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REVIEW NEMATODES IN TEA CULTIVATION: PATHOGENESIS AND PLANT DÉFENSE RESPONSES

Purpose. To identify the complex relationship between tea plants and important plant-parasitic nematodes, focusing on the severe damage these pests inflict on roots, as well as the sophisticated defense strategies employed by tea plants, particularly their synthesis of protective secondary metabolites to combat nematode attacks

Results. Plant-parasitic nematodes pose a serious economic danger to *Camellia sinensis*, the world's most important tea crop, resulting in yield losses of 11–55% and up to $1 billion yearly. Stunting, wilting, and decreased tea output are caused by around 80 nematode species that harm roots, including *Pratylenchus*, *Radopholus*, *Meloidogyne*, and *Hemicriconemoides.* Due to their immobility, tea plants have developed complex defense mechanisms. These include the formation of nematicidal secondary metabolites (polyphenols, alkaloids, terpenoids), systemic signaling pathways triggered by phytohormones (ethylene, jasmonate, and salicylic acid) that activate defense genes, and physical barriers such as lignin and suberin in cell walls. Nematode control is also aided by beneficial soil bacteria.

Conclusions. For sustainable management, it is essential to comprehend relationships. In order to secure the economic future of the tea business, future research should take advantage of natural defences to improve integrated pest control.

KEYWORDS: *Camellia sinensis, plant-parasitic nematodes, plant defense, secondary metabolites, integrated pest management*

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Camellia sinensis (L.) O. Kuntze, commonly known as a tea plant, is a perennial evergreen and a crucial long-term investment for agriculture in tropical and subtropical areas worldwide [1, 2]. Tea first grew in southwestern China [3] Over the following centuries, people from different cultures introduced it to new parts of the world, and it is now grown in over 60 countries on five continents [4]. Tea is enjoyed by people across all social classes, geographies, and cultures. Its widespread appeal stems from its unique flavor and significant health benefits, which are attributed to compounds like tea polyphenols, amino acids, and caffeine [5,6]. Insects and pests are significant factors impacting tea production, leading to yield losses ranging from 11% to 55%. These losses are estimated to result in economic losses amounting to approximately $500 million to $1 billion in the tea industry [7]. Among the many factors limiting tea production, plant-parasitic nematodes pose a significant economic threat [8]. The nematode is a significant pathogen, primarily known for devastating tea plantations throughout Asia [9]. The global tea industry faces threats from a diverse range of plant-parasitic nematodes; Sivapalan (1972) [10] recorded over 40 species across 20 genera, while Chen and Chen (1989) [11] reported an even higher number, identifying 82 species linked to tea plants [12].

Plants, being immobile, have evolved defense mechanisms to safeguard themselves against herbivores and microbial infections [13,14]. Due to their immobility, plants face a range of challenges from both living and nonliving factors in their environment, including threats from herbivores, pathogens, drought, salinity, UV exposure, temperature extremes, and nutrient deficiencies [15-17]. The perennial and monoculture nature of tea cultivation contributes to substantial annual crop losses. However, geographical variation in pest diversity is evident, influenced by factors such as climate change, altitude, and plantation age [18].

Two types of pests, namely the piercing-sucking pests and chewing pests, are associated with tea [19].

Plants and insects have coexisted for more than 350 million years, leading to the development of unique survival tactics in both groups as they evolved together [14, 20, 21]. Natural selection has enabled plants to survive changing environments by producing diverse secondary metabolites. These metabolites act as a chemical defense mechanism, protecting the plant from pathogen attack and invasion [22]. This adaptive response enables plants to defend against a wide range of threats, from pathogens and herbivores to environmental stresses like drought, salinity, and extreme temperatures [23, 24].

Classification of Tea pests. Tea pests can be categorized into three groups based on their location of infestation:

1. Root pests such as nematodes, termites, and cockchafer grubs.
2. Stem pests like the red coffee borer and stem borers.
3. Leaf pests including the tea mosquito bug, thrips, jassids, aphids, flush-worms, looper caterpillars, leaf rollers, and various mite species [25].

This review explores the complex relationship between tea plants and important plant-parasitic nematodes, focusing on the severe damage these pests inflict on roots. It also investigates the sophisticated defense strategies employed by tea plants, particularly their synthesis of protective secondary metabolites to combat nematode attacks

Root pests: Pests often affect three layers of plants: the top, midsection, and roots. Pest control often targets the top and intermediate sections of plants, with less emphasis on their roots [26]. Little is known about the interactions of root pests with host plants compared to aboveground insect herbivores [27]. A disturbed soil microflora with limited species diversity and population density of antagonists to fungal root disease agents promotes the spread and incidence of root disease and nematode infections [28]. Deep ploughing and dredging, have been effectively eliminate root pests [29].

Nematodes: Nematodes are the most abundant animals on earth and the dominant component of soil [30]. Nematodes are major pests of tea soil in nurseries and new clearings, invading tea seedlings up to 8-9 months old in young plantations. More than 40 species of plant parasitic nematodes from 20 genera have been found in various tea-growing regions across the world [31]. The activity, diversity, and distribution of soil organisms, including nematodes, are strongly influenced by soil properties. Key physical and chemical parameters such as temperature, moisture, water-holding capacity, pH, and electrical conductivity are vital for soil functioning. These factors directly shape nematode community composition and structure [32].

Nematodes have been shown to lower the leaf area and stem girth of tea plants [33]. Infestation spreads mostly through nursery plants on tea farms [25].

Various types of plant parasitic nematodes have been found in tea soils worldwide. Most of these nematodes have not been shown pathogenic (Table. 1). The following species are known or believed to be pathogenic to tea. Species include Pratylenchus spp., Radopholus similis, Meloidogyne spp., Hemicriconemoides sp, Rotylenchulus reniformis, Heliotylenchus spp., Paratylenchus curvitatus, Hoplolaimus sp. etc.

Pratylenchus sp: *Pratylenchus* is a parasite of the tea plant in several tea-producing nations like as, the Philippines, China, Bangladesh, Taiwan, India, Vietnam, the, and Australia [34], Sri Lanka, Japan and United States [35]. This nematode is a major parasite of tea in Iran [35, 36, 37, 38], Japan [39] and Korea [40]. This worm is known as the 'upcountry species of nematode' because of its prevalence in high-elevation regions (2200-3000 m a.s.l.) [41].

Mode of damage: Plants respond with apparent symptoms only when a significant portion of their root system is damaged or stops functioning. In extreme circumstances, die-back and death can ensue [25]. The symptoms of tea root-lesion disease caused by *Pratylenchus spp*. infection includes stunting, wilting, yellowing, and a decrease in root length. Such symptoms occur when the nematodes eradicate the root system, resulting in root lesions [8].

Plant response: Tea roots have strong cuticle and cell walls, which impede *Pratylenchus* penetration. Infection-trigger Cell walls to reinforced with lignin and suberin, making the plant difficult to penetrate [42]. Tea plants generate secondary metabolites called polyphenols, which have nematicidal characteristics and impede *Pratylenchus* development and reproduction [43]. Tea plants develop a systemic response to *Pratylenchus* infection by activating defense genes and producing signalling molecules such as salicylic acid [44]. Phytohormones like ethylene and jasmonate also resit the *Pratylenchus* infection [45]. Tea plants interact with helpful bacteria in the soil, helping to reduce Pratylenchus numbers [46].

Radopholus similis: The species was initially identified as a tea pest in Java, Indonesia [47]. R. similis was detected in three locations: Bangka, Gambung in West Java, and on tea plantations elsewhere in Java [48]. Steiner and Buhrer (1933) found tea to be a suitable host for this nematode. it is found in Africa, Asia, North, and South America, Australia, and a few European countries [49]. The *Radopholus similis* was reported from 50m to 1000m altitude [50].

Mode of damage: Tea plants infested with R. similis exhibit symptoms similar to those produced by Pratylenchus loosi, including stunting with twiggy branches, defoliation, early blooming, and fruiting. Infested plants have scant and dry roots, as opposed to healthy plants' white, succulent feeder roots. R. similis causes lesions on tea roots, but they are much less than those caused by P. loosi [51].

Plant response: Plants generate secondary metabolites, which help them defend against worm infections. Secondary metabolites mostly consist of alkaloids, terpenoids, and phenylpropanoids [52]. Due to nematode infection, plants accumulate toxins, modify cell wall, and synthesize phytoalexins [53].

Meloidogyne sp: Root-knot nematodes (RKNs), Meloidogyne spp., are among the oldest and most economically important plant-parasitic nematodes (PPNs). They are serious pests in agricultural production, causing annual global losses of USD 157 billion. [54, 55] *M. javanica*, *M. incognita*, and *M. brevicaua* are common root-knot nematodes (RKN) found in tea plants, particularly in India [33] and tea growing regions of Africa [56].

Mode of damage: *Meloidogyne* enters the root and reaches the growing vascular strands at the elongation zone, resulting in many mitotic cycles without cytokinesis, which leads them to expand and become multinucleated (up to >100 nuclei), leading to the creation of "galls" or "root knots" [57]. Several physiological and morphological changes occur during the formation of root knots and turn them into nematode-feeding sites, which give nutrients for the worm's growth [58]. Seedling plants are more vulnerable to root injury (Tabl.) than vegetatively produced clonal tea plants of the same age, perhaps due to their smaller root mass [59].

Plant response: When RKNs infect a host plant, the plant initiates a defense response, both naturally and artificially, through the coordinated expression of multiple plant signaling pathways, including phytohormones such as salicylic acid, ethylene, and jasmonic acid, pathogenesis-related (PR) proteins, and various plant transcription factors. The outcomes of these highly coordinated signaling responses eventually determine the susceptibility or resistance of plants to RKNs [73]. Resistance to the root-knot nematode can be attributed to the hypersensitive response (HR) and higher phenolic levels, which result in barrier deposition (e.g., lignin) [74].

Hemicriconemoides sp: These nematodes, commonly known as 'sheathoid' nemato-

Table

Tea root Nematodes: Host Spectrum, Species Diversity, and host Interactions

Sn	Name	Distribution	No of species	Host range	Symptom	Host defence
1	*Pratylenchus sp.*	Worldwide except. Antarctica [60]	100 species [61]	400 plant species (ornamental, vegetable, tree etc) [62]	Root development disruption, poorly developed foliage [60]	Polyphenols, salicylic acid, Phytohormones like ethylene and jasmonate
2	*Radopholus sp.*	Worldwide mostly tropical and subtropical areas [63]	Around 20 Species [64]	250 plant species [65] like banana, citrus, pepper, coffee, Cucumber [63], tea [66]	Stunting with twiggy branches, defoliation, early blooming, and fruiting [51]	Alkaloids, terpenoids, phenylpropanoids and phytoalexins
3	*Meloidogyne sp.*	Worldwide [67]	Around 100 species [68]	Broad host range [69]	Gall or root-knot, effect root system, and significant yield losses [67]	Salicylic acid, ethylene, jasmonic acid, Phenolic Compound
4	*Hemicriconemoides sp.*	Worldwide [70]	54 Species [71,72]	Higher plants, primarily woody perennials, and vines [70]	Root rot, leaf necrosis, suppressed root growth, lesions, and coarse roots [70]	Alkaloids, terpenoids, and phenylpropanoids

des due to their smooth-annulated outer accessory sheath, are reported worldwide. They are associated with various higher plants, primarily woody perennials, and vines [68]. Hemicriconemoides spp. (Sheathoid nematodes) are sexually dimorphic plant-parasitic nematodes found mostly in warm areas [75] The genus Hemicriconemoides consists of 54 species [71, 72]. Hemicriconemoides is a significant nematode pest of tea in Japan [39]. The nematode has been detected in Taiwan [10] and Iran [76].

Mode of damage: Common symptoms of infestation by these nematodes include root rot, leaf necrosis, suppressed root growth, lesions, and coarse roots [65, 62]. This ectoparasitic nematode feeds only on tea feeder roots. Continuous feeding by this worm causes the sloughing off of the root cortex, producing a brownish discoloured stele [77]. Plants afflicted with these parasites may exhibit symptoms such as stunting, early wilting, leaf yellowing, root deformity, necrosis of cortical root tissues, and nutritional shortages [78].

Plant response: Plants produce secondary metabolites that help them defend against helminth infections. Secondary metabolites mainly consist of alkaloids, terpenoids, and phenylpropanoids [43].

Conclusion

Globally, tea production and economic value (Camellia sinensis) are damaged and tea production reduced up to 11-55%, with some estimates at $1 billion loss, due to yield loss and production reductions as a result of plant-parasitic nematodes. Pathogenic nematodes, including Pratylenchus, Radopholus, Meloidogyne, and Hemicriconemoides, have a lasting and damaging effect, along with wilting and reduced tea production.

Due to these challenges, the tea plant, and by extension the immobilized plant, has come up with a few layers of the defense strategy. The first part of the defense strategy is the production of polyphenols, alkaloids, and terpenoids, which are nematicidal, and the activation of 'systemic' defense along the pathways of the 'phytohormones' ethylene, jasmonate, and salicylic acid. and the lignin and suberin pathways. Defense interactions at this level are further supported by the physical structures and beneficial microbiomes in the soil.

To develop effective and sustainable management approaches, plant-nematode interactions must be understood. Future tea production will be building this 'plant intelligence' and boosting the 'defenses.' Added these to the rest of the Integrated Pest Management (IPM) tea systems, the chance of reduced chemical dependence and economic viability increases and remains sustainable in production worldwide.

Conflict of Interest

The authors declare no conflict of interest regarding the publication of this manuscript. Furthermore, the authors have fully adhered to ethical norms, including avoiding plagiarism, data falsification, and duplicate publication.

Authors Contribution**:** all authors have contributed equally to this work.

In this study, generative artificial intelligence was used only to help find and compile recent academic literature on the subject. The authors, who take full responsibility for the work's intellectual content, personally performed the crucial tasks of data analysis, information synthesis, and drawing scientific conclusions.

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НЕМАТОДИ У ВИРОЩУВАННІ ЧАЮ: ПАТОГЕНЕЗ ТА ЗАХИСНІ РЕАКЦІЇ РОСЛИН (ОГЛЯД)

Мета. Визначити складний зв'язок між чайними рослинами та важливими рослинними паразитичними нематодами, зосереджуючись на серйозній шкоді, яку ці шкідники завдають корінню, також складні захисні стратегії, що використовуються чайними рослинами, зокрема їхній синтез захисних вторинних метаболітів для боротьби з атаками нематод.

Результати. Фітопаразитичні нематоди становлять серйозну економічну загрозу для Camellia sinensis, найважливішої чайної культури у світі, що призводить до втрат врожаю на 11–55% та до 1 мільярда доларів щорічно. Затримка росту, в'янення та зниження врожаю чаю спричинені близько 80 видами нематод, які пошкоджують коріння, включаючи Pratylen-chus, Radopholus, Meloidogyne та Hemicriconemoides. Через свою нерухомість чайні рослини розвинули складні захисні механізми. До них належать утворення нематоцидних вторинних метаболітів (поліфенолів, алкалоїдів, терпеноїдів), системні сигнальні шляхи, що запускаються фітогормонами (етилен, жасмонат та саліцилова кислота), що активують захисні гени, та фізичні бар'єри, такі як лігнін та суберин у клітинних стінках. Контроль нематод також здійснюється корисними грунтовими бактеріями.

Висновки. Для сталого управління важливо розуміти взаємозв'язки. Щоб забезпечити економічне майбутнє чайного бізнесу, майбутні дослідження повинні використовувати природні захисні механізми для покращення комплексної боротьби зі шкідниками.

КЛЮЧОВІ СЛОВА: *Camellia sinensis, рослинні паразитичні нематоди, захист рослин, вторинні метаболіти, інтегрована боротьба зі шкідниками*

Конфлікт інтересів

Автори заявляють, що конфлікту інтересів щодо публікації цього рукопису немає. Крім того, автори повністю дотримувались етичних норм, включаючи плагіат, фальсифікацію даних та подвійну публікацію.

Внесок авторів: всі автори зробили рівний внесок у цю роботу

У цьому дослідженні штучний інтелект використовувався тільки для пошуку та компіляції актуальної наукової літератури за цією темою. Автори, несуть повну відповідальність за інтелектуальний зміст роботи, особисто виконували найважливіші завдання аналізу даних, синтезу інформації та формулювання наукових висновків.

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