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Original Article

Plant parasitic nematodes associated with vegetable crops in the main agroecological zones of Côte d'Ivoire

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Abstract

Vegetable crops in Côte d'Ivoire are attacked by numerous pests, including plant-parasitic nematodes that cause enormous crop losses. A survey was conducted in six agroecological zones (AEZ) to study the plant-parasitic nematodes associated with vegetable crops. 120 soil and root samples of seven plant species belonging to Solanaceae and Cucurbitaceae were collected. These samples were subjected to various laboratory analyses, including extraction, counting, and identifying nematodes. Plant-parasitic nematodes belonging to nine genera have been inventoried: *Meloidogyne*, *Helicotylenchus*, *Radopholus*, *Pratylenchus*, *Hemicycliophora*, *Rotylenchulus*, *Hoplolaimus*, *Xiphinema* and *Heterodera*. Overall, all the populations were abundant in soils (more than 1000 individuals per kilogram) and roots (more than ten individuals per gram). However, segregation between the genera was observed according to the frequency of populations. The genus *Meloidogyne* was the most frequent and abundant in the whole localities and vegetable crops. Frequencies of 91% and 100% were observed for *Meloidogyne* in the roots of tomato and the rhizosphere of zucchini. *Xiphinema*, *Hoplolaimus*, *Heterodera*, and *Rotylenchulus* had very low-frequency values in soils, while the other genera had intermediate frequency values. The Principal Components Analyses based on nematode populations highlighted a strong correlation between the AEZ I and some genera's abundance, notably *Xiphinema* 92% correlated in the roots samples. Similarly, a strong correlation was observed between the abundance of some genera and eggplant; notably, *Meloidogyne* correlated to 83% in the soil samples. This study highlights the importance of plant-parasitic nematodes in Ivorian vegetable crops, hence the need to implement integrated management measures to limit yield losses.

Keywords: Plant parasitic nematodes, Vegetable crops, Density, Frequency, Agroecological zone

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Introduction

Vegetables are essential for human nutrition and health, as they are rich in vitamins, trace elements, fiber, and minerals (Wafi and Nandiyanto, 2023). Growing them contributes significantly to food self-sufficiency and higher incomes for people, especially young people and women, in rural, urban,-and peri-urban areas (Yarou et al., 2017; Touré et al., 2019). In Côte d'Ivoire, the main vegetable crops are tomato (*Solanum lycopersicum* L.), eggplant (*Solanum melongena* L.), chili pepper (*Capsicum* spp.), okra (*Abelmoschus esculentus* L.), amaranth (*Amaranthus* spp. L.), cabbage (*Brassica oleracea* L.), lettuce (*Lactuca sativa* L.), cucumber (*Cucumis sativus* L.) and green bean (*Phaseolus vulgaris* L.) (Dosso et al., 2023). Production of some of these crops, notably tomatoes and eggplant, is estimated at 48,804 tons and 110,380 tons for areas of 4,692 ha and 24,532 ha, respectively. Cucumber production is also estimated at 20,761 tons for an area of 4,358 ha (FAOSTAT, 2021).

Agricultural production worldwide is attacked by numerous pests and various diseases, including plant-parasitic nematodes, which constitute a serious problem especially in terms of food security (Ullah and Khanum, 2022). Plant-parasitic nematodes are present in all types of environment in agricultural regions, attack almost all crops and constitute a major food security and agricultural economy problem (Bashir and Khanum, 2023). Vegetables crops in Côte d'Ivoire are not spared. Nematodes most often attack underground organs and are present in most plant tissues, making them difficult to manage (Ali, 2015). The damage caused by these parasites is considerable, estimated at 30% of global agricultural production (Sikora et al., 2023), representing annual crop losses of several million tons, with higher figures in tropical regions (Morales-aranibar et al., 2023). Among nematodes, root-knot nematodes of the *Meloidogyne* genus have been reported to be the most widespread worldwide (Gaur, 2023).

Root-knot nematodes (RKN) are sedentary parasites of the roots of plants and are considered some of the most damaging pests in agriculture. RKN targets the root vascular system, causing above-ground symptoms of growth stunting, wilting, chlorosis, and reduced crop yields Tapia-Vázquez et al., 2021). It increases the susceptibility of infected plants to phytopathogenic bacteria, fungi, and viruses (Oliveira et al., 2021). What is more, *Meloidogyne* is polyphagous, causing damage to both field crops and food and vegetable crops, particularly coffee, bananas, and yam (Kouakou et al., 2016; Yéo et al., 2018; Morales-aranibar et al., 2023). Also, *Meloidogyne* prevalence was 25% in cassava crop in Nigeria (Onwuachusi et al., 2023). According to many authors, it has proved abundant in market gardening (El-Nuby et al., 2019). Other genera of nematodes have also been associated with vegetable crops, including *Hemicycliophora*, *Tylenchorhynchus*, *Tylenchus*, *Scutellonema*, *Helicotylenchus*, *Rotylenchulus*, *Pratylenchus* (Touré et al., 2019).

Studies on nematodes in Côte d'Ivoire, particularly nematodes associated with vegetable crops, are limited. They have focused on crops other than vegetables, particularly rice, banana, sugar cane, and, more recently, yams and tomatoes. Moreover, most of these studies were conducted in well-defined areas of the country. In Côte d'Ivoire, where market gardening plays a crucial role in food security and the economy, little work has been done on nematodes in the market gardening sector, particularly on their diversity, frequency, density, and distribution in the main agroecological zones (AEZs). This study aims to improve the productivity of vegetable crops in Côte d'Ivoire by better understanding plant-parasitic nematodes dynamic for sustainable management of their impact on agrosystems.

Material and Methods

Study sites and sampling

The study was carried out in 37 localities (Figure 1) spread over six of the seven Ivorian agroecological zones (AEZs) (Halle and Bruzon, 2006). The surveyed agroecological zones constitute the main vegetable production areas.

The survey sampled roots and soil from seven vegetable crop species. These species were the most frequently encountered in the market gardening areas. They belong to two botanical families, Solanaceae and Cucurbitaceae. The Solanaceae include eggplant, chili pepper, tomatoes,—and pepper, while the Curcubitaceae include zucchini, cucumbers, and calabash.

Sampling was performed over two consecutive years, from June to December, a rainy season favorable for vegetable production and plant parasitic nematodes in Côte d'Ivoire. Soil and root samples were collected simultaneously from the same plant during the flowering and harvesting stages at 20 cm depth, using a trowel. Five soil and root sub-samples were collected in each locality for any visited vegetable crop plot.

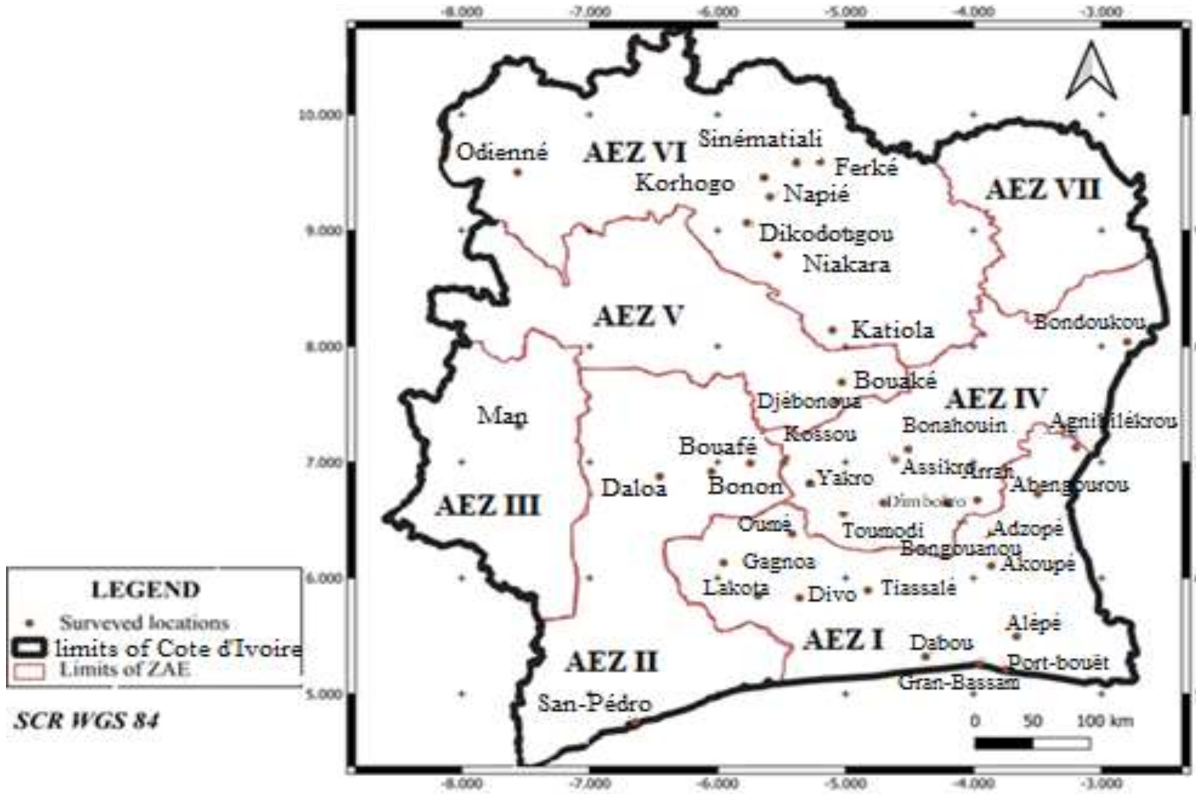

Figure-1: Agroecological zones surveyed and locations sampled

AEZ I: Southern dense rainforest area; Altitude: 0-200m; Rainfall: 1400-2500mm; Annual temperature: 29±5,6°C.
AEZ II: Western dense rainforest area; Altitude: ~1000m; Rainfall: 1300-1750mm; Annual temperature: 23.5±13.4°C.
AEZ III: Western semi-mountainous forest area; Altitude: >1000m; Rainfall: 1300-2300mm; Annual temperature: 24.5±7.7°C.
AEZ IV: Semi-deciduous dense rainforest area; Altitude: 0-200m; Rainfall: 1300-1750mm; Annual temperature: 23.5±1.4°C.
AEZ V: Transitional Forest area; Altitude: Rainfall: 300-600m; 1300-1750mm; Annual temperature: 23,5±13,4°C.
AEZ VI: Humid tropical savanna area; Altitude: 300-500m; Rainfall: 1150-1350mm; Annual temperature: 26.7±1.1°C.
Bolou et al. (2016)

Each plot's root sub-samples were mixed to form a composite sample. Soil subsamples were treated similarly. A total of 120 samples were collected. The composite samples were then packed in hermetically sealed plastic bags, labeled, and placed in a refrigerated cooler before being sent to the laboratory for various analyses.

Sample preparation and nematode extraction

Each composite root sample in the laboratory was carefully washed with tap water to remove adhering soil particles before being cut into 1-2 cm pieces. Soil samples per plot were mixed by hand and sieved using a coarse mesh sieve (2 mm) to remove large particles and plant residues.

Followingly, soil nematodes were extracted using the modified Baerman method (Coyne et al., 2010), and root nematodes using the double-centrifugation method (Coolen and D'Herde, 1972). Samples of 100 g and 20 g of soil and roots were used respectively for extraction. The soil sample was laid on tissue paper, and the whole was placed on a sieve + plastic plate set. Water was added to the plate to moisten the soil and allow the nematodes to migrate into the liquid. After 48 h in the dark, the nematodes were collected from the liquid using a 5 µm sieve. The root sample was ground, filtered through a battery of sieves (500, 80, 40, and 32 µm), and centrifuged twice at 2,500 rpm for 5 min. Chemical kaolin (5 g) and magnesium sulfate (450 g/l) were added to fix the nematodes during centrifugation. The nematodes were also collected using a 5 µm sieve.

Identification and counting of nematodes

Based on the morphology of adults and juveniles, Nematode identification was figured out using the keys of Hunt et al. (2002) and Mekete et al. (2012). Nematode counting per genus was performed thrice using a 1 ml gridded mounting plate and a light microscope at Gx40 and Gx100 magnifications. Values of the three replicates were used to calculate the average number N of nematodes per 100 g of roots or soil, according to:

$N = 100\,(n \times v)/m$ (Yéo et al., 2018):

N: number of nematodes per 100 g of roots or soil; n: mean number of nematodes in 1 ml of suspension; v: volume of nematode suspension obtained (ml); m: mass of roots or soil used for extraction.

Data processing and analyses

The counting of nematodes obtained was used to determine their frequencies and average densities. The frequency, expressed as a percentage, corresponds to the number of samples containing a genus of nematode divided by the number of all samples. The mean density is the number of individuals of a nematode genus in the positive samples divided by the number of positive samples (Apalowo et al., 2023).

After determining the density per 100 g of soil or roots, the average values of nematode density were converted in individuals per kilogram (ind.kg^{-1}) of soil or individuals per gram (ind.g^{-1}) of root, then Log(X+1)-transformed to reduce the large variabilities observed in the dataset. A cloud of dots was carried out using frequency values on axis X and the transformed abundance values on axis Y. The projections of the nematodes as individuals in this cloud of dots allow the segregation of different groups of nematodes based on their frequency and abundance. We consider that a population is frequent if its frequency is up to 30% both in soil and in roots. A population is considered abundant if its abundance is up to 1000 ind.kg^{-1} of soil (that corresponds to Log(X+1) up to 3) or its abundance is up to 10 ind.g^{-1} of roots that corresponds to Log(X+1) up to 1 (De Guiran, 1983).

Two principal component analyses were also carried out using the overall Log(X+1)-transformed average values of nematode density based on one hand on the AEZ considered individuals and the other hand on crops considered as the individuals. These analyses were performed using the Rstudio version 4.1.2 (2021-11-01) software and Inkscape version 1.2.2 for formatting graphics.

Results

Nine genera of plant-parasitic nematodes belonging to the order Rhabditida were associated with vegetable crops grown in the six agroecological zones. The plant-parasitic nematodes were observed in 120 samples of soil and roots.

Vegetable crop-associated plant parasitic nematodes on a national scale

Overall, nine plant-parasitic nematode genera of the order Rhabditida belonging to six families were identified in the soil rhizosphere and roots of the sampled vegetable plants. It was about *Meloidogyne* (Meloidogynidae), *Heterodera* (Heteroderidaea), *Helicotylenchus*, *Hoplolaimus* and *Rotylenchulus* (Hoplolaimidae), *Radopholus* and *Pratylenchus* (Pratylenchidae), *Hemicycliophora* (Criconematidae) and *Xiphinema* (Longidoridae). According to the status of parasitism and mobility, these nematodes were divided into five groups: the migratory endoparasitic nematodes (*Pratylenchus* and *Radopholus*) and the sedentary endoparasites (*Meloidogyne* and *Heterodera*), the sedentary semi-endoparasites (*Hemicycliophora*) and the migratory semi-endoparasites (*Hoplolaimus*, *Helicotylenchus*, and *Rotylenchulus*) and the migratory ectoparasites (*Xiphinema*).

The frequency and abundance analysis, both in soil and roots, allowed the segregation of different groups of plant-parasitic nematodes associated with vegetable crops (Figure 2). The first group comprised *Meloidogyne* spp., the most frequent genus in the rhizosphere and the roots. In the last case especially, the abundance of *Meloidogyne* populations was far superior to those of the other genera (Figure 2B). Although they were overall less frequent (inferior to 30%), the abundances of the other genera were also significant both in the soils and in the roots when they were presented. No segregation was highlighted between the other nematode genera regarding population frequency and abundance in roots. At variance, the rhizosphere harbored two groups of nematodes concerning frequency. *Pratylenchus* spp., *Radopholus* spp., *Helicotylenchus* spp., and *Hemicycliophora* spp. had intermediate frequency values. The other nematode genera (*Xiphinema*, *Hoplolaimus*, *Heterodera*, and *Rotylenchulus*) had low-frequency values.

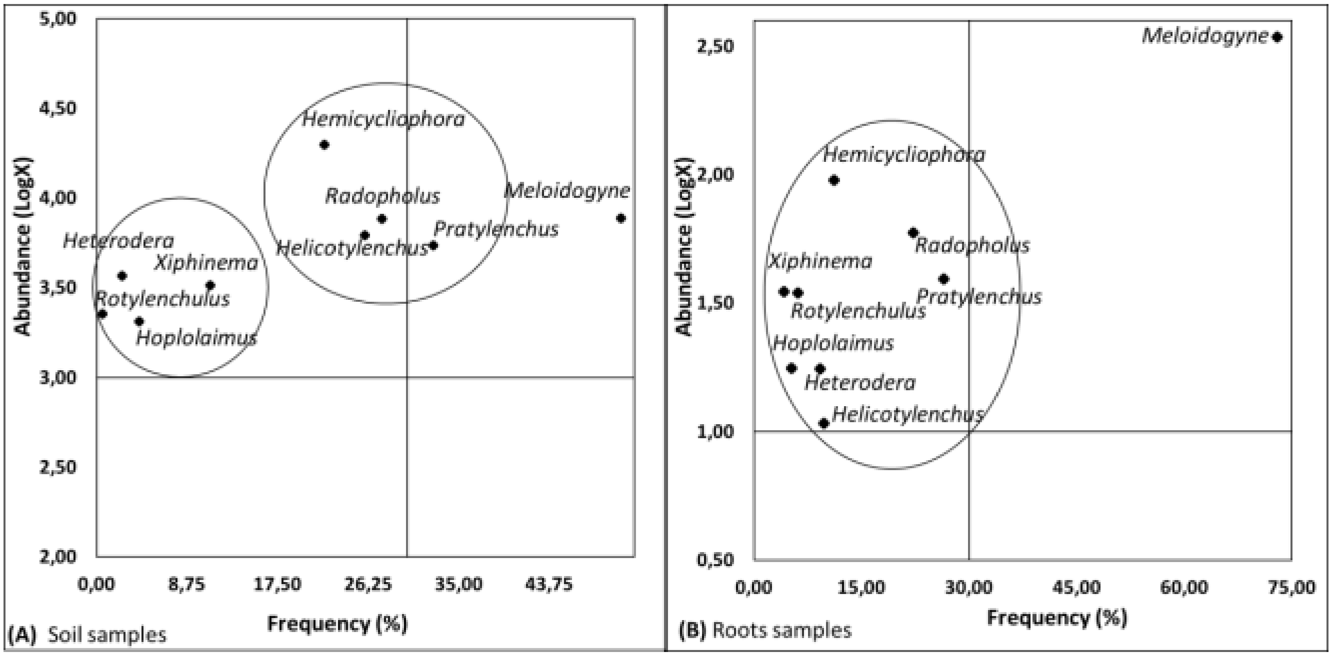

Figure-2: Frequencies and abundances of plant-parasitic nematodes in soil samples (A) and roots samples (B) on a national scale.

Average values of nematode density were determined by individual number/kg of soil or individual number/g of root, then transformed using the Log(X+1) function.

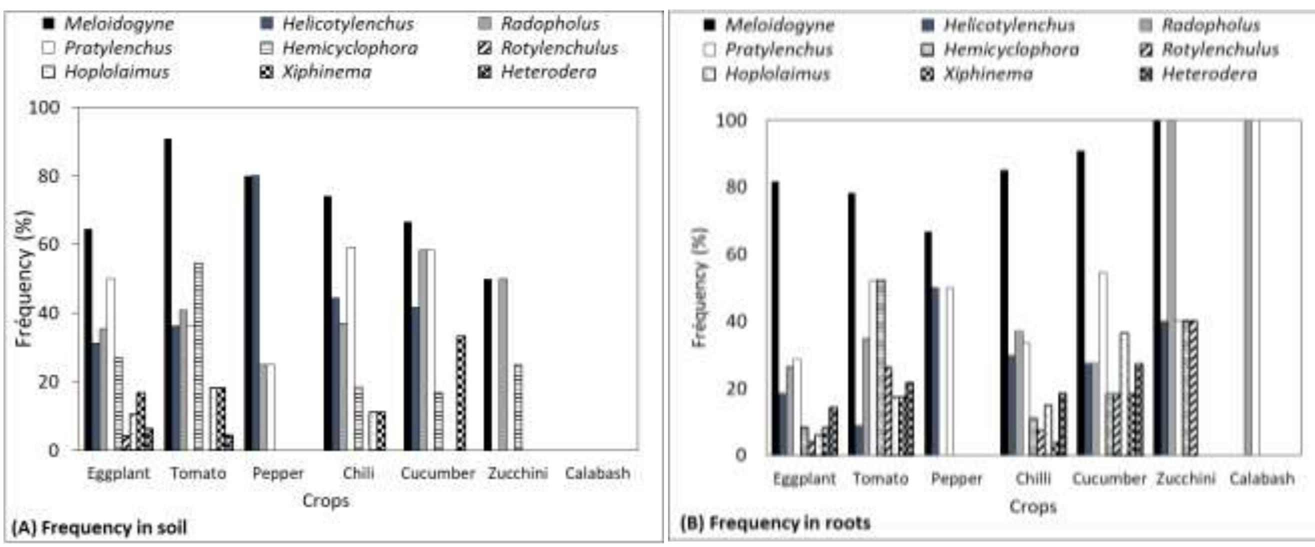

Figure-3: Nematode frequencies (%) in the rhizosphere (A) and crop roots (B)

Crop related frequencies of plant parasitic nematodes

The analysis of the frequencies of plant-parasitic nematodes relative to the crops shows that all nine nematode genera were observed in eggplant, tomato, and cucumber. The genera *Meloidogyne, Pratylenchus*, *Radopholus,* and *Helicotylenchus* can be considered major as they were more or less frequent and observed in almost all vegetable crops. Indeed, the high frequency of *Meloidgyne* was 100 % and 91% in roots and soil samples, respectively. The least frequent were *Rotylenchulus*, *Hemicycliophora, Heterodera, Xiphinema,* and *Hoplolaimus* (Figure 3A and 3B)

Segregation of the agroecological zones based on plant parasitic nematode abundances

A PCA was carried out from the Log(X+1)-transformed averages of the abundances of the genera for each AEZ. The PCA shows that 80.6% of the total variability observed is represented in the first place, which is a good representation of the variability in a large part of the active dataset. The abscissa axis that expressed 57.22% of the variability carries factual information. Consequently, the analysis description can only be restricted to this axis (Figure 4A).

This dimension opposes AEZ I (characterized by a strongly positive coordinate) to AEZ III (characterized by a strongly negative coordinate) on the axis 1. The AEZ I shares high values of the abundance of *Xiphinema* in roots (Xiph._R), *Rotylenchulus*, and *Heterodera* in soil (Roty._S and Hete._S). About AEZ III, it shares low values of abundances of *Meloidogyne* and *Helicotylenchus* in roots (Melo._R; Heli._R) and soil (Melo._S; Heli._S) and *Radopholus* and *Pratylenchus* in soil. A third group comprised the other AEZs with low abundance values for the genus *Rotylenchulus* in the roots (Figure 4B).

Segregation of the vegetable crops based on plant parasitic nematode abundances

The PCA from the Log(X+1)-transformed averages of the genera's abundances and related crops shows that 83.49% of the total variability was due to the first plane. More than the AEZ-related PCA, here, the abscissa axis expressed a greater, more significant variability (66.81%) than in the case of the AEZ-related PCA. Consequently, the analysis description has only been restricted to this axis (Figure 5A).

Axis 1 is strongly correlated with the abundance of *Heterodera* in roots (Hete._R; 92%), the abundance of *Xiphinema* in soil (Xiph._S; 96%), and in roots (Xiph._R; 91%). This axe opposes eggplant and chili, which correlate positively and negatively to the axis. Moreover, based on the significance of the links between axis 1 and the crops considered individuals, the main groups discriminated against are zucchini, chili, and eggplant. Zucchini is characterized by the low population density of *Helicotylenchus* in soil (Heli._S) and roots (Heli._R) and *Pratylenchus* in soil (Prat._S). Chilli is characterized by low population density of *Radopholus* (Rado._R), *Rotylenchulus* (Roty._R), and *Hemicycliophora* (Hemi._R) in roots. Eggplant is characterized by high populations of *Heterodera* in roots (Hete._R), *Xiphinema* in soil (Xiph._S) and in roots (Xiph._R), *Hoplolaimus* in roots (Hopl._R), *Hemicycliophora* in soil (Hemi._S) and *Meloidogyne* in soil (Melo._S) (Figure 5B).

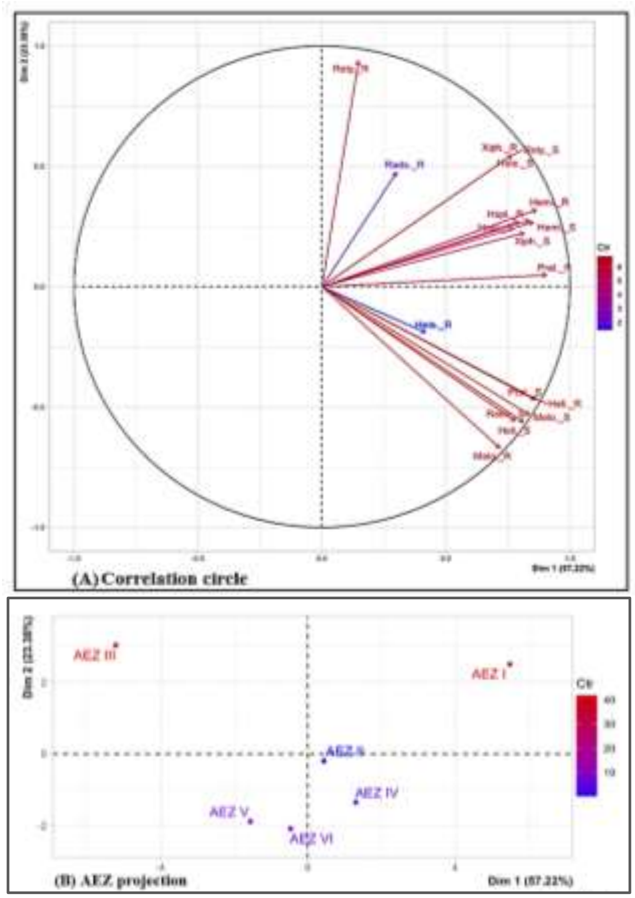

Figure-4: (4A) Correlation circle of nematode abundances in soil and roots and (4B) projection of the agroecological zones based on nematode abundances.

Melo: Meloidogyne, Helico: Helicotylenchus, Rado: Radopholus, Praty: Pratylenchus, Hemi: Hemicycliophora, Roty: Rotylenchulus, Hoplo: Hoplolaimus, Xiphi: Xiphinema, Hetero: Heterodera; R: Root, _S: Soil; AEZ: Agroecological Zone

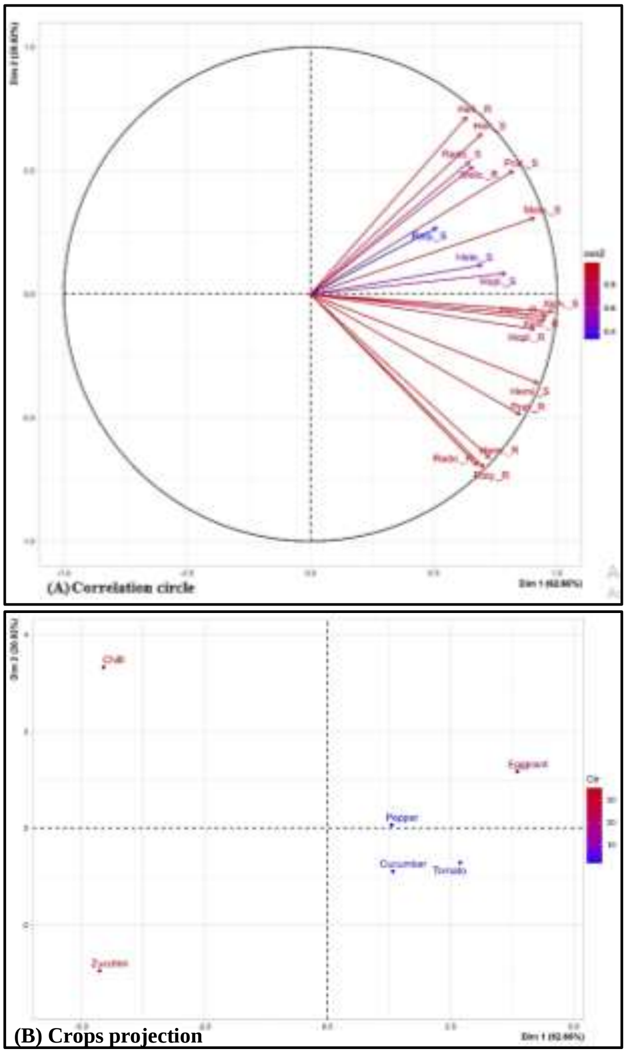

Figure-5: (5A) Correlation circle of nematode abundances in soil and roots and (5B) projection of the crops based on nematode abundances.
Melo: Meloidogyne, Helico: Helicotylenchus, Rado: Radopholus, Praty: Pratylenchus, Hemi: Hemicycliophora, Roty: Rotylenchulus Hoplo: Hoplolaimus, Xiphi: Xiphinema, Hetero: Heterodera; _R: Root, _S: Soil

Discussion

This study revealed the presence of nine genera of plant-parasitic nematodes associated with vegetable crops in six agroecological production zones of Côte d'Ivoire. All the regions surveyed presented potential phytosanitary risks due to nematodes. The populations of these pests were abundant in the samples where present and able to induce yield losses. They were above the tolerance thresholds, 100 to 1000 individuals.kg^{-1} of soil and 10 to 100 individuals.g^{-1} of roots (De Guiran, 1983). Among the identified genera, the root-knot nematodes (*Meloidogyne* spp.) were the most frequent and abundant in vegetable crops and the agroecological zones. This sedentary endoparasitic nematode is known as the most dominant and economically damaging in many countries on several crops as it has a broad host range (Isgouhi and Teixeir, 2019). It causes poor plant growth, reduced crop quality and yield, and reduced resistance to other stresses such as drought and diseases. Several studies demonstrated the association of large numbers of *Meloidogyne* with vegetable crops, especially Solanaceae, Cucurbitaceae, and Composeae (Bui et al., 2022), as reported in this study. Very high population densities (45,000 individuals.g-1) of *Meloidogyne* spp. were associated with pepper crops in Niger (Haougui et al., 2013). The genus *Meloidogyne* was also frequent in eggplant (55.8%) and watermelon (61.9%) in Egypt (El-Nuby et al., 2019). It was also frequent in rice crops at 49% in India (Nisa et al., 2022) and dominant in yam crops, with four individuals per gram of peels (Kouakou et al., 2016).

Another damaging group of plant parasitic nematodes in vegetable crops in Côte d'Ivoire included *Pratylenchus*, *Radopholus*, and *Helicotylenchus*. They were overall abundant but moderately frequent. The root lesion (*Pratylenchus* spp.) and the burrowing (*Radopholus* spp.) nematodes are migratory endoparasitic nematodes that feed on cortical tissues. They are known in Cote d'Ivoire for causing damage to tomato and banana crops (Kakou et al., 2021; Yéo et al., 2018). *Radopholus similis* and *Pratylenchus coffeae*, for instance, have been known for a long as the main harmful nematodes in plantain and bananas in Cote d'Ivoire (Adiko and N'Guessan, 2000). The genera *Pratylenchus* and *Meloidogyne* are known as the most damaging nematodes in sugar cane (Cadet and Spaull, 2005). *Meloidogyne* spp., *Pratylenchus* spp., and *Radopholus* spp. are known as damaging nematodes of many crops. Thus, their prevalence in the different studied areas can predict significant losses related to their action on vegetable crops in Côte d'Ivoire. As far as concern, the spiral nematode (*Helicotylenchus*), despite its significant frequency, has an impact that could be less important on vegetable crops. Indeed, *Helicotylenchus* spp. is a migratory ectoparasitic nematode that stylet is short so that its action on roots could be less damaging.

The genera *Hemicyclophora, Heterodora, Hoplolaimus, Rotylenchulus,* and *Xiphinema* are considered in this study as minor plant-parasitic nematodes for vegetable crops in Côte d'Ivoire. These results corroborate many authors who found low population densities (Anwar and McKenry, 2012; Indarti et al., 2023; Mokrini et al., 2019). The low frequency of these nematode genera suggests that they are not very likely to be associated with vegetable crops and do not threaten their production (Marquez et al., 2021). However, the dagger nematode, *Xiphinema*, harms many vegetable crops because of its virus vector status, including *Tobacco Ring spot Nepovirus* (TobRSV), which infects tomatoes, tobacco, and soybeans. It has a significant economic impact on cucurbits (Wang et al., 2002). The most attacked crops were eggplant, tomato, and cucumber, with eggplant the most susceptible to various genera, including *Meloidogyne* and *Xiphinema*. The differences in population density could be linked to plant resistance degree concerning root structure (Anwar and McKenry, 2002). These results are aligned with previous studies that found more plant-parasitic nematode genera associated with tomato, eggplant, cucumber, and watermelon, while pepper recorded low densities (El-Nuby et al., 2019). Under controlled conditions in India, nematodes were most prevalent in tomatoes, pepper, and Cucurbitaceae, whereas *Meloidogyne incognita* was the most important nematode (Singh and Sharma, 2015). Our results are also in line with those of Anwar et al. (2007), who found that eggplant and tomato are good hosts for *Meloidogyne incognita*, unlike chili, due to the significantly higher reproduction indices of *M. incognita* in tomato and eggplant roots compared with chili.

Furthermore, this study also highlighted differences between agroecological zones of Côte d'Ivoire based on nematode population characteristics. The PCA isolated the AEZ I from the others as the most infested. This zone constitutes an essential basis of vegetable crop production, where production is mainly provided from the overexploited urban and peri-urban areas. The zone is characterized by intensive cropping systems compared to AEZ III, where the cropping systems are extensive. The succession of plant parasitic nematode-sensitive crops is also an increasing factor in nematode populations. The AEZ I is a wet zone where the soil is ferralitic and sandy-textured (Kouakou et al., 2021). Several authors showed strong correlations between nematode abundance, soil texture, and organic matter composition. Indeed, nematodes are more frequently found in sandy textured soils, as they can enhance their mobility. A part of AEZ III that was opposite to AEZ I, the other agroecological zones, are also potentially nematode-damage susceptible zones where vegetable crop production is also significant.

This study shows that nematodes are a severe problem for Ivorian agriculture, particularly market gardening, and could cause substantial economic losses. Adopting an integrated management strategy could reduce the impact of these parasites. This strategy can be implemented by combining control methods such as fallowing, crop rotation, and applying plant extracts with a nematicidal effect.

Conclusion

It can be concluded from the present study that nine genera of nematodes are associated with vegetable crops and are variably distributed in the agroecological zones studied. The most dominant genus is *Meloidogyne*, found in all localities and almost all crops sampled. This study reveals that the diversity of the nematode fauna depends on many factors, including the host plant, cropping systems, and soil type. The high abundance and frequency of nematodes found deserve particular attention from the Ivorian agricultural authorities in implementing vegetable crop development programs. These parasites must be considered major vegetable pests, and management strategies must be adopted to limit their impact. Further studies on the severity, dynamics, and integrated management of these nematodes, especially *Meloidogyne*, are needed for more sustainable production of vegetable crops.

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Contribution of Authors

Sandrine YA: Wrote the protocol, conducted the study, collected data, performed the statistical analysis and wrote the first draft of the manuscript
Gnenakan Y: Analyzed and interpreted data

Jacob N: Analyzed and interpreted data
Eric-Olivier T: Supervised study, interpreted data and edited manuscript
Martial KKFJ: Performed literature review, edited and finalized the manuscript
Gilchrist KEY: Performed literature review, edited and finalized the manuscript
Urbain KKU: Analyzed and interpreted data
Junior KD: Performed literature review, edited and finalized the manuscript
Théodore KK: Performed literature review, edited and finalized the manuscript
Kouabenan A: Conceived the idea, developed research methodology and read and approved the final manuscript

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