.org/licenses/by-nc-nd/4.0/) License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.  
© 2023 The Authors. *Plant Pathology* published by John Wiley & Sons Ltd on behalf of British Society for Plant Pathology.

In 2005–2006, researchers and farmers reported a high incidence of a new syndrome in soybean fields (Meyer et al., 2008). This disease occurred in warm and humid areas of the states of Maranhão, Tocantins, Pará and north of Mato Grosso. The losses reached 100% in some areas and the disease was referred to as Soja Louca II on that occasion (Favoreto & Meyer, 2018; Gilioli et al., 2007; Meyer, Favoreto, Klepker, et al., 2017). After a meticulous investigation, Meyer, Favoreto, Klepker, et al. (2017) reported *A. besseyi* (Christie, 1942) as the causal agent of the green stem and foliar retention (GSFR) of soybean. In 2018 and 2021, *A. besseyi* was reported to be infecting aerial parts of cotton and parasitizing common bean (*Phaseolus vulgaris*) (Favoreto et al., 2018, 2021). In fields, symptomatic plants can be distributed in patches, along the rows or uniformly (Meyer, Favoreto, Klepker, et al., 2017). *A. besseyi* is an emergent plant pathogen in Brazilian agriculture, and therefore the present review aims to summarize information on *A. besseyi*, describe its key characteristics, the main management strategies and highlight future research priorities.

## 2 | GENERAL CHARACTERISTICS AND TAXONOMY

*A. besseyi* ranges in length from 0.4 to 1.2 mm, has a large metacarpus and pharyngeal glands commonly overlapping the intestine dorsally. The stylet is slender with small, but distinct knobs (Christie, 1942; De Jesus & Cares, 2016). When heat relaxed, the females are straight or slightly ventrally arcuate, whereas males present a typical 'walking stick' shape (De Jesus & Cares, 2016). *A. besseyi* can be distinguished from some *Aphelenchoides* species by the presence of lateral field with four lines and a stellate mucro at the tail. When compared to *A. ritzemabosi* (a close relative), *A. besseyi* presents a shorter post-vulvar uterine sac and the excretory pore is usually positioned near the anterior edge of the nerve ring (EPPO, 2017; Kohl, 2011). The reproduction of *A. besseyi* is amphimictic, but not uncommonly they reproduce through parthenogenesis (De Jesus & Cares, 2016).

*Aphelenchoides* species share several characteristics and lack definitive traits, making accurate taxonomic delineation of *A. besseyi* using morphology alone difficult (De Jesus & Cares, 2016; Inomoto, 2016; Xu et al., 2020). For example, *A. besseyi*'s stellate mucro tail differentiates it from some species (such as *A. fragarie* and *A. ritzemabosi*) but is shared among others (such as *Aphelenchoides fujianensis* and *Aphelenchoides goodeyi*).

De Jesus and Cares (2016) used both morphology and molecular methods to characterize different *Aphelenchoides* spp. populations extracted from rice and forage grass seeds in Brazil. Based on morphological and phylogenetic analyses, the populations were separated into two groups: group-rice and group-forage. Bayesian phylogenetic analysis based on SSU and mtCOI clustered the forage populations with a similar species; *A. fujianensis*, suggesting a possible misidentification of *Aphelenchoides* specimens in Brazil. Similarly, two cryptic species were recognized by molecular delimitation methods from *A. besseyi* haplotypes, with limited support from morphological traits (Xu et al., 2020). Some populations

of *A. fujianensis* and *A. besseyi* were assigned as *A. pseudogoodeyi*, a new species (Oliveira et al., 2019). Moreover, on analysing populations that had been previously identified as *A. besseyi*, Subbotin et al. (2021) discovered that there was a species complex containing several cryptic species: *A. besseyi* sensu stricto, *Aphelenchoides oryzae*, *Aphelenchoides pseudobesseyi* sp. n. and other putative undescribed species. Furthermore, the population from Brazil previously identified as *A. besseyi* was found to be *A. pseudobesseyi* and they cannot be easily distinguished using morphological features. When inoculated on soybean, the plants showed similar symptoms to those described by Meyer, Favoreto, Klepker, et al. (2017).

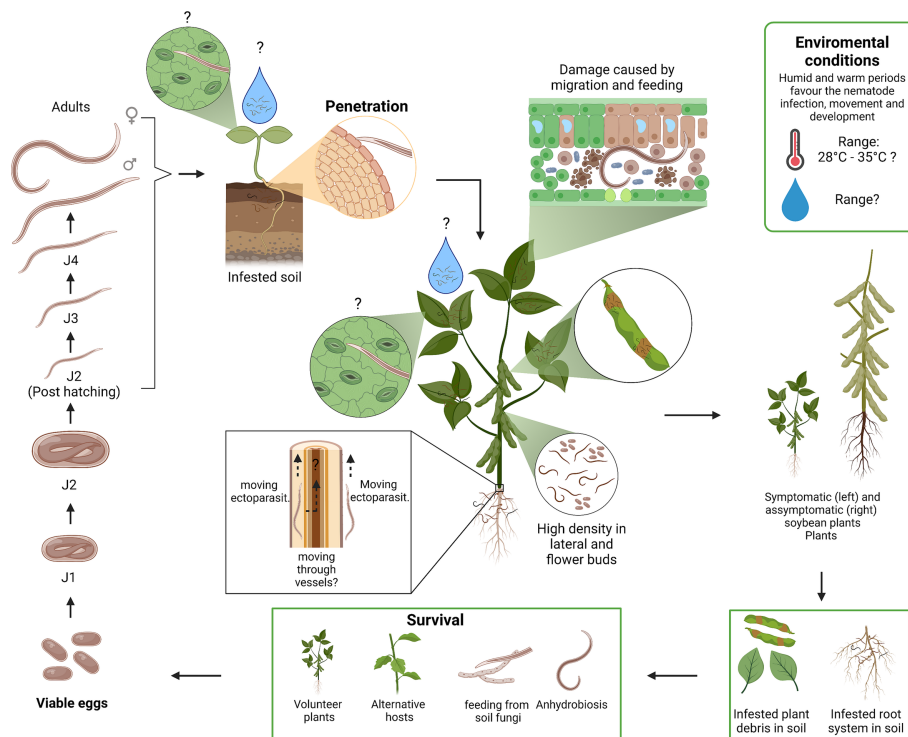
## 3 | LIFE CYCLE

Different from most PPNs (e.g., *Pratylenchus* spp. and *Meloidogyne* spp.), *Aphelenchoides* species vary in their life cycle (Xu et al., 2020). They can display facultative ecto-endoparasitism and survive and multiply in soil by feeding from saprophytic fungi (Cares et al., 2008; De Jesus & Cares, 2016).

Interestingly, it has been reported that nematodes reach upper parts of the plant by moving ectoparasitically in some crops (e.g., rice and common bean; Araya, 2008; De Jesus & Cares, 2016; Hoshino & Togashi, 2020), while endoparasitically, through the cortical cells, on others (e.g., soybean; Calandrelli et al., 2023; Favoreto & Meyer, 2019). Experimental evidence showed that migratory stages penetrate soybean roots and hypocotyls (Calandrelli et al., 2023; Da Silva & Machado, 2022). Calandrelli et al. (2023) also observed nematodes inside xylem vessels; however, it is not clear to what extent xylem vessels play a role in a nematode's movement within the plant and whether/how this influences disease development. Moreover, nematodes consistently display the ability to infect and migrate ectoparasitically (Meyer, Favoreto, Klepker, et al., 2017; Oliveira et al., 2019; Subbotin et al., 2021). There is a need to clarify to what extent ectoparasitism contributes to disease or dispersion by splashing in agriculture (Kohl, 2011) as this has profound implications for management strategies.

After infection, nematodes spread to most aerial parts of the plant (stems, petioles, nodes and leaves) 4 days after inoculation (Calandrelli et al., 2023; Favoreto et al., 2017; Favoreto & Meyer, 2019). Favoreto et al. (2017) suggested that nodes and racemes were the main tissues for nematode feeding and reproduction, which was further confirmed by Calandrelli et al. (2023). Therewith, symptoms start to develop, becoming more evident at the beginning of the reproductive stage (R1).

Taken together, we propose a model life cycle of *A. besseyi* on soybean (Figure 1) in order to highlight the gaps in our current understanding. For example, with regards to inoculum maintenance, *A. besseyi* is likely to survive in hosts plants and saprophytically, feeding from soil fungi (Figure 1; Oliveira et al., 2022). It is currently not understood which conditions (e.g., soil organic matter, humidity and temperature) are favourable for the nematode's survival in the soil. Although some weeds have been identified as good hosts of *A. besseyi* (Meyer, Favoreto, Klepker, et al., 2017),



**FIGURE 1** A proposed model life cycle of *Aphelenchoides besseyi* on soybean based on the limited information available. Unknowns, indicated by question marks, are highlighted for three aspects of the infection biology: penetration, survival and environmental conditions. Created by the authors using Biorender (BioRender.com). [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

the knowledge regarding its host range needs to be expanded to be fully used by field agronomists to make informed disease management decisions. Volunteer plants could also have a role in population build-up and maintenance in the area, and, therefore, could be a target for intervention.

Based on our current understanding, temperatures higher than 28°C are required for GSFR development (Da Silva & Machado, 2022). Although numbers can increase on *Fusarium* at 25°C, symptoms and reproduction on soybean and common bean were observed at 30 ± 5°C (Calandrelli et al., 2023; da Silva & Machado, 2022; Favoreto et al., 2021; Meyer, Favoreto, Klepker, et al., 2017). This indicates that the disease develops at 28–35°C, but it needs further investigation.

High humidity is required for disease development, but a range is yet to be defined. Greenhouse experiments so far have used humidifiers or misting systems to maintain high humidity and maximize infections (Calandrelli et al., 2023; Da Silva & Machado, 2022; Favoreto et al., 2021; Meyer, Favoreto, Klepker, et al., 2017). A well-defined range would not only be useful during experiments, but also help predict conditions that favour disease outbreaks.

## 4 | HOST RANGE

*A. besseyi* was first reported in strawberry by Christie, in 1942. To date, over 100 different host associations have been reported, including grasses, ornamentals, vegetables and beans (De Jesus & Cares, 2016; International Plant Protection Convention - IPPC, 2016; Kohl, 2011). However, the majority of the losses worldwide were

reported in rice (Kohl, 2011), in which it causes white tip disease. In Brazil, *A. besseyi* has been reported in rice, strawberry, horseradish, garlic, ornamental plants and also associated with seeds of graminaceous cover crops (Cares et al., 2008). According to De Jesus and Cares (2016), high densities of *A. besseyi* are frequently found in rice, especially flooded rice. In the few registers available, losses of up to 50% in upland rice in Brazil were reported (Tiware & Khare, 2003). An updated host list of *A. besseyi* is summarized in Table 1.

The polyphagous trait of this nematode is apparent in the distribution of hosts across several orders of the phylum (Figure 2a), with most hosts in Poales (27.4%) and Asterales (17.7%) (Figure 2b). As symptoms caused by nematodes are generally overlooked, the number of hosts is probably underestimated. Additionally, *A. besseyi* is often reported as a free-living nematode due to its fungivorous ability, concealing its parasitic relationship with plants.

Despite the importance of *A. besseyi* to a variety of hosts, the present review will focus on three previously unreported crops that host this parasite (common bean, soybean and cotton), and the previously reported relationship with rice (*Oryza sativa*), as it highlights important characteristics of *A. besseyi* that pertain to distribution and spread.

## 5 | HOW DID THE PROBLEM ARISE?

Data from 1977 indicate that *A. besseyi* was widespread in rice fields in central-west Brazil, wherein 70% of examined samples were infested with *A. besseyi* (Huang et al., 1977). In this period, it was common for growers to save a portion of the harvested seeds to use in the next

TABLE 1 Plant species reported as hosts of *Aphelenchoides besseyi*.

Plant species	Common name	Country of report	References
<i>Abelmoschus esculentus</i>	Okra	Pakistan	Samina & Iqbal, 2019
<i>Allium cepa</i>	Onion	Thailand	Bridge et al., 1990; Fortuner & Williams, 1975
<i>Allium sativum</i> <sup>a</sup>	Garlic	Brazil	da Silveira & Curi, 1990
<i>Amaranthus viridis</i>	Slender amaranth or green amaranth	Brazil	da Silva, Calandrelli, França, et al., 2018
<i>Armoracia rusticana</i>	Horseradish	Brazil	da Silveira & Curi, 1990; Escuer & Bello, 2000
<i>Asplenium dentatum</i> var. <i>jamaicense</i>	Spleenworts	USA	Kohl, 2011; Sánchez-Monge et al., 2015
<i>Asplenium nidus</i>	Bird's nest fern or nest fern	Brazil, Taiwan	da Silva, Calandrelli, Favoreto et al., 2018; Favoreto & Meyer, 2018; UC Davis Database, 2022
<i>Avena sativa</i>	Oat	Brazil, India	Calandrelli et al., 2018; Khan et al., 2012
<i>Begonia</i> sp.	Begonia	Brazil	Oliveira & Kubo, 2006
<i>Boehmeria nivea</i>	Ramie	Philippines	Fortuner, 1970; Fortuner & Williams, 1975
<i>Brachiaria brizantha</i> <sup>a</sup> (syn. <i>Urochloa brizantha</i> )	Palisade grass	Brazil	Marchi et al., 2007; Monteiro et al., 2014
<i>Brachiaria decumbens</i> <sup>a</sup> (syn. <i>Urochloa decumbens</i> )	Signal grass	Brazil	Marchi et al., 2007; Oliveira et al., 2009
<i>Brachiaria</i> sp. <sup>a</sup> (syn. <i>Urochloa</i> sp.)	Brachiaria	Costa Rica	Sánchez-Monge et al., 2015; Solano & Solís, 2013
<i>Brassica pekinensis</i>	Chinese cabbage	Philippines	Fortuner & Williams, 1975
<i>Bulbostylis burchellii</i> <sup>a</sup>	Little sedge	South Africa	Girgan et al., 2018
<i>Ctenanthe oppenheimiana</i>	Giant bamburanta or never never plant	Brazil	da Silveira & Curi, 1990; Oliveira & Kubo, 2006
<i>Calendula officinalis</i> <sup>a</sup>	Calendula	Cuba	Pérez & Fernández, 2004
<i>Callistephus chinensis</i>	China aster	Cuba	Pérez & Fernández, 2004
<i>Capsicum annuum</i>	Bell pepper	Malaysia	Bridge et al., 2005; Escuer & Bello, 2000
<i>Chrysanthemum × morifolium</i>	Chrysanthemum	USA	Fortuner & Williams, 1975
<i>Chrysanthemum maximum</i>	Shasta daisy	USA	Fortuner & Williams, 1975
<i>Chrysanthemum</i> sp.	Chrysanthemum	Brazil	da Silva, Calandrelli, Favoreto et al., 2018; Favoreto & Meyer, 2018; Goodey et al., 1965; Sánchez-Monge et al., 2015
<i>Cibotium</i> sp.	Manfern	USA	Kohl, 2011; Sánchez-Monge et al., 2015
<i>Coleus blumei</i>	Coleus	USA	Fortuner & Williams, 1975; Goodey et al., 1965
<i>Colocasia esculenta</i>	Taro or yam	Not found	Bridge et al., 1990
<i>Commelina benghalensis</i>	Benghal dayflower	Brazil	da Silva, Calandrelli, França, et al., 2018
<i>Cucumis sativus</i>	Cucumber	Not found	Kohl, 2011
<i>Cyperus iria</i>	Grasshopper's cyperus	Japan	Fortuner & Williams, 1975; Goodey et al., 1965
<i>Cyperus longus</i> <sup>a</sup>	Sweet cyperus	South Africa	Girgan et al., 2018
<i>Cyperus</i> sp.	Flatsedges	Comoros Islands	Fortuner & Williams, 1975
<i>Dahlia pinnata</i>	Garden dahlia	Not found	Goodey et al., 1965; Kohl, 2011; Sánchez-Monge et al., 2015
<i>Dahlia variabilis</i>	Dahlia	USA	Fortuner & Williams, 1975
<i>Dendrobium nobile</i>	Noble dendrobium	USA	Uchida & Sipres, 1998
<i>Dianthus caryophyllus</i>	Carnation or clove pink	Cuba	Pérez & Fernández, 2004
<i>Digitalis sanguinalis</i>	Foxgloves	Not found	Goodey et al., 1965; Kohl, 2011; Sánchez-Monge et al., 2015
<i>Digitaria adscendens</i>	Southern crabgrass	Japan	Fortuner & Williams, 1975
<i>Digitaria sanguinalis</i>	Hairy crabgrass	Japan	Fortuner & Williams, 1975; Goodey et al., 1965
<i>Dioscorea cayenensis</i>	Yellow yam or yellow Guinea yam	Brazil	Noronha et al., 2020
<i>Dioscorea trifida</i>	Yam or mapuey	Guadeloupe	Bridge et al., 1990; Fortuner & Williams, 1975; Kermarrec & Anais, 1974; Noronha et al., 2020
<i>Erechtites praealta</i>	American fireweed	USA	Fortuner & Williams, 1975; Goodey et al., 1965; Kohl, 2011
<i>Euchlaena mexicana</i>	Teosinte	India	Khan et al., 2012

(Continues)

TABLE 1 (Continued)

Plant species	Common name	Country of report	References
<i>Ficus elastica</i>	Rubber tree	USA	Fortuner & Williams, 1975; Goodey et al., 1965; Kohl, 2011; Marlatt, 1970
<i>Fragaria × ananassa</i>	Strawberry	Brazil, USA	Favoreto & Meyer, 2018; Fortuner & Williams, 1975; Goodey et al., 1965; Kohl, 2011; Oliveira et al., 2019
<i>Fragaria grandiflora</i> <sup>a</sup>	Strawberry	Taiwan	Sánchez-Monge et al., 2015; UC Davis Database, 2022
<i>Fragaria</i> sp.	Strawberry	USA	Christie, 1942; Kohl, 2011; Sánchez-Monge et al., 2015
<i>Fragaria vesca</i> <sup>a</sup>	European strawberry	Not found	Sánchez-Monge et al., 2015; UC Davis Database, 2022
<i>Gerbera jamesonii</i>	Gerbera daisy	Cuba, USA	Oliveira et al., 2019; Pérez & Fernández, 2004
<i>Gerbera</i> spp.	Gerbera	Cuba	Pérez & Fernández, 2004
<i>Glycine hispida</i>	Soybean	Senegal	Fortuner & Williams, 1975
<i>Glycine max</i>	Soybean	Brazil	Favoreto et al., 2017; Favoreto & Meyer, 2017; Meyer, Favoreto, Klepker, et al., 2017
<i>Gossypium hirsutum</i>	Cotton	Brazil	Favoreto et al., 2017, 2018
<i>Hibiscus brachenridgei</i>	Hibiscus	USA	Fortuner & Williams, 1975
<i>Hibiscus</i> sp. <sup>a</sup>	Hibiscus	Not found	Sánchez-Monge et al., 2015
<i>Hydrangea macrophylla</i>	Big-leaf hydrangea	USA	Fortuner & Williams, 1975; Goodey et al., 1965; Kohl, 2011
<i>Hydrangea</i> sp.	Hydrangea	USA	Escuer & Bello, 2000
<i>Impatiens balsamina</i>	Garden balsam, rose balsam or touch-me-not	USA	Fortuner & Williams, 1975; Goodey et al., 1965; Kohl, 2011
<i>Imperata cylindrica</i>	Cogon grass	Comoros Islands	Fortuner & Williams, 1975
<i>Ipomoea batatas</i>	Sweet potato	Pakistan	Bridge et al., 1990; Fortuner & Williams, 1975
<i>Jasminum simplicifolium</i>	Wax jasmine or Australian wax jasmine	USA	Kohl, 2011; Sánchez-Monge et al., 2015
<i>Jasminum</i> sp.	Jasmine	USA	Kohl, 2011; Sánchez-Monge et al., 2015
<i>Lactuca sativa</i>	Garden lettuce, lettuce	Brazil	da Silveira & Curi, 1990; Escuer & Bello, 2000
<i>Lemna</i> sp.	Common duckweed	USA	Kohl, 2011; Sánchez-Monge et al., 2015
<i>Leonotis nepetifolia</i>	Lion's tail	Brazil	da Silva, Calandrelli, França, et al., 2018
<i>Leucanthemum maximum</i>	Shasta daisy or max chrysanthemum	New Zealand	Goodey et al., 1965; Kohl, 2011; Sánchez-Monge et al., 2015
<i>Lycopodium clavatum</i>	Club moss, elk moss, ground-pine	USA	Kohl, 2011; Sánchez-Monge et al., 2015
<i>Lygodium circinnatum</i>	Climbing fern	USA	Goodey et al., 1965; Kohl, 2011; Sánchez-Monge et al., 2015
<i>Nicotiana tabacum</i> <sup>a</sup>	Tobacco	Not found	Sánchez-Monge et al., 2015; UC Davis Database, 2022
<i>Oryza sativa</i>	Rice	India	Goodey et al., 1965; Khan et al., 2012; Kohl, 2011; Sánchez-Monge et al., 2015
<i>Panicum bisulcatum</i>	Black-seed panic	Japan	Fortuner & Williams, 1975
<i>Panicum crus-galli</i> var <i>frumentacea</i> (syn. <i>Echinochloa crus-galli</i> )	Barnyard-grass or cockspur grass	Japan	Fortuner & Williams, 1975
<i>Panicum maximum</i> <sup>a</sup>	Guinea grass	Brazil	Marchi et al., 2007; Oliveira et al., 2009
<i>Panicum miliaceum</i> <sup>a</sup>	Proso millet or common millet	India	Sánchez-Monge et al., 2015; UC Davis Database, 2022
<i>Panicum</i> sp.	Millet	Israel, Japan	Escuer & Bello, 2000
<i>Pennisetum</i> sp. <sup>a</sup>	Fountain grasses	Not found	International Plant Protection Convention - IPPC, 2016; Sánchez-Monge et al., 2015
<i>Pennisetum typhoides</i>	Bulrush millet, pearl millet, spiked millet or cattail millet	Not found	Fortuner & Williams, 1975
<i>Phaseolus vulgaris</i>	Common bean or bean	Brazil, Costa Rica	Chaves et al., 2013; Favoreto et al., 2021; Solano & Solís, 2013
<i>Pinus massoniana</i> <sup>a</sup>	Chinese red pine	China	Zhuo et al., 2010
<i>Pinus taeda</i> <sup>a</sup>	Loblolly pine	China	Zhuo et al., 2010
<i>Pluchea odorata</i>	Sweet scent shrubby or camphor-weed	USA	Fortuner & Williams, 1975; Goodey et al., 1965; Kohl, 2011
<i>Polianthes tuberosa</i>	Tuberose	India, USA	Bala et al., 2019; Fortuner & Williams, 1975; Khan et al., 2012

TABLE 1 (Continued)

Plant species	Common name	Country of report	References
<i>Pycreus polystachyus</i> (syn. <i>Cyperus polystachyos</i> )	Manyspike flatsedge	Comoros Islands	Fortuner & Williams, 1975
<i>Raphanus sativus</i>	Radish	Brazil	Favoreto & Meyer, 2018
<i>Rosa</i> sp.	Rose	USA	Kohl, 2011; Sánchez-Monge et al., 2015
<i>Rudbeckia hirta</i>	Black-eyed-Susan	USA	Kohl, 2011; Sánchez-Monge et al., 2015
<i>Saccharum officinarum</i>	Sugarcane	Cuba	da Silveira & Curi, 1990; Fortuner & Williams, 1975
<i>Saintpaulia ionantha</i>	African violet	USA	Fortuner & Williams, 1975; Oliveira & Kubo, 2006
<i>Secale cereale</i>	Rye	Brazil	Favoreto & Meyer, 2018
<i>Setaria italica</i>	Foxtail millet	Japan	Fortuner & Williams, 1975
<i>Setaria</i> sp.	Green foxtail	Israel, Japan	Escuer & Bello, 2000
<i>Setaria viridis</i>	Green foxtail	Japan	Fortuner & Williams, 1975; Goodey et al., 1965; Kohl, 2011
<i>Solenostemon scutellarioides</i>	Coleus or painted-nettle	Not found	Goodey et al., 1965; Kohl, 2011; Sánchez-Monge et al., 2015
<i>Sporobolus indicus</i>	Smut grass	USA	Kohl, 2011; Sánchez-Monge et al., 2015
<i>Sporobolus</i> sp.	Smut grasses	Not found	Sánchez-Monge et al., 2015
<i>Sporobolus poiretii</i>	Smut grass	USA	Fortuner & Williams, 1975
<i>Stylosanthes hamata</i> <sup>a</sup>	Caribbean stylo	Australia	Gokte et al., 1992
<i>Synedrellopsis grisebachii</i>	Agriãozinho	Brazil	da Silva, Calandrelli, França, et al., 2018
<i>Tagetes</i> sp.	Marigold	USA	Fortuner & Williams, 1975; Goodey et al., 1965 Kohl, 2011
<i>Theobroma cacao</i> <sup>a</sup>	Cacao tree	Brazil	da Silveira & Curi, 1990
<i>Tithonia diversifolia</i>	Mexican-sunflower or shrub sunflower	USA	Fortuner & Williams, 1975; Goodey et al., 1965; Kohl, 2011
<i>Torenia fournieri</i>	Bluewings or wishbone flower	USA	Fortuner & Williams, 1975; Goodey et al., 1965; Kohl, 2011
<i>Tradescantia pallida</i>	Purpleheart	USA	Kohl, 2011; Sánchez-Monge et al., 2015
<i>Triticum aestivum</i>	Wheat	Brazil	Favoreto & Meyer, 2018
<i>Vanda</i> sp.	Orchid	Not found	Goodey et al., 1965; Kohl, 2011
<i>Vanda</i> sp. × Luma	Orchid	USA	Fortuner & Williams, 1975
<i>Vanda</i> sp. × Miss Deum	Orchid	USA	Fortuner & Williams, 1975
<i>Vanda</i> sp. × Miss Joaquim	Orchid	USA	Fortuner & Williams, 1975
<i>Vanda</i> sp. × Miss Joaquim × Kapoho	Orchid	USA	Fortuner & Williams, 1975
<i>Vanda</i> sp. × Rose Marie	Orchid	USA	Fortuner & Williams, 1975
<i>Vanda</i> sp. × Trimeril	Orchid	USA	Fortuner & Williams, 1975
<i>Vigna unguiculata</i>	Cowpea	Brazil	Favoreto et al., 2022; Favoreto & Meyer, 2018; Noronha et al., 2023
<i>Zea mays</i>	Maize	Thailand	Bridge et al., 1990; Fortuner & Williams, 1975
<i>Zinnia elegans</i> (syn. <i>Zinnia violacea</i> )	Zinnia	Cuba, USA	Fortuner & Williams, 1975; Pérez & Fernández, 2004
<i>Zinnia violacea</i>	Common zinnia or youth-and-old-age	Not found	Goodey et al., 1965; Kohl, 2011; Sánchez-Monge et al., 2015

<sup>a</sup>Plant species in which the presence of *Aphelenchoides besseyi* has been reported. Nematodes have been discovered in association with the plant tissues and/or seeds, but the parasitic relationship is uncertain.

planting season (Huang et al., 1977). As a seed-transmitted nematode, *A. besseyi* has an outstanding ability to survive in anhydrobiosis for several years on stored rice grain (Hoshino & Togashi, 2020; Wang et al., 2014). Therefore, it is reasonable to postulate that this could have been a key factor in the dissemination of *A. besseyi* across the central-west of Brazil. Another hypothesis widely accepted is that some forage crops had a major influence on the dispersion of *A. besseyi*. *Brachiaria*

spp. (syn. *Urochloa*) (*Brachiaria ruziziensis*, *B. decumbens* and *B. brizantha*, respectively), *Panicum* spp. and other forage grasses are popular cover crop options in Brazil (Kluthcouski et al., 2013). Additionally, legislation is less restrictive about the overall quality of such seeds when compared to major crops (Brazilian Ministry of Agriculture, Livestock and Food Supply, 2008) and *Aphelenchoides* individuals were frequently found on seeds of these crops (Pinheiro et al., 1997). Inoculation of *A.*

## (a) Host range

## (b) Hosts by class and order

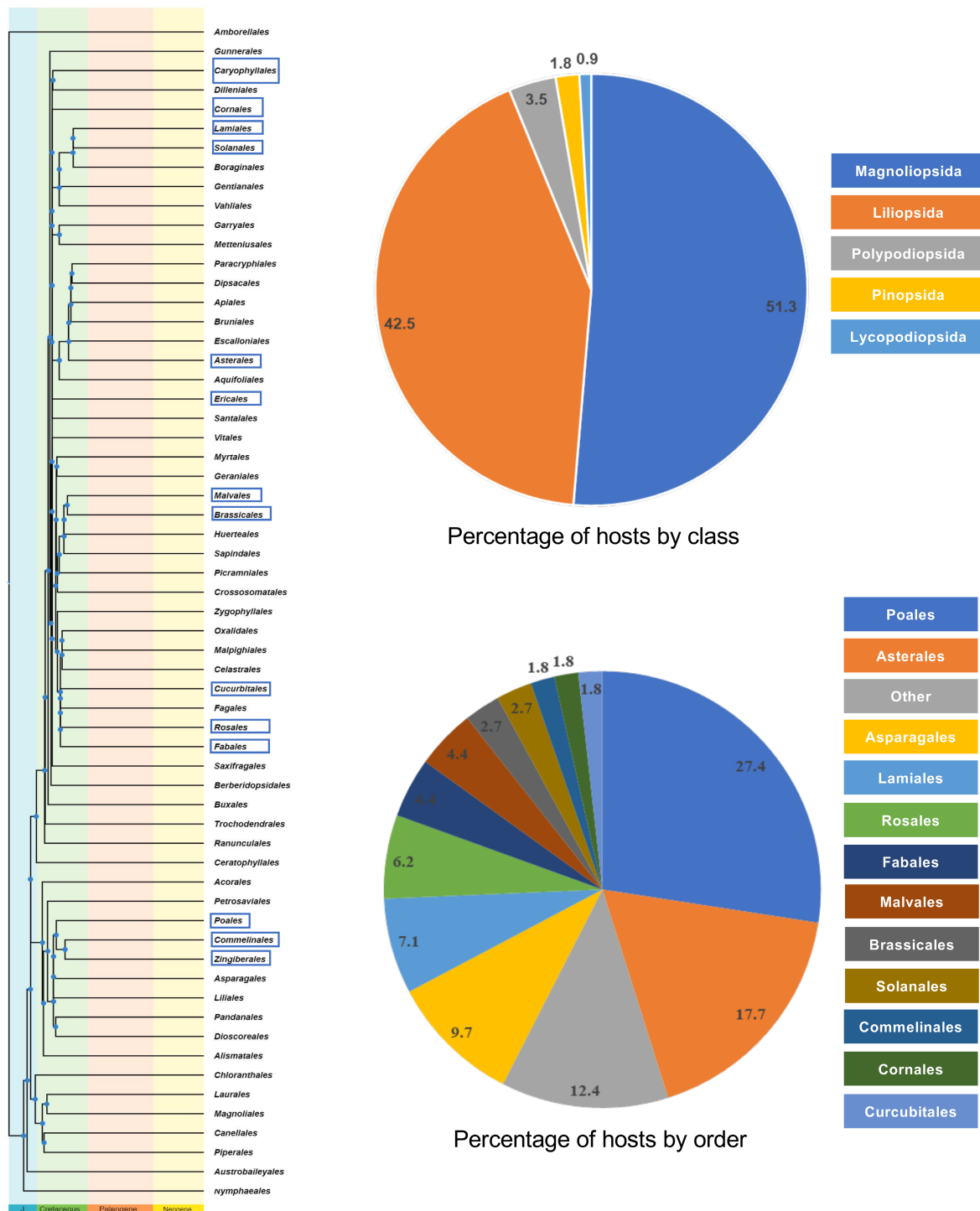


FIGURE 2 (a) Partial phylogenetic time tree of flowering plants (timetree.org; accessed 12th June 2022). The blue boxes highlight the groups that have at least one host species of *Aphelenchoides besseyi*. (b) The percentage of hosts by class and order of plants. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

*besseyi* isolated from forage seeds was able to cause GSFR on soybean (Dr Luciany Favoreto, Embrapa Soja, Londrina—Paraná, Brazil, personal communication, 10/11/2022). Therefore, the use of contaminated forage seeds by farmers could have contributed to *A. besseyi* dispersal.

After the 1980s, damage in rice was dramatically reduced, especially due to the use of pathogen-free seeds and resistant/tolerant rice cultivars (Tülek et al., 2015). Reports of damaged crops caused by *Aphelenchoides* spp. were related to ornamental plants and forage

crops. The first report of *A. besseyi* in soybean was published in 2017, but the discovery of *amachamiento del frijol* (discussed below) was important to find the causal agent of GSFR (Chaves et al., 2013; Meyer, Favoreto, Klepker, et al., 2017). This undoubtedly raised awareness of the nematode, and losses in cotton were published in 2018 (Favoreto et al., 2018). In 2021, the pathogenicity of *A. besseyi* to common bean was demonstrated (Favoreto et al., 2021).

In the early 1990s, *amachamiento del frijol* was first reported in Costa Rica (Morales et al., 1999). The affected plants showed dark green colouration, coriaceous leaves with lesions and deformation, and flowers were aborted with formation of few pods (Chaves et al., 2013; Morales et al., 1999). The causal agent was only discovered years later and reported by Chaves et al. (2013) to be *A. besseyi*. Favoreto et al. (2021) investigated the pathogenicity of *A. besseyi* (soybean population) to *P. vulgaris* 'Jalo Precoce' in greenhouse conditions in Brazil. In addition to typical symptoms of *amachamiento*, the authors observed nematodes inside roots, stems, leaves and inflorescences 7 days after inoculation.

A similar type of GSFR of soybean was reported more than four decades ago, caused by stinkbugs or nutritional disorders (Sosa-Gómez & Moscardi, 1995). However, a new type of GSFR was reported in early 1990s, with no association with these causes. The new GSFR was initially termed Soja Louca II (Gilioli et al., 2007; Meyer, Favoreto, Klepker, et al., 2017). In affected areas, impacted plants remained green, which imposes several difficulties in the harvest process in addition to the direct damage caused by *A. besseyi*. When harvested, green soybeans decrease the quality of good seeds (Meyer et al., 2010). The harvester must not collect these green plants in order to avoid this and to prevent eventual damage to the machinery.

In May 2017, cotton plants exhibiting stunting, loss of floral buds, distortion in leaves and thickened nodes were found in Sapezal (MT, Brazil) (Favoreto et al., 2018). Extraction of cotton tissues revealed *Aphelenchoides* individuals, and morphometric/molecular examinations identified them as *A. besseyi* (Favoreto et al., 2018). Additionally, field surveys indicated that soybean grown in infested areas before or after cotton were also damaged. A soybean–cotton cropping system was already disregarded as a control measure in *P. brachyurus*, *M. incognita* and *Rotylenchulus reniformis*-infested areas (Ferraz et al., 2010), although management tools could be applied to reduce their impacts.

The present scenario is a complex one, but understanding this narrative may inform other susceptible geographies on the dangers of unrecognized disease.

## 6 | MANAGEMENT

### 6.1 | Traditional practices

The management of PPNs is challenging; instead of relying on a single measure, it requires the use of multiple strategies in a compatible manner to reduce or keep the nematode population level low

to avoid economic losses (Ferraz et al., 2010; Sikora et al., 2021; Smith & Reynolds, 1966). Among the most used strategies, chemical nematicides are of health and environmental concern and several have had their use restricted or have been removed from the market. Conversely, new management tools have been integrated over the years, notably the use of biological control agents and induced resistance (Fontana et al., 2021; Kerry, 1992). Nevertheless, an early diagnosis of *A. besseyi* is fundamental to the success of any management tool (Ranulfi et al., 2018). This could be achieved by assessing the population of nematodes through a nematological survey in the area shortly before sowing and at the beginning/end of the harvest period (Santos et al., 2016). Previous records of the area could be useful to management, as they provide information about possible host crops planted in previous years or possible losses caused by *A. besseyi*. Cropping in noninfested areas or during a period of the year not favourable to the disease (e.g., dry season) would be ideal, but may not be feasible in many situations.

Currently, no chemical nematicides are registered for the control of *A. besseyi* in Brazil (Brazilian System of Phytosanitary Agrochemicals, 2022). The only nematicide registered for the management of *Aphelenchoides* sp. is metam sodium to *A. ritzenabosi* in ornamental plants, although novel products are expected to be available in the near future (Desaeger et al., 2020). Regarding cultural practices, rotation/succession with nonhost crops is one of the main tools available to manage PPNs. This is one of the oldest techniques to reduce the damage of pathogens and pests (Chen & Tsay, 2006; Sasanelli et al., 2021). In Brazil, crop rotation/succession has been largely used to manage important species of PPNs, for example, soybean followed by maize/cotton against *H. glycines* (Debiasi et al., 2016; Souza & Inomoto, 2019). However, polyphagous species of nematodes limit the options available to farmers to less profitable crops, such as *Crotalaria* spp. (Asmus et al., 2016; Dias et al., 2010; Rodrigues et al., 2014; Souza & Inomoto, 2019). Some plant species were identified as nonhosts to *A. besseyi* and could be used in its management. The brachiaria grasses (*U. ruziziensis* and *U. brizantha*), some rattlebox species (*Crotalaria juncea*, *C. spectabilis* and *C. ochroleuca*), millet (*Pennisetum glaucum*), maize (*Zea mays*), rice, sorghum (*Sorghum bicolor*) and cowpea (*Vigna unguiculata*) were ranked as poor hosts to *A. besseyi* (Favoreto & Meyer, 2018). These are familiar to farmers and have been used to manage other PPNs. Chaves and Araya (2012) observed the decrease in incidence of *amachamiento* caused by *A. besseyi* in common bean at R8 stage as a result of crop rotation with nonhost crops, especially hot pepper (*Capsicum annuum*) and pumpkin (*Curcubita agryosperma*) (3.7% and 15.4%, respectively), when compared to maize and common bean (63.6% and 62.2%, respectively). Interestingly, the authors observed that rotation with rice led to an intermediary incidence (c.29%) and did not differ statistically to that obtained for pumpkin. The authors pointed out that their use contributed with maintenance of *A. besseyi* in common bean fields. The crop to be used in rotation/succession should be carefully chosen based on the context of the area, including the presence of other PPNs (Inomoto & Asmus, 2010; Souza & Inomoto, 2019).

Sources of genetic resistance are also lacking. For example, no resistant genotypes were reported for cotton. For common bean, Favoreto and Meyer (2019) tested 22 cultivars in greenhouse conditions and *A. besseyi* was pathogenic on all of them. For soybean, Meyer, Favoreto, Calandrelli, et al. (2017) assessed the host status of 64 soybean cultivars to *A. besseyi*. The final population ranged from 0.3 to 16.5 individuals per gram of fresh above-ground tissues. Only two cultivars presented low severity of symptoms. Based on this data, no correlation between resistance and disease severity was found.

There are different types of soil preparations, such as conventional tillage and conservational tillage, which can reduce nematode population and are respectively characterized by a high and low/no degree of soil disturbance, respectively. Tillage can be an effective control method for some PPN species, including *Aphelenchoides* spp. (Minton, 1986). However, depending on the degree and frequency of soil disturbance, tillage could present several negative effects, including soil erosion and reduced soil microbial diversity (De Freitas & Landers, 2014; Govaerts et al., 2006). In some cases, tillage can also have undesirable effects on the nematode populations. *H. glycines* populations in soybean were significantly higher in a conventional tillage system when compared to no-tilled plots (Tyler et al., 1983). For GSFR, Meyer and Klepker (2015) found conventional tillage to be effective when associated with strict weed management and early desiccation before soybean sowing.

## 6.2 | Biological control

Biological control can be defined as the use of living organisms to suppress the population density or impact of a specific pest organism (Poveda et al., 2020). In the past few decades, there has been an increase in the number of studies addressing the biological control of PPNs (Ahmad et al., 2021); however, *A. besseyi* in the context of soybean, cotton and common beans is an unexplored topic. Cotton farmers have been testing several tools to manage *A. besseyi*, including fungus-based nematicides, but without promising results (Machado, 2021). There are nevertheless promising microorganisms that are already used in (and registered to) these crops against other PPNs (e.g., *Meloidogyne* spp. and *P. brachyurus*) and, with proper adaptation, they have the potential to be used for *A. besseyi*. Among them are microbes belonging to the genera *Pochonia*, *Purpureocillium*, *Trichoderma* and *Bacillus* (Fontana et al., 2021; Poveda et al., 2020). Extensive research has shown these genera of microorganisms to be broad-spectrum, environmentally friendly and not harmful to humans (Hernández-Rosas et al., 2020). Based on this premise, it is essential to advance research studying the feasibility of using these biological control agents against the nematode *A. besseyi*.

As an above-ground pathogen, *A. besseyi* migrates from roots to the upper parts of the plant, spending less time in soil than other root-parasitic nematodes. Therefore, to ensure efficacious use of biological control, along with finding an efficient antagonist, it will also be important to identify when (e.g., before, during or after sowing)

and how (e.g., soil drench, seed treatment or spray) it should be applied into the soil to maximize the control. *A. besseyi* develops better in warm and humid conditions, so it is reasonable that the antagonist should be adapted to these conditions as well. We currently do not have enough information about the impact of mycophagy of *A. besseyi* on the efficiency of biological control fungi. Available data point towards *A. besseyi* being more selective to fungi than *A. pseudogoodeyi* (Oliveira et al., 2022), but the feeding plasticity of *A. besseyi* should be considered and host status of biological control fungi should be accessed before using them in infested areas.

## 6.3 | Potential novel solutions

A sustainable future of nematode control may require novel interventions, probably in conjunction with current interventions. Two potential options are discussed: induced resistance and blocking so-called 'parasitism genes'.

The phenomenon of induced resistance has been known for over 100 years, but it is one of the least explored management strategies. In some cases, induced resistance can lead to an improved defence state of plants, termed 'priming'. In this state, plants show a faster and/or stronger defence response upon pathogen and therefore leads to increased resistance or tolerance to biotic and abiotic stresses (Mauch-Mani et al., 2017).

Induced resistance can be triggered by both abiotic (e.g., silicon) and biotic (e.g., endophytic microorganisms) agents, locally or systemically (El-Saadony et al., 2021; Hammerschmidt, 2014). Increased resistance has been achieved to different pathogen groups, including PPNs (Choudhary et al., 2007; Fontana et al., 2021; Miao et al., 2019; Pieterse et al., 2014; Wang et al., 2017). The majority of reports addressing the effect of resistance inducers against PPNs investigated sedentary endoparasites, notably *Globodera* spp., *Heterodera* spp. and *Meloidogyne* spp. (Fontana et al., 2021; Sato et al., 2019). One of the few available works addressing induced resistance to control *A. besseyi* on rice was carried out by Ibrahim and Kurniawati (2020). In this, the seed treatment of chitosan, a known resistance inducer against different pathogens, was effective to control *A. besseyi* in rice. In another case, the exogenous application of benzo-(1,2,3)-thiadiazole-7-carbothioic acid *S*-methyl ester (BTH), methyl jasmonate (MeJa) and ethephon reduced the number of *A. besseyi* per rice plant (Xie et al., 2022). Taken together, the use of resistance inducers to manage *A. besseyi* on soybean, cotton and common bean has clear potential and conveniently, new products have been introduced in the market in recent years.

A long-standing goal of research in plant-parasitic nematology has been to use our understanding of how they infect plants to deliver control. Specifically, PPNs heavily rely on molecules called effectors. Effectors are primarily produced in the dorsal and subventral glands, and delivered into plant host through the stylet (Eves-van den Akker & Jones, 2018). Their role in parasitism is diverse, but usually related to manipulating the host metabolism, and gene expression, and suppressing plant immunity (Eves-van den Akker, 2021;

Molly et al., 2023). Two potential routes to emerge from this understanding: to disrupt the effectors themselves using RNA interference (RNAi), and to disrupt the targets of the effectors in the plant using genome editing (typically CRISPR/Cas).

Importantly, RNAi has been successfully deployed for other migratory endoparasites by Tan et al. (2013): *P. thornei* and *P. zaeae*. In their experiments, the *pat-10* and *unc-97* genes of both nematodes were silenced, resulting in paralysis and uncoordinated movements, to a higher degree in *P. thornei*. Its reproduction was dramatically decreased on carrot minidisks, with a reduction of 77%–81%. Taken together with the fact that transgenic expression of double-stranded RNA in planta has been used for a variety of PPNs (Eves-van den Akker, 2021; Molloy et al., 2023), there is clear potential for novel control solutions.

Similarly, effectors can be disrupted indirectly by disrupting their targets in the host using CRISPR/Cas9. Deleting or altering so-called susceptibility genes (*S* genes) within the host that the pathogen relies on for successfully infecting the plant can give rise to novel sources of resistance. For example, *SIWRKY45*, a negative regulator of jasmonic acid signalling, is targeted by *M. incognita* and deleting the gene by CRISPR/Cas9 leads to a reduction in gall index and nematode number (Huang et al., 2022). Another example is that of the metabolic pathway for vitamin B5 synthesis, which is incomplete in the beet cyst nematode *H. schachtii*, and the nematode depends on the host plant for the early steps of the pathway. Furthermore, deleting these early steps in the host leads to a reduction in nematode infection (Siddique et al., 2022).

Therefore, the identification of effectors and their targets in important hosts plants may play a role in the development of novel strategies for *A. besseyi*.

In the last decade, some progress has been made in this regard. Transcriptomic analysis of *A. besseyi* revealed 13 potential effectors from 41 candidate effector homologues. Among them, six had an unknown role, whereas the other seven presented varied functions, such as protein degradation and binding of host fatty acids (Wang et al., 2014). Huang et al. (2022) investigated the role of a new effector in rice parasitism, a serine carboxypeptidase termed *AbSCP1*. In situ hybridization and reverse transcription-quantitative PCR showed that this effector is exclusively expressed in oesophageal glands and upregulated in juveniles of *A. besseyi*. RNAi-treated nematodes, presenting reduced *AbSCP1* expression, presented lower reproduction and were less pathogenic on rice.

Although very promising, these strategies are likely in the distant future and will require continued advances in our understanding of *A. besseyi* infection biology.

## 7 | CONCLUSIONS AND FUTURE DIRECTIONS

The foliar nematode *A. besseyi* is an overlooked and emergent pathogen in Brazil. In warm and humid areas of the country it could lead to great losses, especially for common bean, soybean and cotton in an intense cropping system with a sequence of susceptible plants. Few

management tools are available to manage *A. besseyi* in Brazil; currently, no chemical nematicides are registered and genetic resistance is still unknown. Biological control and induced resistance are interesting tools, but they need further investigation. Cultural practices are the only available measures: tillage, which should be carefully considered due to its generally negative impact on overall soil health, and crop rotation with nonhost plants, which could help in decreasing nematode density in infested areas. Management should be carried out in an integrative approach to alleviate the losses caused by *A. besseyi*.

*A. besseyi* was first reported infesting strawberries in the United States, but the majority of the damage has been reported worldwide in rice. Currently, 113 plants are known to be hosts of *A. besseyi*, including important crops and weeds. The polyphagous trait of this nematode, as emphasized by the distribution of the plants parasitized, is a major challenge for its control and spread. Here, we raise the hypothesis that the dispersion of *A. besseyi* in Brazil could have happened by contaminated rice seeds and/or forage seeds (i.e., brachiarias). This needs to be confirmed through future research.

New genetic technologies could help in the control of *A. besseyi*. Here, RNAi and CRISPR/Cas9 are highlighted and can be achieved by understanding the molecular mechanisms of attack used by *A. besseyi* (i.e., effectors) and their targets within the plant. However, they are long-term and demand high collective effort from the scientific community.

Altogether, addressing the following knowledge gaps is paramount to developing future control measures against this threat: (a) which *Aphelenchoides* spp. are present and studied in Brazil, (b) which species are responsible for the greatest losses, (c) how can we optimize diagnosis, (d) which control measures are most effective against *Aphelenchoides* spp., (e) clarification of the host–parasite interaction(s), and most importantly, (f) is what happened in Brazil prophetic of other geographical regions?

## ACKNOWLEDGEMENTS

The authors would like to thank Dr Anindya Kundu, Dr Min-Yao Jhu and Dr Mário Inomoto for their valuable suggestions to the manuscript. Work on PPNs at the University of Cambridge is supported by DEFRA licence 125034/359149/3 and funded by BBSRC grants BB/R011311/1, BB/S006397/1 and BB/X006352/1, a Leverhulme grant RPG-2023-001 and a UKRI Frontier Research Grant EP/X024008/1. V.H.M.S. is supported by the European Union's Horizon 2020 research and innovation programme under grant agreement 101025218. S.M.P. would like to thank the National Council for Scientific and Technological Development (CNPq) of Brazil for the funding under grant 2020-2080.

## DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analysed.

## ORCID

Victor Hugo Moura de Souza  <https://orcid.org/0000-0002-7576-4676>

## REFERENCES

- Ahmad, G., Khan, A., Khan, A.A., Ali, A. & Mohamad, H.I. (2021) Biological control: a novel strategy for the control of the plant parasitic nematodes. *Antonie Van Leeuwenhoek*, 114, 885–912.
- Araya, C. (2008) Enfermedades y su combate. In: Hernández, J. & Ramírez, L. (Eds.) *Cultivo del frijol (Phaseolus vulgaris)*. San José, Costa Rica, Instituto Nacional de Innovación y Transferencia e Tecnología Agropecuaria (INTA): Manual de recomendaciones técnicas de cultivo de frijol, pp. 63–72.
- Asmus, G.L., Inomoto, M.M. & Borges, E.P. (2016) Manejo de *Pratylenchus brachyurus* com crotalária ou milho em área de produção de soja. *Embrapa Agropecuária Oeste*. Available at: <http://www.infoteca.cnptia.embrapa.br/infoteca/handle/doc/1054764> [Accessed 19th October 2023].
- Bala, S., Nihal, R. & Khan, M. (2019) Pathogenicity and population dynamics of foliar nematode, *Aphelenchoides besseyi* infecting tuberoses in West Bengal, India. *Journal of Environmental Biology*, 40, 1159–1163.
- Brazilian Ministry of Agriculture, Livestock and Food Supply (2008) Normas e Padrões para comercialização de sementes de espécies forrageiras de clima tropical. Available at: <https://www.gov.br/agricultura/pt-br/assuntos/insumos-agropecuarios/insumos-agricolas/sementes-e-mudas/publicacoes-sementes-e-mudas/INN30de21demaide2008.pdf> [Accessed 19th October 2023].
- Brazilian Ministry of Agriculture. (2015) *Ministério da Agricultura mapeia principais pragas das lavouras brasileiras*. Livestock and Food Supply (MAPA): Ministry of Agriculture.
- Brazilian System of Phytosanitary Agrochemicals. (2022) Ministry of Agriculture. *Livestock and Food Supply (AGROFIT - MAPA/Brazil)*.
- Bridge, J., Luc, M. & Plowright, R.A. (1990) Nematode parasites of rice. In: Luc, M., Sikora, R.A. & Bridge, J. (Eds.) *Plant parasitic nematodes in subtropical and tropical agriculture*. Wallingford: CAB International, pp. 69–108.
- Bridge, J., Plowright, R.A. & Peng, D. (2005) Nematode parasites of rice. In: Luc, M., Sikora, R.A. & Bridge, J. (Eds.) *Plant parasitic nematodes in subtropical and tropical agriculture*. Wallingford: CAB International, pp. 87–130.
- Calandrelli, A., da Silva, M.C.M., França, P.P., Favoreto, L. & Meyer, M.C. (2018) Hospedabilidade de arroz e aveia branca a populações de *Aphelenchoides besseyi*. *Jornada Acadêmica da Embrapa Soja*, 13, 223–228.
- Calandrelli, A., Silva, M., Miamoto, A., Rinaldi, L., Favoreto, L., Meyer, M. et al. (2023) Host-parasite relationship between *Aphelenchoides besseyi* and soybean. *Nematology*, 25, 33–44.
- Cares, J.E., Santos, J.R.P. & Tenente, R.C.V. (2008) Taxonomia de Nematóides de Sementes, Bulbos e Caules - Parte II. *Revisão Anual de Patologia de Plantas*, 16, 39–84.
- Chaves, N.F. & Araya, C.M. (2012) Efecto de la rotación de cultivos en la incidencia del amachamiento (*Aphelenchoides besseyi* Christie) en frijol. *Agronomía Costarricense*, 36, 61–70.
- Chaves, N.F., Cervantes, E., Zabalgoeazcoa, I. & Araya, C. (2013) *Aphelenchoides besseyi* Christie (Nematoda: Aphelenchoididae), agente causal del amachamiento del frijol comun. *Tropical Plant Pathology*, 38, 243–252.
- Chen, P. & Tsay, T.T. (2006) Effect of crop rotation on *Meloidogyne* spp. and *Pratylenchus* spp. populations in strawberry fields in Taiwan. *Journal of Nematology*, 38, 339–344.
- Choudhary, D.K., Prakash, A. & Johri, B.N. (2007) Induced systemic resistance (ISR) in plants: mechanism of action. *Indian Journal of Microbiology*, 47, 289–297.
- Christie, J.R. (1942) A description of *Aphelenchoides besseyi* n. sp., the summer-dwarf nematode of strawberries, with comments on the identity of *Aphelenchoides subtenuis* (cobb, 1926) and *Aphelenchoides hodsoni* Goodey, 1935. *Proceedings of the Helminthological Society of Washington*, 9, 82–84.
- da Silva, M.C.M., Calandrelli, A., Favoreto, L. & Meyer, M.C. (2018) Patogenicidade de populações de *Aphelenchoides besseyi* Christie, 1942 a diferentes espécies de plantas. *Congresso Brasileiro de Nematologia*, 35, 133 Available from: <https://ainfo.cnptia.embrapa.br/digital/bitstream/item/181687/1/p-133-Anais-35CBN.pdf> [Accessed 19th October 2023].
- da Silva, M.C.M., Calandrelli, A., França, P.P., Favoreto, L. & Meyer, M.C. (2018) Ocorrência de *Aphelenchoides besseyi* em espécies de plantas invasoras. *Jornada Acadêmica da Embrapa Soja*, 13, 229–234.
- da Silva, S.A. & Machado, A.C.Z. (2022) Santino's growth chamber: a chamber for studies with *Aphelenchoides besseyi* on plants. *MethodsX*, 9, 101780.
- da Silveira, S.G.P. & Curi, S.M. (1990) Two hosts of *Aphelenchoides besseyi* in Brazil. *Nematologia Brasileira*, 14, 146–150.
- de Freitas, P.L. & Landers, J.N. (2014) The transformation of agriculture in Brazil through development and adoption of zero tillage conservation agriculture. *International Soil and Water Conservation Research*, 2, 35–46.
- de Jesus, D.S. & Cares, J.E. (2016) Gênero *Aphelenchoides*. In: de Oliveira, C.M.G., dos Santos, M.A. & Castro, L.H.S. (Eds.) *Diagnose de Fitonematoides*. Campinas, SP: Editora Millennium.
- Decraemer, W. & Geraert, E. (2006) Ectoparasitic nematodes. In: *Plant nematology*. Wallingford: CAB International, pp. 153–184.
- Desaeger, J., Wram, C. & Zasada, I. (2020) New reduced-risk agricultural nematicides – rationale and review. *Journal of Nematology*, 52, 1–16.
- Dias, W.P., Garcia, A., Silva, J.F.V. & de Carneiro, G.E. (2010) Nematóides em soja: identificação e controle. *Embrapa Soja. Circular Técnica*, 76. Available at: <http://www.infoteca.cnptia.embrapa.br/infoteca/handle/doc/854178> [Accessed 19th October 2023]
- El-Saadony, M.T., Abuljadayel, D.A., Shafi, M.E., Albaqami, N.M., Desoky, E.-S.M., El-Tahan, A.M. et al. (2021) Control of foliar phytoparasitic nematodes through sustainable natural materials: current progress and challenges. *Saudi Journal of Biological Sciences*, 28, 7314–7326.
- EPPO. (2017) PM 7/39 (2) *Aphelenchoides besseyi*. *EPPO Bulletin*, 47, 384–400.
- Escuer, M. & Bello, A. (2000) Nematodos del género *Aphelenchoides* de interés fitopatológico y su distribución en España. *Boletín de Sanidad Vegetal Plagas*, 26, 47–63.
- Eves-van den Akker, S. (2021) Plant-nematode interactions. *Current Opinion in Plant Biology*, 62, 102035.
- Eves-van den Akker, S. & Jones, J.T. (2018) Sex: not all that it's cracked up to be? *PLoS Genetics*, 14, e1007160.
- Favoreto, L., Bueno, R., Calandrelli, A., França, P.P., Meyer, M.C. & Machado, A.C.Z. (2022) *Aphelenchoides besseyi* parasitizing cowpea (*Vigna unguiculata*) in Brazil. *Plant Disease*, 106, 1555–1557.
- Favoreto, L., Faleiro, V.O., Freitas, M.A., Brauwiers, L.R., Galbieri, R., Homiak, J.A. et al. (2018) First report of *Aphelenchoides besseyi* infecting the aerial part of cotton plants in Brazil. *Plant Disease*, 102, 2662.
- Favoreto, L., Faleiro, V.O., Freitas, M.A., Galbieri, R., Brauwiers, L.R., Homiak, J.A. et al. (2017) Identificação taxonômica de *Aphelenchoides* sp. infectando plantas de algodoeiro no Mato Grosso. *Congresso Brasileiro de Fitopatologia*, 50 Available from: <http://www.alice.cnptia.embrapa.br/alice/handle/doc/1078798> [Accessed 19th October 2023].
- Favoreto, L. & Meyer, M.C. (2017) "Soja Louca II" – green stem and foliar retention – a new soybean disease in Brazil. *Nematropica*, 47, 13.
- Favoreto, L. & Meyer, M.C. (2018) Diagnose, hospedeiros e manejo de *Aphelenchoides besseyi*. In: XXXV Congresso Brasileiro de Nematologia. Brasília: EMBRAPA, pp. 60–62 Available at: <http://www.alice.cnptia.embrapa.br/alice/handle/doc/1094187> [Accessed 19th October 2023]
- Favoreto, L. & Meyer, M.C. (2019) Desvendando a Soja Louca II. In: XXXVI Congresso Brasileiro de Nematologia, pp. 1–4 Available at: <http://www.alice.cnptia.embrapa.br/alice/handle/doc/1110585> [Accessed 19th October 2023].

- Favoreto, L., Meyer, M.C., Calandrelli, A., Maia da Silva, M.C., Aleandro da Silva, S. & Machado, A.C.Z. (2021) *Aphelenchoides besseyi* parasitizing common bean in Brazil. *Plant Disease*, 105, 748–751.
- Ferraz, S., de Freitas, L.G., Lopes, E.A. & Dias-Arieira, C.R. (2010) *Manejo sustentável de fitonematoides*. Viçosa, MG: Editora UFV.
- Fontana, D.C., de Paula, S., Torres, A.G., de Souza, V.H.M., Pascholati, S.F., Schmidt, D. et al. (2021) Endophytic fungi: biological control and induced resistance to phytopathogens and abiotic stresses. *Pathogens*, 10, 570.
- Fortuner, R. (1970) On the morphology of *Aphelenchoides besseyi* Christie, 1942 and *A. siddiqii* n.sp. (Nematoda, Aphelenchoidea). *Journal of Helminthology*, 44, 141–152.
- Fortuner, R. & Williams, K.J. (1975) Review of the literature on *Aphelenchoides besseyi* Christie, 1942, the nematode causing white tip disease in rice. *Nematology*, 44, 1–40.
- Gilioli, J.L., Prince, P., Gilioli, B.L. & Gilioli, A.L. (2007) Quais as causas da soja louca? In: *XXIX Reunião de Pesquisa de Soja da Região Central do Brasil*. pp. 61 Available at: [https://ainfo.cnptia.embrapa.br/digital/bitstream/CNPSO-2009-09/27822/1/resumos\\_rpsrcb\\_2007.pdf](https://ainfo.cnptia.embrapa.br/digital/bitstream/CNPSO-2009-09/27822/1/resumos_rpsrcb_2007.pdf) [Accessed 19th October 2023].
- Girgan, C., Swart, A., Marais, M. & Fourie, H. (2018) *Aphelenchoides* spp. (Nematoda: Aphelenchida) and *Panagrolaimus leperisini* (Nematoda: Rhabditida) found associated with grass seeds in the Telperion nature reserve, South Africa. *Zootaxa*, 4370, 137–155.
- Gokte, N., Mathur, V.K., Lal, A. & Rajan. (1992) On the occurrence of *Aphelenchoides besseyi* and some free living nematode species in *Stylosanthes hamata* seeds. *Nematologia Mediterranea*, 20, 63.
- Goodey, J.B., Franklin, M.T. & Hooper, D.J. (1965) *T. Goodey's the nematode parasites of plants catalogued under their hosts*, 3rd edition. Farnham: Commonwealth Agricultural Bureaux.
- Govaerts, B., Mezzalama, M., Sayre, K.D., Crossa, J., Nicol, J.M. & Deckers, J. (2006) Long-term consequences of tillage, residue management, and crop rotation on maize/wheat root rot and nematode populations in subtropical highlands. *Applied Soil Ecology*, 32, 305–315.
- Hammerschmidt, R. (2014) Introduction: definitions and some history. In: Walters, D.R., Newton, A.C., Lyon, G.D. (Eds.) *Induced resistance for plant defense*. Chichester, UK: John Wiley & Sons, Ltd, pp. 1–10.
- Hernández-Rosas, F., Figueroa-Rodríguez, K.A., García-Pacheco, L.A., Velasco-Velasco, J. & Sangerman-Jarquín, D.M. (2020) Microorganisms and biological pest control: an analysis based on a bibliometric review. *Agronomy*, 10, 1808.
- Hoshino, S. & Togashi, K. (2020) Effects of temperatures on survival of *Aphelenchoides besseyi* in prolonged storage of rice grains. *Nematology*, 22, 1169–1177.
- Huang, C.S., Cupertino, F.P. & Martinelli, N.M. (1977) Incidence of white-tip nematode, *Aphelenchoides besseyi*, in stored rice seed from central-West Brazil. *Pans*, 23, 65–67.
- Huang, H., Zhao, W., Qiao, H., Li, C., Sun, L., Yang, R. et al. (2022) SIWRKY45 interacts with jasmonate-ZIM domain proteins to negatively regulate defense against the root-knot nematode *Meloidogyne incognita* in tomato. *Horticulture Research*, 9, uhac197.
- Ibrahim, A.Y. & Kurniawati, F. (2020) The efficacy of chitosan to control nematode *Aphelenchoides besseyi* Christie through seed treatment. *IOP Conference Series: Earth and Environmental Science*, 468, 012025.
- Inomoto, M.M. (2016) Técnicas clássicas da diagnose de fitonematoides. In: de Oliveira, C.M.G., dos Santos, M.A. & Castro, L.H.S. (Eds.) *Diagnose de Fitonematoides*. Editora Millennium: Campinas, SP, pp. 255–276.
- Inomoto, M.M. & Asmus, G.L. (2010) Host status of graminaceous cover crops for *Pratylenchus brachyurus*. *Plant Disease*, 94, 1022–1025.
- International Plant Protection Convention – IPPC. (2016) Diagnostic protocols for regulated pests (DP 17): *Aphelenchoides besseyi*, *A. fragariae* and *A. ritzemabosi*. Available at: [https://www.ippc.int/static/media/files/publication/en/2016/11/DP\\_17\\_2016\\_En\\_2016-11-01\\_iaK6Hls.pdf](https://www.ippc.int/static/media/files/publication/en/2016/11/DP_17_2016_En_2016-11-01_iaK6Hls.pdf) [Accessed 19th October 2023].
- Jones, J.T., Haegeman, A., Danchin, E.G.J., Gaur, H.S., Helder, J., Jones, M.G.K. et al. (2013) Top 10 plant-parasitic nematodes in molecular plant pathology. *Molecular Plant Pathology*, 14, 946–961.
- Kermarrec, A. & Anais, A. (1974) Presence of *Aphelenchoides besseyi* in foliage and tubers of yam (*Dioscorea trifida*) in the French West Indies. *Nematropica*, 4, 2–3.
- Kerry, B.R. (1992) Biological control of nematodes: prospects and opportunities. In: Maqbool, M.A. & Kerry, B.R. (Eds.) *Plant nematode problems and their control in the near east region*. Karachi, Pakistan: FAO Plant Production and Protection Paper. Available from: <https://www.fao.org/3/v9978e/v9978eOb.htm#biological%20control%20of%20nematodes:%20prospects%20and%20opportunities> [Accessed 31st October 2023]
- Khan, M.R., Handoo, Z.A., Rao, U., Rao, S.B. & Prasad, J.S. (2012) Observations on the foliar nematode, *Aphelenchoides besseyi*, infecting tuberose and rice in India. *Journal of Nematology*, 44, 391–398.
- Kluthcouski, J., Cordeiro, L.A.M., Ceccon, G. & de Oliveira, P. (2013) Braquiária na agropecuária brasileira: uma história de sucesso. In: Ceccon, G. (Ed.) *Consórcio milho-braquiária*. Brasília, DF: Embrapa. Available at: <http://www.infoteca.cnptia.embrapa.br/infoteca/handle/doc/982611> [Accessed 19th October 2023]
- Kohl, L.M. (2011) Foliar nematodes: a summary of biology and control with a compilation of host range. *Plant Health Progress*, 12. Available from: <https://doi.org/10.1094/PHP-2011-1129-01-RV>
- Machado, A.C.Z. (2021) Problems and solutions to integrated nematode management of root-knot, reniform and lesion nematodes in cotton in Brazil. In: Sikora, R., Desaeer, J. & Molendijk, L. (Eds.) *Integrated nematode management: state-of-the-art and visions for the future*. Wallingford: CABI International, pp. 73–79.
- Marchi, C., Fernandes, C., Borges, C., Santos, J., Jerba, V., Trentin, R. et al. (2007) Phytopathogenic nematofauna of commercial seeds of tropical forages. *Pesquisa Agropecuária Brasileira*, 42, 655–660.
- Marlatt, R.B. (1970) Transmission of *Aphelenchoides besseyi* to *Fiscus elastica* leaves via *Sporobolus poiretti* inflorescences. *Phytopathology*, 60, 543–544.
- Mauch-Mani, B., Baccelli, I., Luna, E. & Flors, V. (2017) Defense priming: an adaptive part of induced resistance. *Annual Review of Plant Biology*, 68, 485–512.
- Meyer, M.C., Almeida, A.M.R., Gazziero, D.L.P. & de Lima, D. (2010) *Soja louca II: um problema de causa desconhecida*. Londrina, PR: Embrapa Soja. Available at: <https://ainfo.cnptia.embrapa.br/digital/bitstream/item/35775/1/Folder-Soja-louca11.pdf> [Accessed 19th October 2023].
- Meyer, M.C., Favoreto, L., Calandrelli, A. & da Silva, M.C.M. (2017) Reação de cultivares de soja ao nematoide *Aphelenchoides besseyi*. In: *Congresso Brasileiro de Fitopatologia*. Uberlândia, MG - Brazil: 50° Congresso Brasileiro de Fitopatologia, p. 50. Available at: <http://www.alice.cnptia.embrapa.br/alice/handle/doc/1078811> [Accessed 19th October 2023]
- Meyer, M.C., Favoreto, L., Klepker, D. & Marcelino-Guimarães, F.C. (2017) Soybean green stem and foliar retention syndrome caused by *Aphelenchoides besseyi*. *Tropical Plant Pathology*, 42, 403–409.
- Meyer, M.C., Gilioli, J.L. & Prince, P.C. (2008) Efeito de doses de herbicidas e sistemas de semeadura na incidência de retenção foliar e haste verde, em cultivares de soja, no Maranhão e Tocantins. In: *XXX Reunião de Pesquisa de Soja da Região Central do Brasil*. Londrina, Brazil: EMBRAPA Soja, pp. 133–136.
- Meyer, M.C. & Klepker, D. (2015) Efeito do manejo de solo e sistemas de cultivo na incidência de Soja Louca II. In: *Congresso Brasileiro de Fitopatologia*. Uberlândia, Brazil: 50° Congresso Brasileiro de Fitopatologia, p. 48 Available at: <https://ainfo.cnptia.embrapa.br/digital/bitstream/item/130590/1/430-1.pdf> [Accessed 19th October 2023].
- Miao, G., Han, J., Zhang, K., Wang, S. & Wang, C. (2019) Protection of melon against *Fusarium* wilt-root knot nematode complex by endophytic fungi *Penicillium brefeldianum* HS-1. *Symbiosis*, 77, 83–89.

- Minton, N.A. (1986) Impact of conservation tillage on nematode populations. *Journal of Nematology*, 18, 135–140.
- Molloy, B., Baum, T. & Eves-van den Akker, S. (2023) Unlocking the development-and physiology-altering 'effector toolbox' of plant-parasitic nematodes. *Trends in Parasitology*, 39, 732–738.
- Monteiro, T., Nasu, E., Guimarães, C., Neves, W., Mizobutsi, E. & Freitas, L. (2014) Redução de inóculo de *Aphelenchoides besseyi* em sementes de *Brachiaria brizantha* tratadas com óleos essenciais. *Ciência Rural*, 44, 1149–1154.
- Morales, F.J., Araya, C.M., Hernandez, J.C., Arroyave, J.A., Cuervo, M., Velasco, A.C. et al. (1999) Etiología del amachamiento del frijol común en Costa Rica. *Manejo Integrado de Plagas*, 52, 42–48.
- Nicol, J.M., Turner, S.J., Coyne, D.L., den Nijs, L., Hockland, S. & Maafi, Z.T. (2011) Current nematode threats to world agriculture. In: Jones, J., Gheysen, G. & Fenoll, C. (Eds.) *Genomics and molecular genetics of plant-nematode interactions*. Dordrecht: Springer Netherlands, pp. 21–43.
- Noronha, M.A., Assunção, M.C., Costa, M.G.S., Muniz, M.F.S., Favoreto, L., Sercero, B.C. et al. (2020) First report of *Aphelenchoides besseyi* causing leaf spot on yam (*Dioscorea cayenensis*) in Brazil. *Plant Disease*, 104, 3083–3084.
- Noronha, M.A., Assunção, M.C., Muniz, M.S. et al. (2023) *Aphelenchoides besseyi* causing leaf spot on cowpea under field conditions in Brazil. *Australasian Plant Disease Notes*, 18, 11.
- Oliveira, C. & Kubo, R. (2006) Novos assinalamentos de nematóides de parte aérea (*Aphelenchoides* spp.) em plantas de begônia no Brasil. *Revista Brasileira de Horticultura Ornamental*, 12, 134–137.
- Oliveira, C.J., Schumacher, L.A., Peres, N.A., Brito, J.A., Suarez, M. & Desaegeer, J. (2022) Feeding selectivity of *Aphelenchoides besseyi* and *A. pseudogoodeyi* on fungi associated with Florida strawberry. *Plant Disease*, 106, 1929–1934.
- Oliveira, C.J., Subbotin, S.A., Alvarez-Ortega, S., Desaegeer, J., Brito, J.A., Xavier, K.V. et al. (2019) Morphological and molecular identification of two Florida populations of foliar nematodes (*Aphelenchoides* spp.) isolated from strawberry with the description of *Aphelenchoides pseudogoodeyi* sp. n. (Nematoda: Aphelenchoididae) and notes on their bionomics. *Plant Disease*, 103, 2825–2842.
- Oliveira, C.M.G., Kanazawa, T.Y. & Consoli, E.A. (2009) *Identificação molecular de Aphelenchoides besseyi* em sementes de forrageiras. São Paulo: Centro Experimental Central do Instituto Biológico.
- Pérez, A. & Fernández, E. (2004) Nuevos hospedantes de *Aphelenchoides besseyi* (CHRISTIE, 1942) en Cuba. *Fitosanidad*, 8, 45–46.
- Pieterse, C.M.J., Zamioudis, C., Berendsen, R.L., Weller, D.M., van Wees, S.C.M. & Bakker, P.A.H.M. (2014) Induced systemic resistance by beneficial microbes. *Annual Review of Phytopathology*, 52, 347–375.
- Pinheiro, F.P., Vianello, R.P., Ebeidalla, F.S. & Tenente, R.C.V. (1997) Thermal seed treatments to eradicate *Aphelenchoides besseyi* from *Brachiaria dictyoneura*. *Nematologia Brasileira*, 21, 92–97.
- Poveda, J., Abril-Urias, P. & Escobar, C. (2020) Biological control of plant-parasitic nematodes by filamentous fungi inducers of resistance: *Trichoderma*, mycorrhizal and endophytic fungi. *Frontiers in Microbiology*, 11, e00992.
- Ranulfi, A.C., Senesi, G.S., Caetano, J.B., Meyer, M.C., Magalhães, A.B., Villas-Boas, P.R. et al. (2018) Nutritional characterization of healthy and *Aphelenchoides besseyi* infected soybean leaves by laser-induced breakdown spectroscopy (LIBS). *Microchemical Journal*, 141, 118–126.
- Rodrigues, D.B., Dias-Arieira, C.R., Vedoveto, M.V.V., Roldi, M., Molin, H.F.D. & Abe, V.H.F. (2014) Crop rotation for *Pratylenchus brachyurus* in soybean. *Nematropica*, 44, 146–151.
- Samina, S. & Iqbal, E. (2019) Nematode fauna of Kurram agency, Pakistan. *Pakistan Journal of Nematology*, 37, 1–20.
- Sánchez-Monge, A., Flores, L., Salazar, L., Hockland, S. & Bert, W. (2015) An updated list of the plants associated with plant-parasitic *Aphelenchoides* (Nematoda: Aphelenchoididae) and its implications for plant-parasitism within this genus. *Zootaxa*, 4013, 207–224.
- Santos, M.A., Castro, L.H.S. & Guimarães, E.C. (2016) Diagnose de fitonematoides no campo, técnicas de amostragem e geoestatística. In: de Oliveira, C.M.G., dos Santos, M.A. & Castro, L.H.S. (Eds.) *Diagnose de fitonematoides*. Campinas, SP: Editora Millennium.
- Sasanelli, N., Konrat, A., Migunova, V., Toderas, I., Iurcu-Straistaru, E., Rusu, S. et al. (2021) Review on control methods against plant parasitic nematodes applied in southern member states (C zone) of the European Union. *Agriculture*, 11, 602.
- Sato, K., Kadota, Y. & Shirasu, K. (2019) Plant immune responses to parasitic nematodes. *Frontiers in Plant Science*, 10, e01165.
- Siddique, S., Radakovic, Z.S., Hiltl, C., Pellegrin, C., Baum, T.J., Beasley, H. et al. (2022) The genome and lifestyle-specific transcriptomes of a plant-parasitic nematode and its host reveal susceptibility genes involved in trans-kingdom synthesis of vitamin B5. *Nature Communications*, 13, 6190.
- Sikora, R.A., Molendijk, L.P.G. & Desaegeer, J. (2021) Integrated nematode management and crop health: future challenges and opportunities. In: Sikora, R.A., Desaegeer, J. & Molendijk, L.P.G. (Eds.) *Integrated nematode management: state-of-the-art and visions for the future*. Wallingford: CAB, pp. 3–10.
- Smith, R.F. & Reynolds, H.T. (1966) Principles, definitions and scope of integrated pest control. In: *FAO symposium on integrated pest control*, 1. Rome: FAO, pp. 11–17.
- Solano, O.M.F. & Solís, A.S.Q. (2013) Nematodos asociados a los cultivos de Costa Rica. In: *Ministerio de Agricultura y Ganadería. Servicio Fitosanitario del Estado*.
- Sosa-Gómez, D.R. & Moscardi, F. (1995) Differential foliar retention on soybean by stink bugs (Heteroptera: Pentatomidae). *Anais da Sociedade Entomológica do Brasil*, 24, 401–404.
- Souza, V.H.M. & Inomoto, M.M. (2019) Host suitability of grain sorghum and Sudangrass for *Pratylenchus brachyurus*. *Arquivos do Instituto Biológico*, 86. Available from: <https://doi.org/10.1590/1808-165700262019>
- Subbotin, S.A., Oliveira, C.J., Álvarez-Ortega, S., Desaegeer, J.A., Crow, W., Overstreet, C. et al. (2021) The taxonomic status of *Aphelenchoides besseyi* Christie, 1942 (Nematoda: Aphelenchoididae) populations from the southeastern USA, and description of *Aphelenchoides pseudobesseyi* sp. n. *Nematology*, 23, 381–413.
- Tan, J.-A.C.H., Jones, M.G.K. & Fosu-Nyarko, J. (2013) Gene silencing in root lesion nematodes (*Pratylenchus* spp.) significantly reduces reproduction in a plant host. *Experimental Parasitology*, 133, 166–178.
- Tiwari, S.P. & Khare, M.N. (2003) White tip caused by *Aphelenchoides besseyi*, an important seed borne disease of rice. In: Trivedi, P.C. (Ed.) *Advances in nematology*. Jodhpur: Scientific Publishers, pp. 103–114.
- Tülek, A., Kepenekçi, I., Çiftçigil, T., Sürek, H., Akin, K. & Kaya, R. (2015) Reaction of some rice cultivars to the white tip nematode, *Aphelenchoides besseyi*, under field conditions in the Thrace region of Turkey. *Turkish Journal of Agriculture and Forestry*, 39, 958–966.
- Tyler, D.D., Overton, J.R. & Chambers, A.Y. (1983) Tillage effects on soil properties, diseases, cyst nematodes, and soybean yields. *Journal of Soil and Water Conservation*, 38, 374–376.
- UCDavis Database. (2022) *Host range of a genus and species of plant-feeding nematodes*. Available at: <http://nemalex.ucdavis.edu/Nemabase2010/GenusPageHostRangeResults.aspx?Ngenus=Aphelenchoides> [Accessed 19th October 2023].
- Uchida, J.Y. & Sipres, B.S. (1998) *Foliar nematodes on orchids in Hawaii*. Manoa: University of Hawaii. Cooperative Extension Service, pp. 1–7.
- Wang, F., Li, D., Wang, Z., Dong, A., Liu, L., Wang, B. et al. (2014) Transcriptomic analysis of the rice white tip nematode, *Aphelenchoides besseyi* (Nematoda: Aphelenchoididae). *PLoS One*, 9, e91591.
- Wang, L., Li, H., Zhao, C., Li, S., Kong, L., Wu, W. et al. (2017) The inhibition of protein translation mediated by AtGCN1 is essential for cold tolerance in *Arabidopsis thaliana*. *Plant, Cell & Environment*, 40, 56–68.



- Xie, J., Yang, F., Xu, X., Peng, Y. & Ji, H. (2022) Salicylic acid, jasmonate, and ethylene contribute to rice defense against white tip nematodes *Aphelenchoides besseyi*. *Frontiers in Plant Science*, 12, e755802.
- Xu, X., Qing, X., Xie, J.L., Yang, F., Peng, Y.L. & Ji, H.L. (2020) Population structure and species delimitation of rice white tip nematode, *Aphelenchoides besseyi* (Nematoda: Aphelenchoididae), in China. *Plant Pathology*, 69, 159–167.
- Zhuo, K., Cui, R., Ye, W., Luo, M., Wang, H., Hu, X. et al. (2010) Morphological and molecular characterization of *Aphelenchoides fujianensis* n. sp. (Nematoda: Aphelenchoididae) from *Pinus massoniana* in China. *Zootaxa*, 2509, 9–52.

**How to cite this article:** de Souza, V.H.M., Philadelphi, S.M., Galbieri, R., Sonawala, U. & Eves-van den Akker, S. (2024) An emergent plant-parasitic nematode in Brazil: *Aphelenchoides besseyi*. Current status and research perspectives. *Plant Pathology*, 73, 478–491. Available from: <https://doi.org/10.1111/ppa.13829>