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RESEARCH ARTICLE

Polysaccharide-based compound from the fungus *Pycnoporus sanguineus* for the protection of tomato plants against *Meloidogyne incognita*

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ABSTRACT

New control strategies for *Meloidogyne incognita* are needed to meet the global demand for environmentally safe methods. The objective of this study was to use crude polysaccharide extract (CPE) from the basidiocarp of *Pycnoporus sanguineus* for the control of *M. incognita* in tomato (*Solanum lycopersicum* L.) plants. Concentrations of 0, 100, 200, 400, and 500 mg L^{-1} CPE were used as well as three application methods for nematode control: Root immersion, foliar spraying, and a combination of both, all performed 3 d before pathogen inoculation. The number of galls and egg masses, egg viability, number of eggs and second-stage juveniles (J2) in the soil and root, as well as the reproduction factor, were evaluated. In the assays with different concentrations, reductions were observed in the number of galls (50%), egg masses (67%), nematodes in the soil (64%) and egg viability (76%) in concentrations 400, 500, 500 and 200 mg L^{-1}, respectively. The most efficient application method was the combination of foliar spraying and root immersion using 500 mg L^{-1} CPE, which led to 70% and 74% reductions in root and soil nematodes, respectively, a 62% decline in egg viability, and a 68% decrease in the reproduction factor. These results indicate the potential of crude polysaccharide extract from *P. sanguineus* for the control of *M. incognita* in tomato plants.

Key words: Alternative control, basidiomycete, induced resistance, nematode, *Solanum lycopersicum*.

INTRODUCTION

Plant-parasitic nematodes negatively affect the production of various crops, causing 21.3% annual losses worldwide (Kumar et al., 2020). Root-knot nematodes of the genus *Meloidogyne* Goeldi are the main ones that cause damage to tomato (*Solanum lycopersicum* L.) plants, especially the species *M. incognita* (Kofoid and White) Chitwood and *M. javanica* (Treub) Chitwood (Subedi et al., 2020). These nematodes are root-knot, polyphagous endoparasites that represent a serious threat to global food security (Shukla et al., 2018; Abolusoro et al., 2020).

Given the difficulty in managing nematodes, different control methods are necessary to enable integrated action aimed at reducing populations of this pathogen. One of these methods is the induction of resistance, achieved through chemical products, plant extracts, or substances derived from microorganisms such as viral envelope proteins, fungal or bacterial proteins, lipoproteins, lipopolysaccharides, and exopolysaccharides (Blainski et al., 2018).

Basidiomycetes are fungi known to be reservoirs of bioactive metabolites, and considerable attention has been given to the exploration of these metabolites as an innovative alternative in crop protection (Tsivileva et al., 2024). The use of basidiomycetes for nematode management shows promise, as many basidiomycete macrofungi produce various compounds with nematicidal and insecticidal properties (Themuhi et al., 2020).

The bioactive compound from *Neonothopanus nambi* has been used to control plant diseases, particularly root-knot nematodes (Bua-Art et al., 2010). Root immersion treatment with *Ganoderma lucidum* reduced the infection level of *M. incognita* and promoted eggplant growth (Fatima et al., 2022). Extracts of the *Pleurotus ostreatus*, *P. citrinopileatus*, *P. pulmonarius*, and *Boletus* sp. basidiomycetes were used on lettuce and reduced root-knot nematode infestation (Wille et al., 2019).

Another basidiomycete with potential for nematode control is *Pycnoporus sanguineus*, which shows strong potential to produce natural pigments, especially cinnabarin. This compound, together with other substances produced by the fungus, exhibits antiviral, antioxidant, antifungal, antibacterial, and antiparasitic activities (Pineda-Insuasti et al., 2017). Extracts from *P. sanguineus* can act as resistance inducers and contribute to the management of plant-parasitic nematodes (Barbosa et al., 2021; Tasca et al., 2022; Brito et al., 2025).

The use of polysaccharides extracted from basidiomycetes has shown promise for pathogen control. Polysaccharides are long, complex carbohydrate chains composed of neutral sugars and/or uronic acid monomers linked by glycosidic bonds (Leong et al., 2020). Growing interest has been directed toward carbohydrates due to their role in plant immunity. Some function as inducers of plant defenses (Aguiar et al., 2018; Tsivileva et al., 2024), while others act as signaling molecules in a manner like phytohormones (Trouvelot et al., 2014).

Plants respond to biotic and abiotic stresses through different defense mechanisms (Oliveira et al., 2016). They possess a range of structural and biochemical strategies that contribute to resistance against phytopathogens (Stangarlin et al., 2011). These mechanisms may be pre- or post-formed in relation to the onset of infection, and in cases of induced resistance, it is the post-formed mechanisms that are activated by treatment. Post-formed structural mechanisms include mechanical barriers characterized by increased production and deposition of substances capable of restricting pathogen invasion, such as papillae, halos, lignification, cork layers, abscission layers, tyloses, and exudates like hesperidin. Post-formed chemical barriers involve higher concentrations or activities of defense proteins or enzymes and the synthesis of antimicrobial compounds such as phenols, phytoalexins, pathogenesis-related proteins, reactive oxygen species, terpenes, and others (Pascholati and Dalio, 2018).

The induced resistance strategy consists of stimulating the plant's defense system with elicitors, natural molecules that mimic pathogen attack or a state of danger, or with living organisms (Burketova et al., 2015). Proteins isolated from basidiocarps of *P. sanguineus* can induce peroxidase activity in tomato plants, especially in interaction with *M. javanica*, suggesting active participation in lignification and possible prevention of feeding site formation by nematodes (Brito et al., 2025).

This study aimed to examine the effectiveness of carbohydrates extracted from basidiocarps of *P. sanguineus* for the control of *M. incognita* in tomato plants, seeking an efficient method for nematode control using biomolecules that cause less environmental impact.

MATERIAL AND METHODS

Meloidogyne incognita populations

Meloidogyne incognita, identified based on the configuration of the perineal pattern (Hartman and Sasser, 1985), was obtained from tomato (*Solanum lycopersicum* L.) roots maintained in a greenhouse. For egg and nematode extraction, the roots were washed in running water and ground in a blender in a 0.5% sodium hypochlorite solution for 30 s at low speed (Freitas et al., 2007). The ground material was passed through a 48-mesh sieve over a 500-mesh sieve, and the material retained in the latter was quantified using a Peters chamber.

Extraction of crude polysaccharide extract from *Pycnoporus sanguineus*

Basidiocarps of *P. sanguineus* produced on substrate (Martinazzo-Portz et al., 2025) were dried in an oven at 40 °C for 2 h and ground in a blender. Basidiocarps were bright reddish-orange, with short or sessile pilei, sometimes overlapping, with a leathery to corky consistency (according to Téllez-Téllez et al., 2016). Seventy grams of basidiocarps were ground and added to 2.1 L distilled water and kept at 70 °C for 8 h. Pre-filtration was carried out using a funnel lined with filter paper, followed by vacuum filtration through a 0.45 µm pore membrane. The volume of the solution was reduced in an oven at 55 °C, and three parts (v/v) of absolute analytical-grade ethanol were added to the reduced volume. The mixture was kept at -20 °C for 48 h. After discarding the supernatant, the residue was rotary evaporated at 50 °C and 60 rpm to remove residual ethanol.

The resulting final fraction was dried in an oven at 55 °C, yielding 790 mg crude polysaccharide extract (CPE) (11.3 mg CPE per gram of basidiocarp) of *P. sanguineus*, which were stored in a freezer at -20 °C until use.

The carbohydrates from *P. sanguineus* were diluted to concentrations of 0, 100, 200, 400, and 500 mg L^{-1} using distilled water.

Induction of resistance-concentrations

Susceptible 'Gaúcho' tomato seeds were sown in 128-cell trays containing an autoclaved mixture of soil, sand, and humus in a 2:1:1 ratio. After 30 d, the seedlings were transplanted into 2 L pots using the same substrate.

Fourteen days after transplanting, seedlings received 0 (control), 100, 200, 400, or 500 mg L^{-1} CPE. The application was performed via foliar spraying, using a sprayer to uniformly apply 5 mL each concentration to the plant shoots, ensuring that the solution did not reach the soil. Four days after the CPE application, 2000 eggs + second-stage juveniles (J2) of *M. incognita* were inoculated per pot (Brito et al., 2025), in three openings of 1 cm in diameter and 3 cm in depth in the substrate.

Tomato plants were grown for 60 d in a greenhouse covered with polyethylene plastic and laterally protected with 70% shade cloth. The temperature and relative humidity ranged between 26-32 °C and 60%-70% respectively. To prevent nematode dispersal and maintain experimental integrity, irrigation was controlled, providing water daily in reduced quantities to avoid runoff. Sticky traps were installed to prevent insect attacks, and plant support was provided when necessary to ensure proper development. Nematological analyses were performed after 60 d.

Induction of resistance-application method

An assay was conducted to determine the application method using the concentration 500 mg L^{-1} CPE. Treatments included: Control (distilled water); application to the shoots via foliar spraying with CPE, ensuring that the solution did not reach the soil; and root application, in which seedlings were removed from the tray and their root systems were immersed in CPE for 5 s; and the combination of foliar spraying and root immersion. Three days after treatment, tomato plants were inoculated with *M. incognita* (2000 eggs + J2 per plant) (Brito et al., 2025).

Nematological analyses

To examine the presence of egg masses in the roots, these were stained with Phloxine B (15 mg L^{-1}; Dinâmica Química, Indaiatuba, São Paulo, Brazil) and, after 20 min, washed in running water to remove excess dye (Taylor and Sasser, 1978). The numbers of galls and egg masses were determined under a stereomicroscope (Bel Engineering, Milano, Italy).

After counting the galls and stained egg masses, egg viability was evaluated. The egg masses were removed and placed in wells containing 250 µL distilled water in ELISA plates. The plates were sealed with plastic film and kept in the dark at 25 °C, 95-100% humidity, for 15 d. Viability was determined by counting the hatched juveniles (Kosmann et al., 2017).

Egg and nematode extraction from roots followed Coolen and D'Herde (1972). The centrifugal flotation method in sucrose solution was used to extract eggs and nematodes from the soil (Jenkins, 1964). Quantification was performed using a Peters chamber under an optical microscope.

The reproduction factor (RF) was calculated using the egg and J2 values per root and soil (Oostenbrink, 1966).

Statistical analysis

Data were checked for normality and homogeneity of variance and subjected to ANOVA, followed by regression analysis to assess the effects of CPE concentrations. For the CPE application methods assay, Tukey's test was applied at a 5% probability level. The number of replicates was four to CPE concentrations and six for CPE application methods, where each replicate was a 2 L pot. The Sisvar program (Ferreira, 2011) was used for these analyses. Two experiments were conducted and produced consistent results; data presented are from one of the experiments that showed the lowest coefficient of variation.

RESULTS

Induction of resistance – concentrations

The number of galls was reduced by CPE treatments, with a dose-dependent response (Figure 1). The calculated concentration of 326 mg L^{-1} would provide a 56% reduction in gall formation. Among the concentrations tested, 400 mg L^{-1} resulted in a 50.45% reduction compared with the control. These findings indicate that CPE from *P. sanguineus*, applied to the shoots, may have systemically activated plant defense mechanisms that acted in the roots, affecting nematode penetration or feeding site formation and reducing gall development.

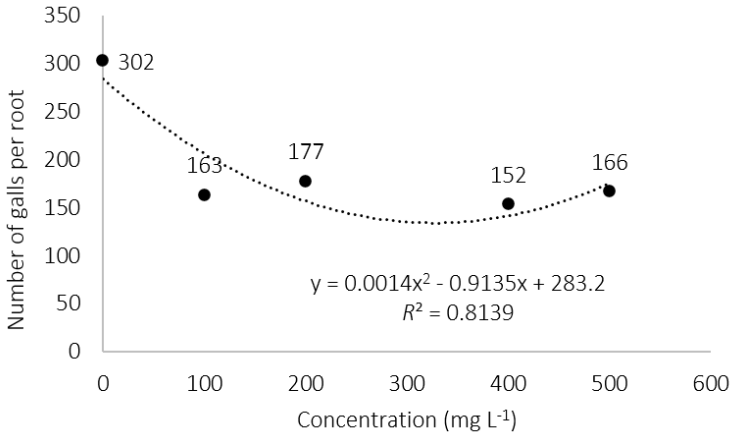

Figure 1. Number of galls of *Meloidogyne incognita* in tomato plants treated with concentrations of crude polysaccharide extract from *Pycnoporus sanguineus*. The treatment was applied by spraying the seedling shoots 4 d before nematode inoculation. Root gall assessment was performed 60 d after seedling transplantation.

The number of egg masses was also reduced by the application of CPE to the shoots (Figure 2). The calculated concentration of 722 mg L^{-1} would lead to complete suppression of egg mass formation. The greatest reduction of 67.46% was observed at 500 mg L^{-1}. These results are relevant because they suggest a limitation in nematode reproduction, likely associated with the reduction in the number of galls formed.

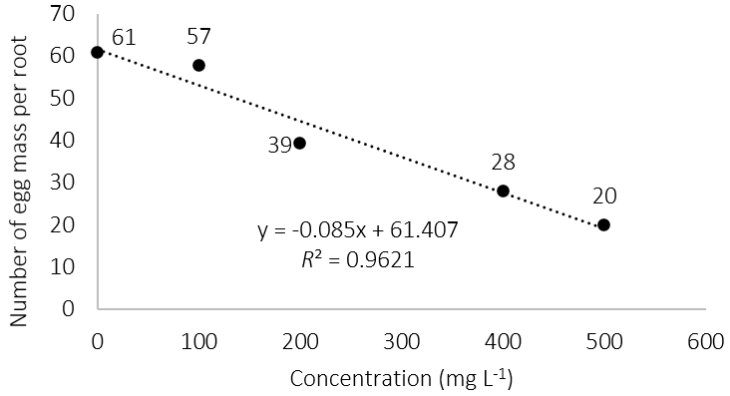

Figure 2. Number of *Meloidogyne incognita* egg masses in tomato plants treated with concentrations of crude polysaccharide extract from *Pycnoporus sanguineus*. The treatment was applied by spraying the seedling shoots 4 d before nematode inoculation. Egg mass assessment per root was performed 60 d after seedling transplantation.

The nematode population in the soil was also affected by the inducing effect of *P. sanguineus* CPE applied to the shoots (Figure 3). The greatest reduction occurred at 500 mg L^{-1}, with a 64.39% decrease compared with the control. This result may be related to reductions in both the *M. incognita* population and its reproductive cycle, due to fewer galls and egg masses and consequently fewer nematodes in the soil.

Egg viability was also affected by the resistance-inducing treatment with *P. sanguineus* (Figure 4). The concentration estimated to result in the lowest viability was 306 mg L^{-1}, with a reduction of 61%. The concentration of 200 mg L^{-1} was the most effective in reducing the number of hatched juveniles, causing it to decrease by 76.35%.

For nematodes in the roots, there was nonsignificant effect (p = 0.3681; CV = 6.34%) of CPE concentrations (data not shown).

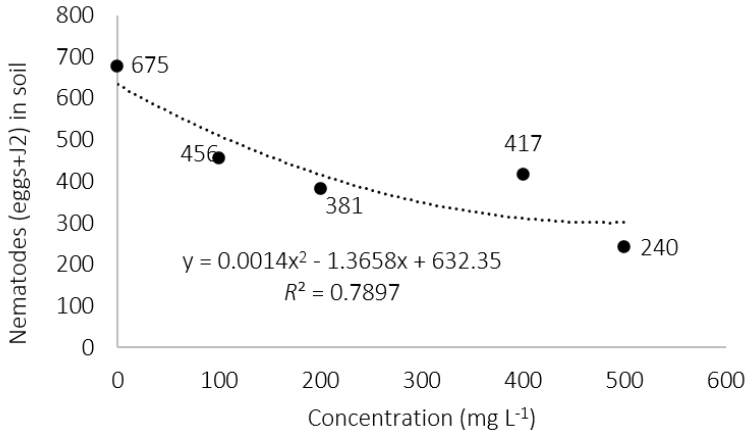

Figure 3. Number of eggs and second-stage juveniles (J2) of *Meloidogyne incognita* produced in tomato soil treated with concentrations of crude polysaccharide extract from *Pycnoporus sanguineus*. The treatment was applied by spraying the seedling shoots 4 d before nematode inoculation. Soil nematode assessment was performed 60 d after seedling transplantation.

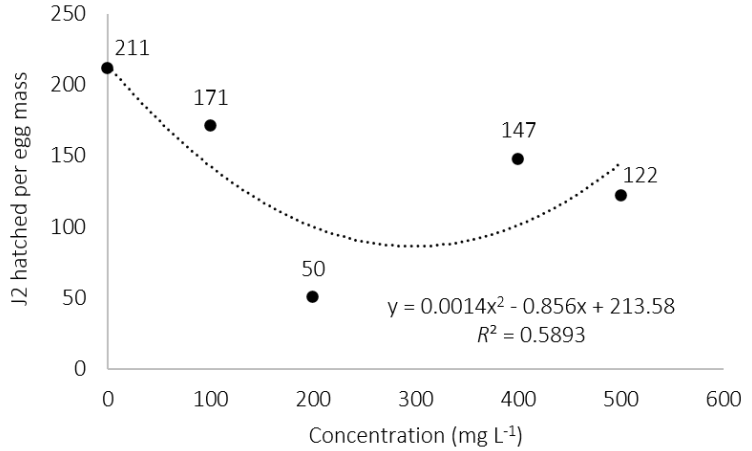

Figure 4. Viability of *Meloidogyne incognita* eggs produced in tomato plants treated with concentrations of crude polysaccharide extract from *Pycnoporus sanguineus*. The treatment was applied by spraying the seedling shoots 4 d before nematode inoculation. Egg viability was assessed 15 d after incubation in water in microplates.

Induction of resistance – application methods

In the assay evaluating CPE application methods, there was no effect on the number of galls (p = 0.3837; CV = 14.53%) or egg masses (p = 0.4154; CV = 18.93%) (data not shown). However, for nematodes in the roots, a difference was observed between the control and the treatment combining CPE application to both shoots and roots, resulting in a 70% reduction in nematode numbers (Figure 5). The effectiveness of this combined treatment may reflect a dual mechanism: Application to the shoots likely induced resistance, while application to the roots may have had a direct nematicidal effect, reducing nematode penetration.

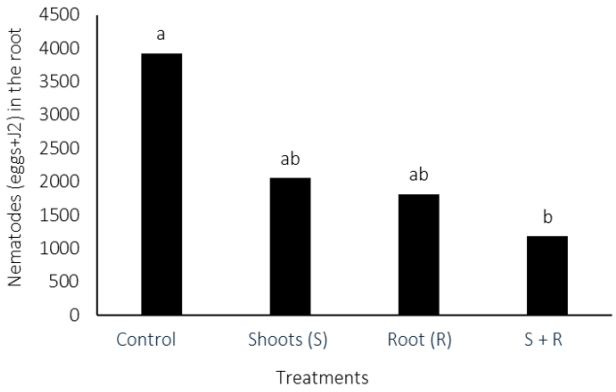

Figure 5. Number of eggs and second-stage juveniles (J2) of *Meloidogyne incognita* in tomato roots treated by different methods with crude polysaccharide extract from *Pycnoporus sanguineus*. The treatment occurred 3 d before nematode inoculation. CV: 7.58%. Root nematode assessment was performed 60 d after seedling transplantation.

The same behavior was observed for the nematode count in the soil, where the treatment combining the application of carbohydrates to the shoots and root reduced the number of nematodes by 74% (Figure 6). The lower nematode count in the soil can be attributed to reduced pathogen reproduction promoted by the treatment, thereby decreasing the population present in the pots. Additionally, the product's nematicidal effect likely contributed to this decline. This reduction in the soil nematode population is a crucial finding, as it suggests a potentially lower infection rate by these pathogens in future growing cycles and reduced reinfection during the current cycle. This could provide a meaningful advantage for crop health and productivity in the medium to long term.

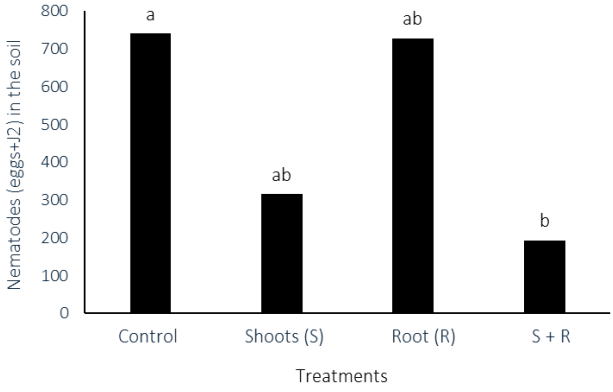

Figure 6. Number of eggs and second-stage juveniles (J2) of *Meloidogyne incognita* produced in tomato soil treated by different methods with crude polysaccharide extract from *Pycnoporus sanguineus*. The treatment occurred 3 d before nematode inoculation. CV: 9.46%. Soil nematode assessment was performed 60 d after seedling transplantation.

The analysis of egg viability showed that all treatments involving the application of *P. sanguineus* carbohydrates reduced the number of J2 hatched per egg mass, with an average reduction of 61% across the three treatments (Figure 7). Low egg viability can lead to a substantial decrease in nematode inoculum. Although gall formation and egg mass production did not show significant differences, unviability prevents J2 hatching, disrupting the pathogen's life cycle and consequently reducing its infestation potential in subsequent cycles.

In the calculation of the reproduction factor, it was evident that the root immersion and shoot spraying + root immersion treatments reduced the reproduction factor to values below 1 (Figure 8). This result indicates that the treatments lowered the initial inoculum, demonstrating the effectiveness of *P. sanguineus* carbohydrates in controlling *M. incognita* in tomato plants.

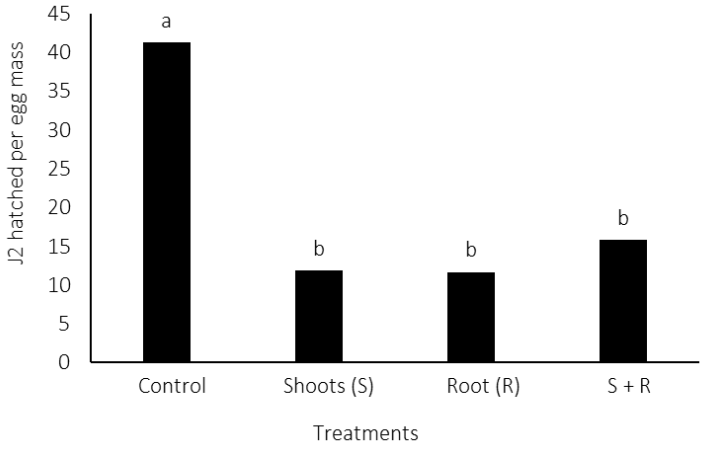

Figure 7. Viability of *Meloidogyne incognita* eggs produced in tomato plants treated by different methods with crude polysaccharide extract from *Pycnoporus sanguineus*. The treatment occurred 3 d before nematode inoculation. CV: 49.12%. The number of J2 hatched per egg mass was counted after 15 d of incubation in microplates.

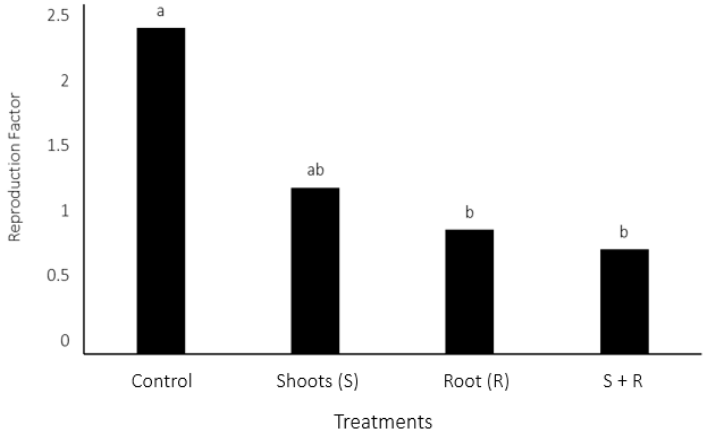

Figure 8. Reproduction factor (RF) of *Meloidogyne incognita* in tomato plants treated by different methods with crude polysaccharide extract from *Pycnoporus sanguineus*. The treatment occurred 3 d before nematode inoculation. CV: 37.49%. The reproduction factor was assessed 60 d after seedling transplantation.

DISCUSSION

The nematicidal potential of basidiomycete fungi has been widely reported, primarily due to their capacity to parasitize plant-parasitic nematodes (Elkhateeb et al., 2021; Santana-Santos et al., 2022). In this biological control process, saprophytic basidiomycetes—organisms that degrade dead organic substrates—may attack living organisms as an alternative nutrient source, increasing their chances of survival under conditions of low nutrient availability (Dix and Webster, 1995). Basidiomycetes such as *Daedalea quercina*, *Fomitopsis pinicola*, and *Gymnopilus junonius* fall into this category (Balaes and Tănase, 2016). However, research has increasingly focused on the use of bioactive compounds extracted from basidiomycetes for nematode control (Wille et al., 2019), which may contribute to the development of new molecules for commercial phytosanitary products (Soliman et al., 2022).

Compounds excreted by basidiomycete fungi or extracted from their basidiocarps may display direct toxic activity against nematodes, as observed for the crude polysaccharide extract (CPE) extracted from *Pycnoporus sanguineus* in our study. Bioactive compounds with nematicidal properties have also been identified in other basidiomycetes (Degenkolb and Vilcinskas, 2015). For example, compounds extracted from the luminescent mushroom *Neonothopanus nambi*, at a concentration of 500 mg L^{-1}, caused 100% mortality of *Meloidogyne incognita* second-stage juveniles (J2) after only 1 min of exposure, and concentrations of 100 and 50 mg L^{-1} resulted in total mortality after 30 and 48 h, respectively (Bua-Art et al., 2010). Filtrates from the culture medium of other basidiomycetes, e.g., *Lentinula edodes*, *Pleurotus pulmonarius*, *P. ostreatus*, *P. djamor*, and *Coprinus comatus*, reduced the mobility of *Meloidogyne* spp., yielding up to 100% immotile J2 of *M. javanica* after 24 h of exposure (Hahn et al., 2019). Culture filtrates of *Ganoderma lucidum*, *Lentinula edodes*, and *Schizophyllum commune* caused mortality rates of 93.50%, 90.83%, and 83.50%, respectively, in J2 of *Meloidogyne* spp. (Themuhi et al., 2020). On the other hand, protein fractions of *P. sanguineus* obtained by gel filtration chromatography, with molecular masses of 4.81, 47.98, 0.17, 25.78, 4.25, and 4 kDa, showed no nematostatic or nematocidal effect against *M. javanica* and *M. incognita* (Brito et al., 2025). On the other hand, Talaska et al. (2025) reported that *P. sanguineus* applied as basidiocarp powder in the seedling transplanting hole reduced egg masses of *M. incognita* in tomato plants by 41%, particularly at a concentration of 750 mg basidiocarp powder per hole.

In our study, the resistance-inducing effect of *P. sanguineus* CPE was evident. When applied to the aerial plant shoots, they interfered with the infectious process of *M. incognita* in tomato roots, reducing the number of galls, egg masses, soil nematodes, egg viability, and the reproduction factor.

Reduction in gall formation has also been reported by Bua-Art et al. (2010) using an extract from the basidiomycete *N. nambi* to control *M. incognita*, where treatments of 100 and 500 mg L^{-1} completely prevented gall formation in tomato plants, while lower concentrations (10 and 50 mg L^{-1}) still significantly reduced the number of galls compared to the control. A decrease in egg mass formation was also observed for *M. javanica* when fungal filtrates of *P. ostreatus*, *P. sajor-caju*, and *P. florida* were applied (Heydari et al., 2006).

Reducing egg mass in the roots is an effective strategy for lowering inoculum levels for subsequent crops, which is fundamental for nematode management. This approach contributes significantly to agricultural sustainability and productivity by interrupting the pathogen life cycle, lowering initial inoculum, and minimizing soil proliferation. According to Wille et al. (2019), basidiomycetes or their metabolites can markedly interfere with plant-parasitic nematodes by impairing juvenile motility and penetration, affecting host attraction, and even influencing J2 hatching, or causing nematode death.

Other studies on basidiomycetes for nematode control also report effects on gall formation and egg masses. Exhausted substrate from edible mushroom cultivation reduced *Meloidogyne* spp. Galls by 96% with 100 g per pot, and by 91% with 50 g per pot (Bakr and Mahdy, 2022). *Pycnoporus sanguineus* basidiocarp powder, delivered in gelatin capsules, reduced M. *incognita* gall formation in tomato plants by 11% and 14% at concentrations of 500 and 750 mg per transplanting hole, respectively (Talaska et al., 2025). Similarly, extracts from *Ganoderma lucidum* basidiocarps reduced egg mass formation, egg viability, and increased *M. incognita* mortality (Themuhi et al., 2020; Akshaya et al., 2021). Basidiocarps of *G. lucidum* also caused high mortality of *M. incognita* juveniles in eggplant when different concentrations of culture filtrates were applied (Fatima et al., 2022). *Pleurotus ostreatus* significantly reduced the number of *M. javanica* eggs per gram of treated soil, demonstrating the efficacy of fungal metabolites in nematode management (Abbasi et al., 2014).

Although these studies used *P. ostreatus* and lettuce as the host plant, Wille et al. (2019) observed strong nematicidal activity against *M. incognita*, with over a 70% reduction in the reproduction factor, reinforcing the potential of basidiomycetes such as *P. sanguineus* for biological control of the pathogen. Additionally, *Neolentinus ponderosus* showed high nematicidal activity in vitro and in vivo (approximately 97% and 50%, respectively), likely due to secondary metabolites produced by this basidiomycete (Montañez-Palma et al., 2021).

Regarding application methods, the efficiency of combined treatment of shoot spraying and root immersion was likely due to a dual mechanism: Shoot application induced systemic resistance, while root immersion exerted a direct, though modest, nematicidal effect, preventing nematode penetration.

Overall, these results highlight the significant potential of *P. sanguineus* for nematode control, combining both direct effects on the pathogen and indirect effects through resistance induction. Previous studies have reported similar results for *P. sanguineus* in controlling nematodes of the genus *Meloidogyne* (Barbosa et al., 2021), but no studies have focused exclusively on carbohydrates extracted from *P. sanguineus* basidiocarps, as in the present work.

Although our study evaluated only morphophysiological variables, Brito et al. (2025) demonstrated that proteins from *P. sanguineus* extracts increased peroxidase activity in tomato plants treated and inoculated with *M. javanica*, suggesting that resistance induction may involve specific biochemical pathways. Thus, further histological and biochemical analyses are recommended to elucidate the mechanisms activated by *P. sanguineus* carbohydrates, alongside chemical characterization of these carbohydrates, which is underway by our research group.

CONCLUSIONS

The results demonstrate the potential of crude polysaccharide extracted from *Pycnoporus sanguineus* basidiocarps as resistance-inducing agents for controlling *Meloidogyne incognita* in tomato plants when applied via root immersion at seedling transplantation, followed by shoot spraying.

Author contributions

Conceptualization: B.L.O., J.R.S. Methodology: B.L.O., R.P. Formal analysis: B.L.O., T.M.M. Investigation: B.L.O. Resources: J.R.S. Data curation: B.L.O. Writing-original draft: B.L.O. Writing-review & editing: T.M.M., J.R.S. Supervision: J.R.S., O.J.K. Project administration: J.R.S. Funding acquisition: J.R.S. All co-authors reviewed the final version and approved the manuscript before submission.

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