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Correlations Between *Pratylenchus* and *Meloidogyne* Populations, Soil Chemical Properties, Soil Texture, and Nutritional Status of Soybean Crops in Paraguay

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Abstract

Nematodes cause great damage to soybean crops in Paraguay. Studies have investigated correlations between phytonematodes and soil chemical and physical properties, but little is known about correlations with the nutritional status of soybean crops. This study aimed to assess correlations between *Pratylenchus*, *Meloidogyne*, soil chemical properties, soil texture, and the nutritional status of soybean. The experiment was carried out in Paraguay in areas of commercial soybean cultivation infested with nematodes, totaling 83 collection sites. Analyses of nematodes in soil and root samples, chemical characterization of soil acidity, fertility, and texture, and chemical characterization of soybean leaves were performed, totaling 36 variables. Data were subjected to principal component analysis. Soil Al^{3+} favored the development of *Pratylenchus* populations. Organic carbon negatively influenced *Meloidogyne*. K^+ and Mg^{2+} negatively affected *Pratylenchus* and *Meloidogyne*, respectively. *Pratylenchus* and *Meloidogyne* correlated negatively with clay contents. In sandy soils, there was a negative correlation between *Pratylenchus* and sand content. *Pratylenchus* and *Meloidogyne* led to an increase in foliar Ca and a decrease in foliar P. Soil fertility management can be used as part of the integrated management of *Pratylenchus* and *Meloidogyne*. It is worth mentioning that, in field studies, the complexity of biotic and abiotic factors in the crop system may contribute to diverging results, making it difficult to establish a single response pattern, especially when some factors affect others.

Keywords: root-knot nematode, lesion nematode, soil fertility, leaf chemistry

1. Introduction

The yield of soybean is influenced by interactions between several factors, including plant genotype, climate conditions, biotic stress (diseases and pests), and soil chemical and physical properties (Hansel et al., 2021). Plant-parasitic nematodes are important biotic factors in soybean production, causing losses of up to 5.3 billion dollars in Brazil (Syngenta et al., 2022). Among the nematodes able to infect soybean, some of the most damaging species are members of the genera *Pratylenchus* and *Meloidogyne*, which have a wide range of hosts and occur in virtually all cropping areas (Favoreto et al., 2019). The lesion nematode, *Pratylenchus brachyurus*, is a migrating endoparasite that penetrates and moves within host roots, rupturing cortical tissues and producing symptoms of necrosis (Favoreto et al., 2019). *Meloidogyne*, commonly known as root-knot nematode, is the genus of greatest economic importance worldwide (Ferraz & Brown, 2016). These sedentary endoparasites induce abnormal root growth and deformation, leading to the formation of nodules known as galls (Jones et al., 2013). Both parasites impair water and nutrient absorption by host roots, causing stunted growth and, in some cases, even plant death (Favoreto et al., 2019).

Knowledge of soil physical and chemical properties allows to understand the dynamics of nutrient release and uptake, water permeability, and retention capacity. Assessment of nutrient levels in soybean leaf tissues serves to gain insight into the crop's productive potential (Oliveira Junior et al., 2020). Previous studies investigated associations of *Pratylenchus* and *Meloidogyne* with soil physical (Galbieri et al., 2016; Noronha et al., 2020; Leiva et al., 2020; Dias-Arieira et al., 2021) and chemical properties (Guzmán, 2008; Leiva et al., 2020; Noronha et al., 2020; Dias-Arieira et al., 2021). *Pratylenchus* is reported to correlate positively with sandy (Leiva et al., 2020; Dias-Arieira et al., 2021) and clay sandy soils (Gallardo et al., 2015). Findings regarding organic matter and soil pH are not conclusive, with reports of negative (Leiva et al., 2020; Dias-Arieira et al., 2021) and positive correlations between *Pratylenchus* and organic matter (Franchini et al., 2018; Noronha et al., 2020) as well as negative (Osseni et al., 1997) and positive correlations between the nematode and soil pH (Noronha et al., 2020). *Meloidogyne* is consistently associated with sandy soils (Guzmán et al., 2008; Galbieri et al., 2016; Noronha et al., 2020). The species *M. incognita*, *M. javanica*, *M. arenaria*, and *M. hapla* show a negative correlation with soil organic matter (Guzmán et al., 2008). Research suggests that nematode genus is not significantly correlated with soil pH (Guzmán et al., 2008). Furthermore, soil pH does not seem to interfere with nematode development or penetration in host roots (Melakeberhan et al., 2004), although a recent study found a positive relationship (Noronha et al., 2020).

Investigations on soil nutrients showed that nitrogen (N) and phosphorus (P) may directly influence nematode abundance, due to a decrease in the diversity of plant-parasitic as well as bacteriophagus and fungivorous nematode genera when these nutrients are found in lower concentrations (Nisa et al., 2021). However, chemical phosphorus fertilizer (P_2O_5) was reported to increase the number of second-stage juveniles (J2) of *M. javanica* in soil (Hemmati & Saeedizadeh, 2020).

Despite an extensive number of studies, there is little information available on the relationship between nematodes and the nutritional status of soybean. Available studies focus primarily on root-knot nematodes (Carneiro et al., 2002). This study aimed to assess correlations between nematodes of the genera *Pratylenchus* and *Meloidogyne*, soil chemical properties, soil texture, and the nutritional status of soybean crops in naturally infested fields in Paraguay.

2. Method

The study was carried out through collections performed at the major areas of grain production in Paraguay (MAG, 2014), more specifically in departments located in the northern (Amambay), eastern (Canindeyú and Alto Paraná), and southern (Itapúa) agroecological regions of eastern Paraguay. These regions are characterized by diverse climates: humid mesothermal climate in the North, humid mesothermal forest climate in the East, and hot humid temperate climate in the South. The average annual rainfall in all three regions is 1600 mm (MAG, 2014). Soils have sandstone or basalt as parent materials and are classified as Rhodic Kandiudox Oxisol (Latosol) and Rhodic Paleudult Ultisol (Nitosol) (Santos et al., 2018).

Samples were collected from soybean production areas previously identified to be infested with plant-parasitic nematodes. A total of 83 collection sites were sampled: 44 in Amambay, 36 in Canindeyú, 2 in Alto Paraná, and 1 in Itapúa. At each collection site, a sample consisting of at least four subsamples was collected when soybean crops were between R1 and R4 stages. A shovel and bucket were used for the collection of soil and root samples for nematode analysis. About 1 kg of soil was collected from around the roots of soybean plants at 0-20 cm depth, as well as about 30 g of root material, with care to include secondary roots.

For analysis, soil samples were homogenized and a 200 cm^3 aliquot was subjected to nematode extraction (Jenkins, 1964). Roots were divided into 10 g fragments, ground in a blender, and centrifuged in sucrose solution (Coolen & D'Herde, 1972). Subsequently, nematodes were identified at the genus level and quantified in a Peters' chamber under an optical microscope at 10× magnification.

Sampling for analysis of soil chemical parameters (acidity and fertility) was carried out at the same time and site of sample collection for nematode analysis but from between crop rows. Soil samples were collected using open tubular manual sampler at 0-20 cm depth. Soil chemical parameters were determined by methods described in Raij et al. (1997). Texture analysis was performed using 20 g of soil according to the modified method of Camargo et al. (1986).

The results were used to calculate sum of bases (SB), base saturation (BS), total cation-exchange capacity (TCEC), effective cation-exchange capacity (ECEC), and Al saturation (Teixeira et al., 2017). Potential acidity (H + Al) was estimated using a pH SMP correlation curve (Steiner et al., 2009).

Nutrient analysis of soybean: leaves were collected at the same time of sample collection for nematode analysis. Each sample consisted of at least 35 newly mature trifoliate leaves without the petiole, corresponding to the third and fourth leaves from the apex (Malavolta et al., 1997). Nitrogen was quantified by the semi-micro-Kjeldahl method (Kjeldahl, 1883); P by the metavanadate colorimetric method; K^+, Ca^{2+}, Mg^{2+}, Fe^{2+}, Cu^{2+}, Zn^{2+}, and

Mn^{2+} by atomic absorption spectrophotometry; SO_4^{2-} by barium sulfate turbidity; and BO_3^{3-} by the azomethine colorimetric method (Malavolta et al., 1997).

2.1 Data Analysis

Three groups of variables were analyzed. The first group comprised the sum of *Pratylenchus* and *Meloidogyne* numbers in soil and root samples. Only samples containing nematodes from these genera were considered at this stage of analysis. The second group comprised soil attributes related to acidity, fertility and texture (sand, silt, and clay contents). The third group comprised variables related to soybean nutrition, including foliar macronutrients (N, P, K, Ca, Mg, and S) and micronutrients (B, Fe, Cu, Zn, and Mn). The data were analyzed separately according to two groups of soil texture. The first group included sandy soils, comprising 16 sites with a clay content of less than 150 g kg^{-1}. The second group included clay soils, comprising 67 sites with clayey or very clayey texture (clay contents equal to or greater than 350 g kg^{-1}) (Santos et al., 2018).

Data on soil physical properties were presented by textural classes (sandy and clay soils) in a descriptive table. Nematode, soil, and soybean nutrition data were subjected to principal component analysis (PCA) using Statistica software (version 7). PCA results were presented as vector graphs.

3. Results

Pratylenchus was detected in 76 root samples (91.57% of collection sites) and 20 soil samples (24.10% of collection sites), whereas *Meloidogyne* was found in 18 root samples (21.69% of collection sites) and 17 soil samples (20.48% of collection sites). *Pratylenchus* densities ranged from 4 to 1552 nematodes per gram of root and from 80 to 800 nematodes per 200 cm^3 of soil, whereas *Meloidogyne* densities ranged from 4 to 5616 nematodes per gram of root and from 80 to 77280 nematodes per 200 cm^3 of soil. It is noteworthy that, of the 83 samples, 98% contained mixed nematode populations, with 2, 3, and 4 genera of phytonematodes detected in 24%, 66%, and 7% of samples, respectively. In addition to *Pratylenchus* and *Meloidogyne*, other nematode genera were identified in root and soil samples as shown in Figure 1.

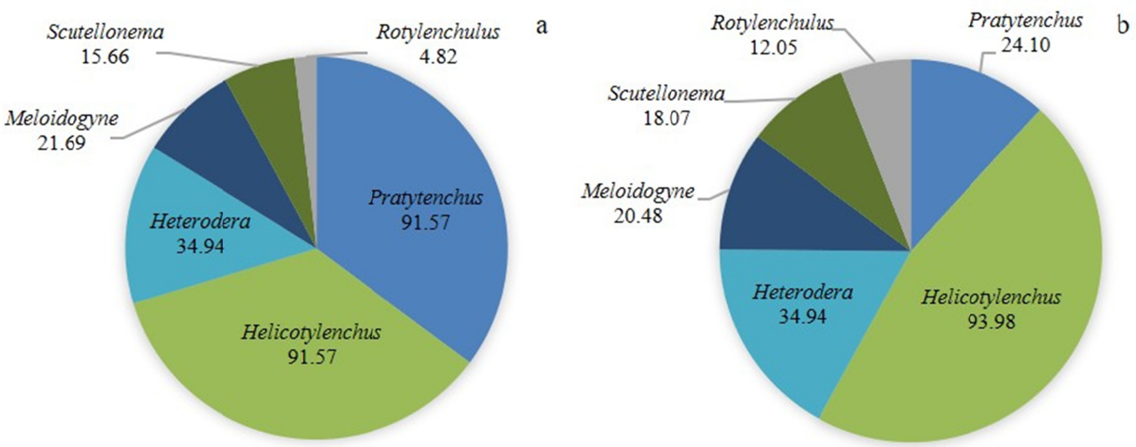

Figure 1. Frequency of occurrence (%) of nematode species in the samples in root (A) and soil (B) samples

Soil texture analysis revealed that 16 samples were sandy (clay content below 150 g kg^{-1}) and 67 samples were clayey (clay content above 350 g kg^{-1}). Minimum, mean, and maximum values of soil chemical properties in sandy and clay soils are shown in Table 1.

Table 1. Minimum, mean, and maximum values of chemical properties of sandy and clay soils analyzed in the study

Value	pH ($CaCl_2$)	Al	H + Al	OC	OM	BS	Al saturation	SB	ECEC	TCEC
		-- $cmol_c\ dm^{-3}$ --		$g\ dm^{-3}$	---------------- % ----------------			---------- $cmol_c\ dm^{-3}$ -----------		
Sandy soils										
Min	4.05	0.00	0.22	7.20	1.24	8.43	0.00	0.72	1.42	3.40
Mean	5.26	0.07	3.55	13.98	2.41	46.18	4.40	2.69	2.76	6.24
Max	6.97	0.70	7.82	28.56	4.92	96.64	49.30	6.48	6.48	8.54
Clay soils										
Min	4.60	0.00	0.22	17.52	3.02	41.88	0.00	4.73	4.99	11.29
Mean	5.49	0.02	4.30	29.89	5.15	70.55	0.28	10.61	10.63	14.92
Max	7.18	0.26	7.77	55.44	9.56	98.47	5.21	17.80	17.80	21.92

Value	P	S	K	Ca	Mg	B	Cu	Fe	Mn	Zn	Clay
	--- $mg\ dm^{-3}$ ---		-------- $cmol_c\ dm^{-3}$ --------			------------------------ $mg\ dm^{-3}$ ------------------------					-- $g\ kg^{-1}$ --
Sandy soils											
Min	7.63	1.59	0.11	0.30	0.21	0.27	0.36	26.85	4.26	0.24	44
Mean	29.19	3.29	0.23	1.82	0.65	0.44	1.00	199.68	48.24	1.62	82
Max	107.4	5.56	0.42	5.53	0.99	0.72	2.33	517.20	160.44	4.17	110
Clay soils											
Min	5.27	1.87	0.16	3.20	0.96	0.43	2.28	16.87	64.15	2.03	371
Mean	18.91	12.34	0.70	8.01	1.90	0.79	12.64	57.37	206.78	8.24	550
Max	54.90	44.53	1.41	14.56	4.21	1.71	38.16	154.80	419.40	24.84	673

Note. OC, organic carbon; OM, organic matter; SB, sum of bases; BS, base saturation; ECEC, effective cation-exchange capacity; TCEC, total cation-exchange capacity.

3.1 PCA of Pratylenchus, Meloidogyne, Texture, and Soil Chemical Properties

PCA of *Pratylenchus* population and soil chemical attributes revealed that, in sandy soils, there was a weak positive correlation between *Pratylenchus* and pH SMP as well as a weak negative correlation between the nematode and OC, TCEC, and H + Al (Figure 2a). In clay soils, there was a strong positive correlation between *Pratylenchus* and Al^{3+} and a weak correlation with H + Al and Al saturation, as well as a weak negative correlation between the nematode and pH SMP and pH $CaCl_2$ (Figure 2b).

In sandy soils, a weak negative correlation was observed between *Meloidogyne* and TCEC and OC (Figure 2c). Similarly, in clay soils, there was a negative but strong correlation between *Meloidogyne* and OC, as well as a weak negative correlation of the nematode with TCEC, ECEC, and SB (Figure 2d).

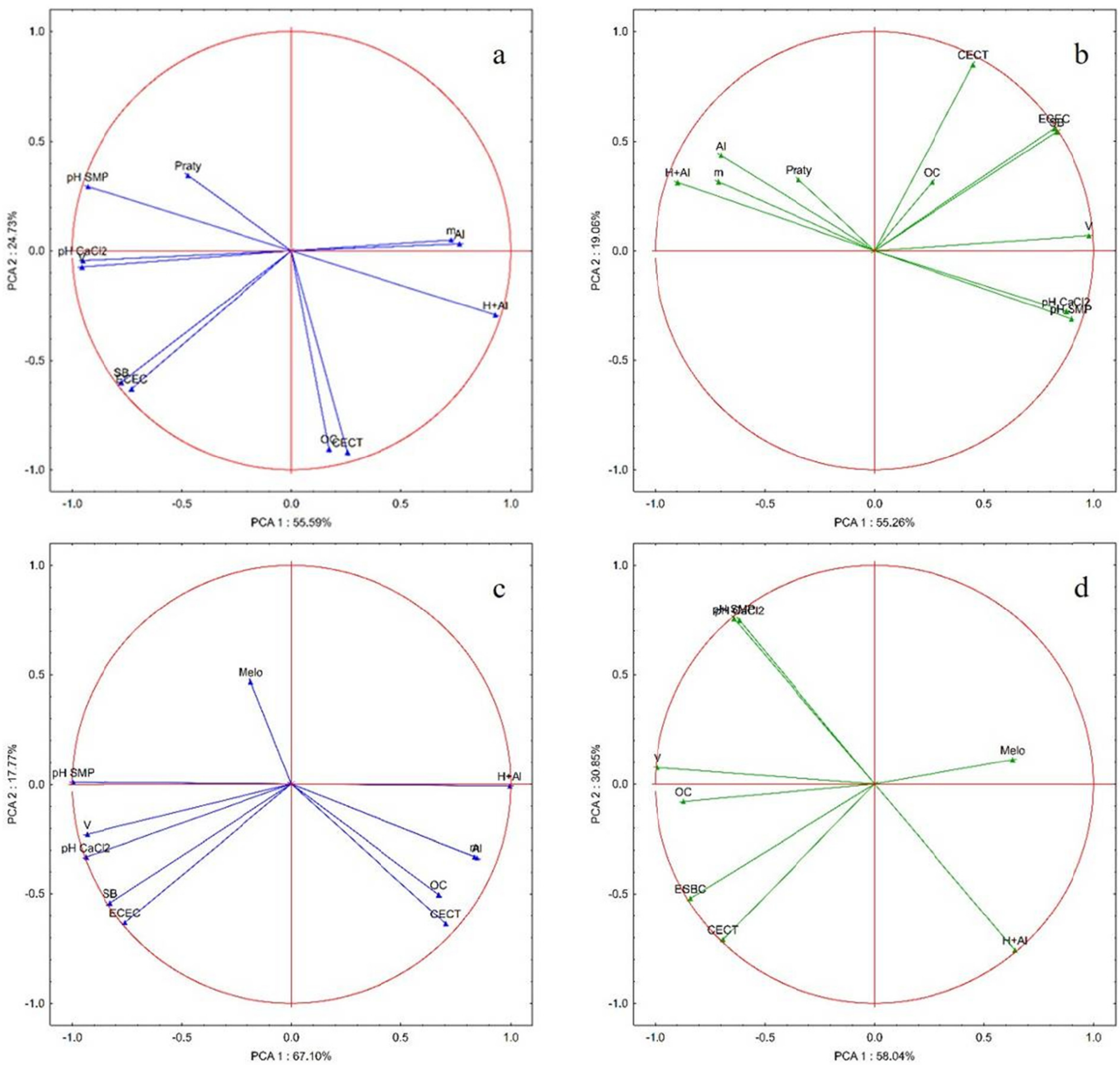

Figure 2. Principal component analysis (PCA) biplot of *Pratylenchus* and *Meloidogyne* populations and soil chemical properties represented by vectors. *Pratylenchus* in (a) sandy and (b) clay soils. *Meloidogyne* in (c) sandy and (d) clay soils

Note. Praty, *Pratylenchus*; Melo, *Meloidogyne*; Al, aluminum; Al sat, Al saturation; H + Al, potential acidity; TCET, total cation-exchange capacity; ECEC, effective cation-exchange capacity; SB, sum of bases; BS, base saturation; OC, organic carbon

Pratylenchus correlated negatively with both sand and clay contents (Figures 3a and 3b, respectively). The correlation between *Meloidogyne* and sandy soil was weak and poorly explained by PCA (Figure 3c). By contrast, *Meloidogyne* had a negative correlation with clay soils (Figure 3d).

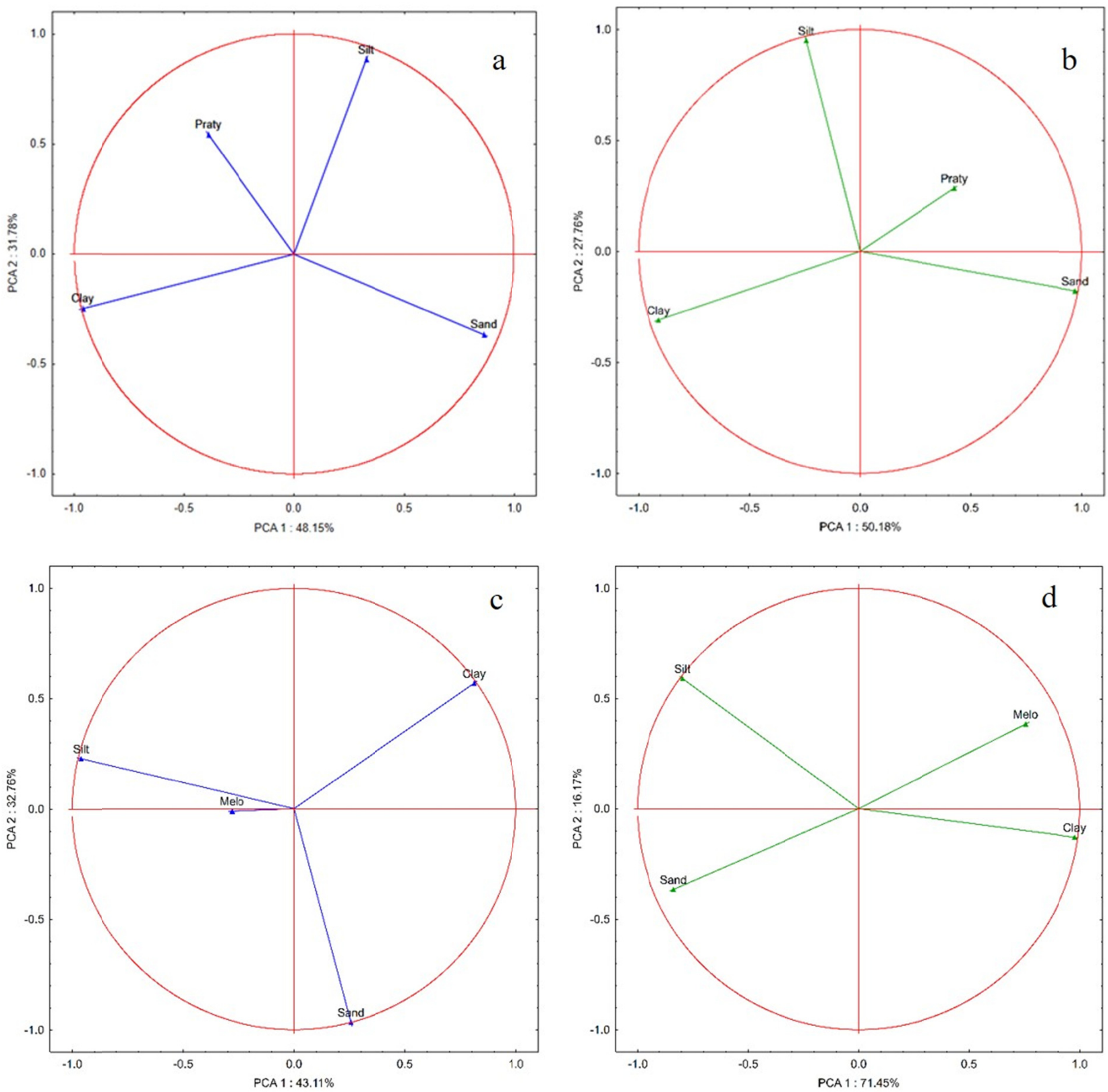

Figure 3. Principal component analysis (PCA) biplot of *Pratylenchus* and *Meloidogyne* populations and soil texture represented by vectors. *Pratylenchus* in (a) sandy and (b) clay soils. *Meloidogyne* in (c) sandy and (d) clay soils

Note. Praty, *Pratylenchus*; Melo, *Meloidogyne*.

3.2 PCA of Pratylenchus, Meloidogyne, and Soil Macronutrients and Micronutrients

There was a weak positive correlation between *Pratylenchus* and Mg^{2+} and a weak negative correlation with PO_4^{3-} in sandy soils (Figure 4a). This nematode also correlated strongly and negatively with K^+ in clay soils (Figure 4b). In sandy soils (Figure 4c), there was a weak positive correlation between *Meloidogyne* and Ca^{2+} and Mg^{2+}, as well as a weak negative correlation with SO_4^{2-}. In clay soils, *Meloidogyne* had a strong negative correlation with Mg^{2+}, a weak negative correlation with Ca^{2+}, and a weak positive correlation with PO_4^{3-} (Figure 4d).

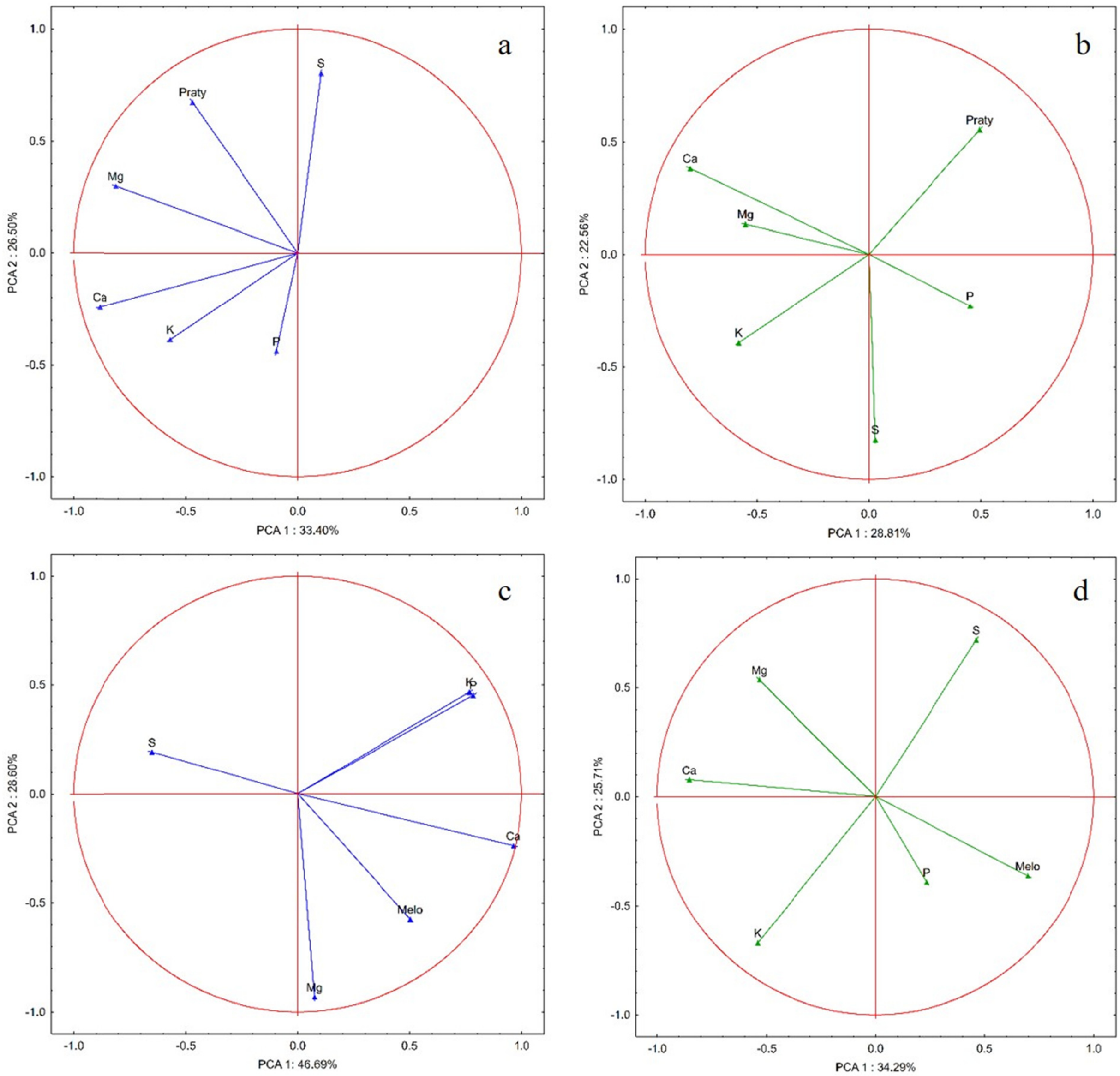

Figure 4. Principal component analysis (PCA) biplot of *Pratylenchus* and *Meloidogyne* populations and soil macronutrient contents represented by vectors. *Pratylenchus* in (a) sandy and (b) clay soils. *Meloidogyne* in (c) sandy and (d) clay soils

Note. Praty, *Pratylenchus*; Melo, *Meloidogyne*; P, phosphorus; K, potassium; Ca, calcium; Mg, magnesium; S, sulfur.

Pratylenchus showed a weak negative correlation with BO_3^{3-} in sandy soils (Figure 5a) and a weak positive correlation with Fe^{2+} in clay soils (Figure 5b). *Meloidogyne* had a weak positive correlation with BO_3^{3-} and Cu^{2+} in sandy soils (Figure 5c) and a strong negative correlation with Mn^{2+} in clay soils (Figure 5d).

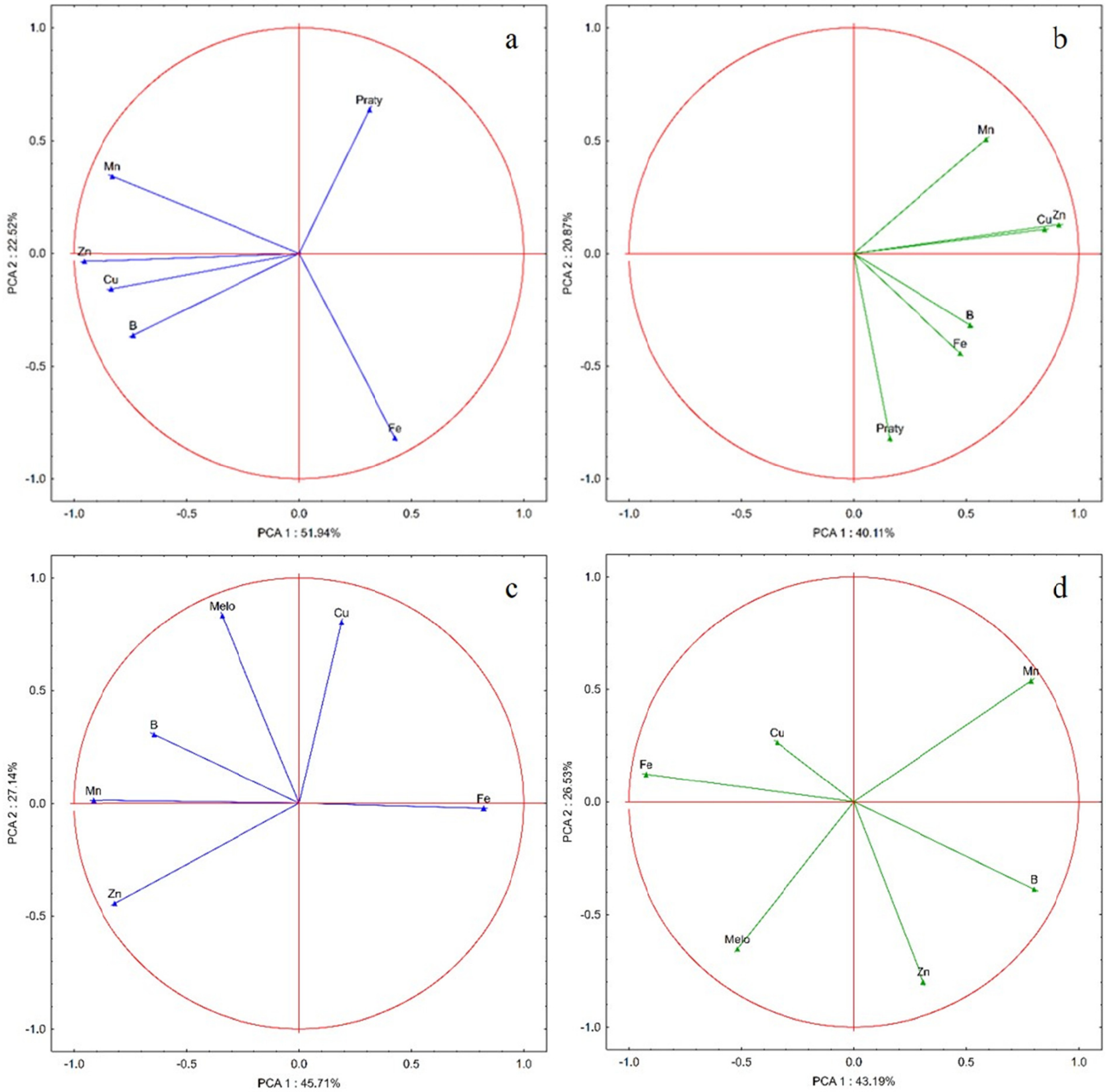

Figure 5. Principal component analysis (PCA) biplot of *Pratylenchus* and *Meloidogyne* populations and soil micronutrient contents represented by vectors. *Pratylenchus* in (a) sandy and (b) clay soils. *Meloidogyne* in (c) sandy and (d) clay soils

Note. Praty, *Pratylenchus*; Melo, *Meloidogyne*; Fe, iron; Cu, copper; Zn, zinc; B, boron; Mn, manganese.

3.3 PCA of Pratylenchus, Meloidogyne, and Foliar Macronutrients and Micronutrients

In sandy soils, *Pratylenchus* had a strong positive correlation with foliar Ca, a strong negative correlation with P, and a weak negative correlation with K (Figure 6a). On the other hand, in clay soils, the nematode correlated weakly and positively with Ca, strongly and negatively with N, K, and S, and weakly and negatively with P (Figure 6b). *Meloidogyne* showed a strong negative correlation with K, a weak negative correlation with P, and a strong positive correlation with Ca^{2+} in sandy soils (Figure 6c). In clay soils, the nematode had a strong negative correlation with S as well as a weak negative correlation with N (Figure 6d).

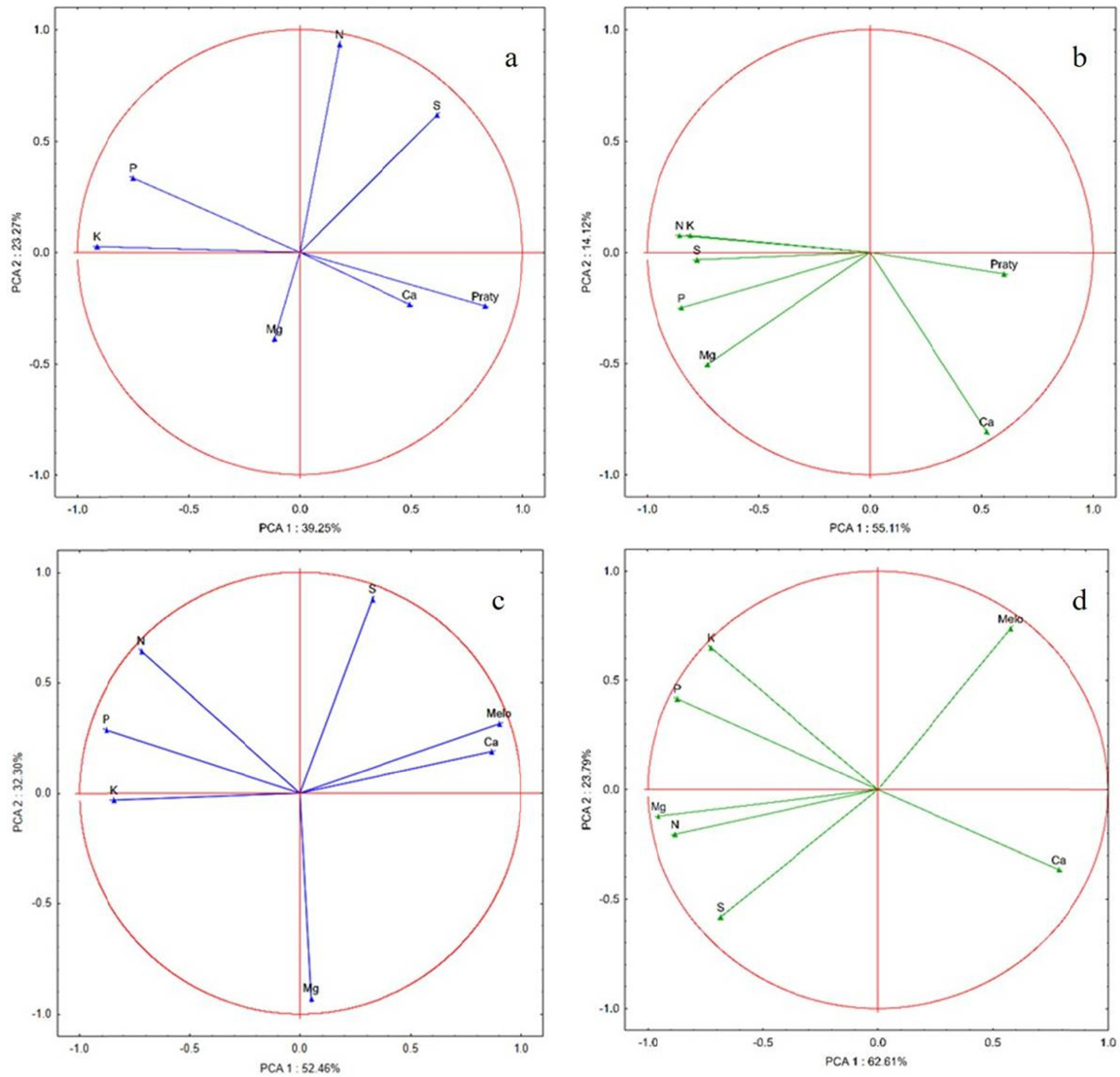

Figure 6. Principal component analysis (PCA) biplot of *Pratylenchus* and *Meloidogyne* populations and foliar macronutrients represented by vectors. *Pratylenchus* in (a) sandy and (b) clay soils. *Meloidogyne* in (c) sandy and (d) clay soils

Note. Praty, *Pratylenchus*; Melo, *Meloidogyne*; N, nitrogen; P, phosphorus; K, potassium; Ca, calcium; Mg, magnesium; S, sulfur.

In sandy soils, a weak positive correlation was observed between *Pratylenchus* and B and a negative correlation between the nematode and Cu (Figure 7a). In clay soils (Figure 7b), *Pratylenchus* had a strong positive correlation with Fe and a weak negative correlation with Mn. *Meloidogyne* correlated strongly and positively with foliar B, strongly and negatively with Fe, and weakly and negatively with Cu in sandy soils (Figure 7c). *Meloidogyne* did not correlate with any foliar micronutrients in clay soils (Figure 7d).

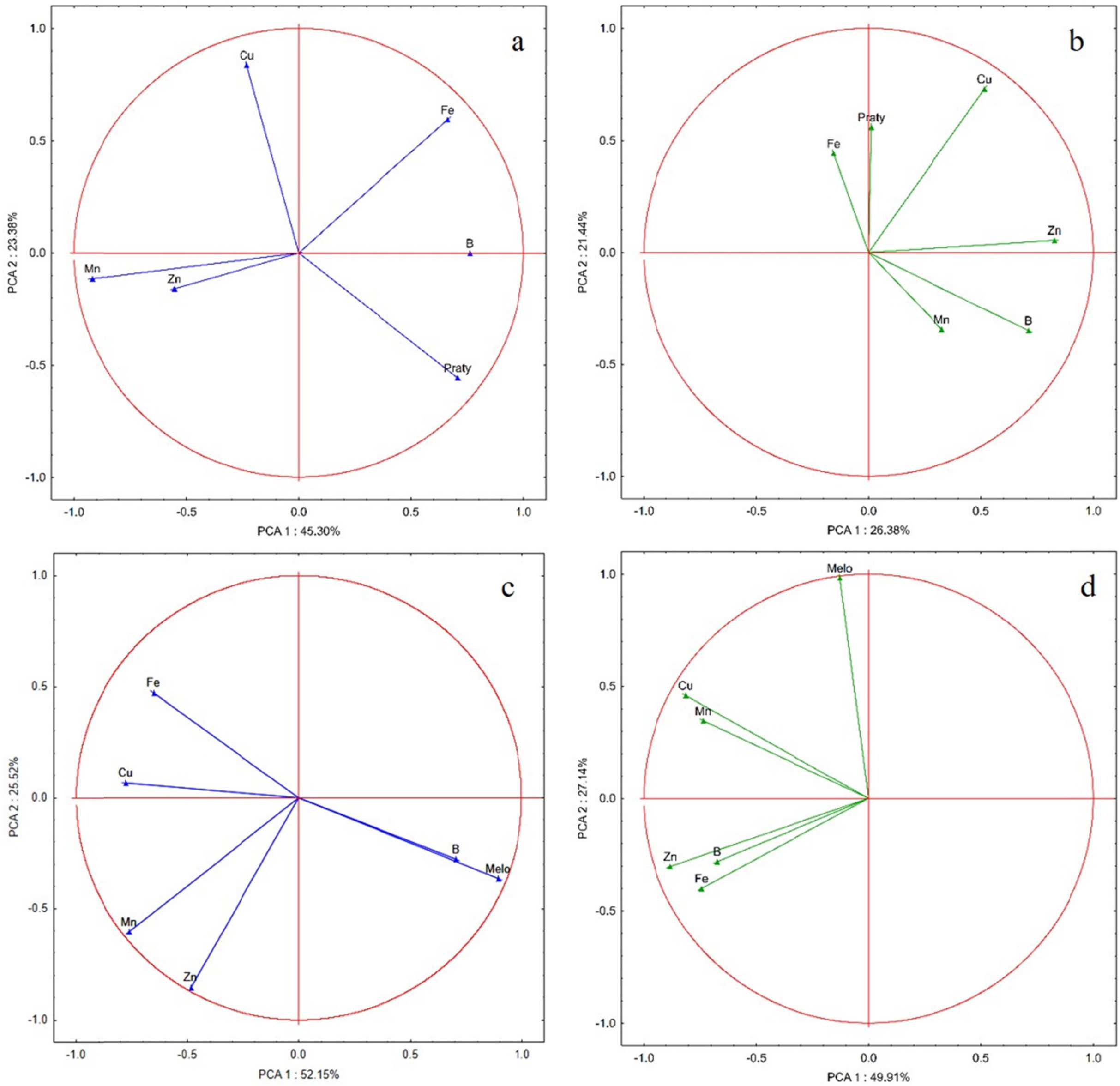

Figure 7. Principal component analysis (PCA) biplot of *Pratylenchus* and *Meloidogyne* populations and foliar micronutrients represented by vectors. *Pratylenchus* in (a) sandy and (b) clay soils. *Meloidogyne* in (c) sandy and (d) clay soils

Note. Praty, *Pratylenchus*; Melo, *Meloidogyne*; Fe, iron; Cu, copper; Zn, zinc; B, boron; Mn, manganese.

4. Discussion

The frequency of *Pratylenchus* and *Meloidogyne* was higher in root samples than in soil samples, which was expected given that these nematodes are endoparasites and spend most of the life cycle inside roots (Jones et al., 2013; Favoreto et al., 2019). Of note, majority of samples (98%) contained mixed populations of nematodes, a result frequently observed in Brazil (Galbieri et al., 2016) and Paraguay (Leiva et al., 2020). Coexistence of these nematodes can be explained by their common hosts, good adaptation to edaphoclimatic conditions of crop regions, and diversity of survival mechanisms, as well as low interspecific competition between these genera (Jones et al., 2013; Favoreto et al., 2019; Ferraz & Brown, 2016).

The properties of soils studied here were compared with reference values for soils in Paraná (Motta & Pauletti, 2017) and Mato Grosso do Sul and Santa Catarina States (Santos et al., 2016), states of Brazil closest to the studied areas of the Paraguay. It was observed that the values of soil chemical properties varied greatly in sandy soils, ranging from very low, moderate to high (Table 1). The exceptions were Al^{3+}, which showed very low or low values in all soils, TCEC and Mg^{2+}, which did not have high values, and BO_3^{3-}, which ranged from medium to very high in sandy soils. In clay soils, on the other hand, fertility variables were found to be high. We observed high or very high OC and ECEC levels. TCEC, pH $CaCl_2$, Ca^{2+}, and Mg^{2+} ranged from medium to high. In clay soils, all micronutrients were identified at high or very high levels (Table 1).

The positive correlation between *Pratylenchus* and soil pH and the negative correlation between the nematode and OC in sandy soils (Figure 2a) disagree with previous research (Franchini et al., 2014). However, one study also observed a negative relationship between OC and the lesion nematode (Dias-Arieira et al., 2021), suggesting a possible suppressive effect of organic compounds on phytonematodes, in addition to a beneficial effect of OC on the growth of nematode-antagonistic microorganisms. In clay soils, the positive relationship of *Pratylenchus* with Al^{3+}, H + Al, and Al saturation, as well as the negative relationship between the nematode and pH $CaCl_2$ and pH SMP (Figure 2a), can be attributed to the fact that *Pratylenchus* populations are generally associated with poor, acidic soils. These findings corroborate those of previous studies showing the correlation between soil H + Al and *P. brachyurus* in soybean roots (Franchini et al., 2014) and the negative correlation between nematodes and soil pH (Duddigan et al., 2021).

Given that OC can be used as an estimate of soil organic matter (Motta & Pauletti, 2017), our results for *Meloidogyne* (Figure 2c) agree with those of Guzmán et al. (2008), who observed a negative relationship between root-knot nematodes and soil organic matter content. As previously discussed for *Pratylenchus*, this relationship can be explained by the release of toxic compounds during organic matter decomposition and the increase in soil biological activity (Graham & Strauss, 2021). These findings allow us to infer that conservation practices that increase soil organic matter may contribute to the biological control of nematodes by increasing populations of antagonistic microorganisms that are native to the environment.

Soil acidity and fertility properties showed similar correlations in the PCAs of nematode genera and soil types. There were positive correlations between pH $CaCl_2$ and pH SMP, OC and TCEC, ECEC and SB, and Al^{3+} and Al saturation. pH SMP correlated negatively with H + Al. The negative relationship between H + Al and pH SMP was expected, given that the estimation of potential acidity is based on the correlation between both values, which are negatively related (Steiner et al., 2009). By contrast, ECEC is positively associated with BS, given that ECEC is calculated as the sum of soil and aluminum bases (Teixeira et al., 2017). Furthermore, the low Al content of the study soils might have potentiated this effect, as argued by Motta and Pauletti (2017). TCEC correlates with OC because organic matter promotes an increase in the soil colloidal system, consequently increasing TCEC (Malavolta, 2006; García et al., 2018).

In sandy soils, there was a negative correlation between *Pratylenchus* and sand content (Figure 3a), and, in clay soils, the nematode was negatively associated with clay content (Figure 3b). Previous research reported a positive relationship between *Pratylenchus* and sandy soils (Leiva et al., 2020; Dias-Arieira et al., 2021) and clay sandy soils (Gallardo et al., 2015). In fact, studies have shown that sandy soils favor *Pratylenchus* populations because of the presence of macropores, which improve oxygenation and reduce waterlogging (Leiva et al., 2020). However, this relationship goes beyond soil physical characteristics, as sandy soils generally have limitations regarding organic matter accumulation, porosity, and water retention, factors that may influence nematode populations (Galbieri et al., 2016). The contrasting results indicate that sand content is not necessarily the determining factor for nematode prevalence and that adequate soil management may help maintain nematode population levels below the threshold of economic damage.

Different from our findings, the literature has numerous reports of positive correlations between root-knot nematodes and sandy soils (Guzmán et al., 2008; Galbieri et al., 2016; Noronha et al., 2020). However, as previously mentioned, other factors might have exerted a greater effect on nematode population, mitigating the influence of soil texture. Thus, texture was considered an imperfect quantitative indicator of nematode populations, given that soils of the same texture can vary in structure, porosity, organic matter content, and water retention capacity, influencing nematode movement and development as well as soil microbial populations (Galbieri et al., 2016).

Regarding soil macronutrients, *Pratylenchus* had a weak positive correlation with Mg^{2+} and a weak negative correlation with PO_4^{3-} in sandy soils (Figure 4a). These results disagree with a study demonstrating a strong negative relationship between the nematode and Mg^{2+} in sandy soils (Dias-Arieira et al., 2021). It is known that liming (addition of Ca^{2+} and Mg^{2+}) promotes a linear decrease in nematode populations; that is, high lime rates contribute to reducing *Pratylenchus* populations (Debiasi et al., 2018). This result further supports that various factors associated with the crop system may influence nematode populations, not depending exclusively on the content of a particular nutrient.

A negative correlation between P and nematode population was previously reported (Noronha et al., 2020). Such a relationship can be attributed to the benefits of P to the nutritional balance of soybean, contributing to disease resistance, increasing vigor and the speed of tissue maturation, and shortening the host susceptibility period (Bedendo et al., 2018). In clay soils, a strong negative correlation with K was observed (Figure 4b), as previously reported by Leiva et al. (2020). It is known that K^+ may hinder the establishment of pathogens in host roots, promoting wound healing in plants and decreasing fungi and bacteria penetration (Bedendo et al., 2018). The results of this study indicate a possible suppressive effect of the nutrient on lesion nematodes, added to the effect of K on soybean growth, development, and resistance to abiotic and biotic stresses (Hansel et al., 2021).

In sandy and clay soils, the correlations of *Meloidogyne* with Ca^{2+} (Figure 6c) and with S (Figure 6d) were in accordance with the results of Dias-Arieira et al. (2021), who described a weak positive correlation with Ca^{2+} and a weak negative correlation with S. There is evidence that S deposition may alter the composition of nematode communities (Zhang et al., 2021), explaining the observed negative correlations.

Pratylenchus had a negative correlation with the micronutrient BO_3^{3-} in sandy soils and a positive correlation with Fe^{2+} in clay soils (Figures 7a and 7b). In sandy soils, B levels were medium to very high, indicating a negative effect of the nutrient on *Pratylenchus*, as observed in previous studies on other genera of plant-parasitic nematodes (Couto et al., 2016; El-Batal et al., 2019). B is associated with the synthesis of lignin, a molecule that increases the rigidity of plant cell walls, especially in adventitious roots (Malavolta, 2006). As a result, nematode penetration, movement, and reproduction are negatively affected.

The negative correlation of *Pratylenchus* with micronutrients in clay soils (Figures 7c and 7d) differs from literature reports (Dias-Arieira et al., 2021). High Fe^{2+} levels were shown to increase the severity of soil pathogens, including *Fusarium* and *Verticillium* (Zambolim et al., 2005). It is possible that pathogens had a high use of Fe^{2+}, reducing the availability of the nutrient to plants, thereby negatively affecting phenol and lignin synthesis (Malavolta, 2006).

For *Meloidogyne*, there was a positive correlation with BO_3^{3-} and Cu^{2+} in sandy soils (Figure 5c) and a negative relationship with Mn^{2+} in clay soils (Figure 5d). Because of the complexity of soil activities, it is difficult to establish the exact role of these elements in plant-nutrient-nematode relationships. Thus, studies under controlled conditions should be conducted to elucidate such correlations.

The results of PCA for *Pratylenchus*, *Meloidogyne*, and foliar macronutrients agree with reports showing that plants parasitized by nematodes have reduced nutrient absorption and accumulation (Melakeberhan et al., 1988; Jones et al., 2013; Ferraz & Brown, 2016). Such an effect is potentiated by the negative correlations between nematodes and P (sandy soils), N, K, and S (clay soils) (Figures 6a and 6b).

Of note, there was a weak positive correlation between nematodes and leaf Ca content. It is hypothesized that this was a response of plants to oxidative stress generated by nematode parasitism. Ca is related to the protein calmodulin, which, under abiotic water stress (Hansel et al., 2021) and disease-related biotic stress (Bedendo et al., 2018), acts by stimulating root growth. Thus, calmodulin synthesis might have been a defense mechanism in response to nematode infection. Furthermore, an increase in Ca in soybean shoots was previously reported in plants infected with *Meloidogyne* (Carneiro et al., 2002).

Few studies have investigated correlations between nematodes and micronutrient absorption and accumulation. The results of PCA for *Pratylenchus* and foliar micronutrients confirm that the nematode can compromise micronutrient absorption by plants, possibly affecting several physiological processes. Cu, Mn, and Fe, some of the most affected micronutrients, are essential for numerous physiological processes, including electron transport, protein and carbohydrate metabolism, nitrogen fixation, and oxidation-reduction reactions (Furlani, 2004; Benton, 2012).

5. Conclusions

In clay soils, Al levels favored *Pratylenchus*, whereas OC levels negatively affected *Meloidogyne*. K negatively affected *Pratylenchus*, and Mg negatively affected *Meloidogyne*. High levels of soil Mn^{2+} adversely affected *Meloidogyne*.

Pratylenchus positively influenced foliar Ca in both types of soils, and *Meloidogyne* had the same effect in sandy soils. Similarly, *Pratylenchus* increased Fe absorption in clay soils and *Meloidogyne* increased that of B in sandy soils.

It is worth mentioning that, in field studies, the complexity of biotic and abiotic factors in the crop system may contribute to diverging results, making it difficult to establish a single response pattern, especially when some factors affect others. In this research, we chose to group the data according to soil type (sandy and clay); however, other intrinsic characteristics of the study sites might have directly affected the results.

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