

Soil abiotic factors associated with *Meloidogyne* spp. and *Pratylenchus* spp. populations in sugarcane

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Summary – *Meloidogyne* spp. and *Pratylenchus* spp. are the most damaging plant-parasitic nematodes to sugarcane and the knowledge of soil characteristics that influence the occurrence of these pathogens can be useful in their management. With the objective to investigate the relationships between soil variables and populations of *Meloidogyne* spp. and *Pratylenchus* spp. in sugarcane fields, root-zone soil and root samples were collected from 20 farms located in 16 municipalities in Alagoas state, Brazil. The multivariate regression tree technique was used to model the population density's response variables for *Meloidogyne* spp. and *Pratylenchus* spp. in the root-zone soil and the roots according to sugarcane cultivars, soil organic matter, and soil chemical and physical variables. The results showed the existence of associations between soil factors, sugarcane cultivars and populations of nematodes. Root samples from soils with $K > 37.79 \text{ mmol}_c \text{ dm}^{-3}$, $Al < 5.93 \text{ mmol}_c \text{ dm}^{-3}$ and sugarcane 'RB92579', 'SP753046', 'SP813250' and 'SP921631' showed the lowest *Pratylenchus* spp. population densities. However, the lowest densities in the root-zone were found in soils with sum of bases $> 1.91 \text{ mmol}_c \text{ dm}^{-3}$, Ca:Mg ratio $< 1:2$ and soil organic matter $< 10.7 \text{ g dm}^{-3}$. The lowest population densities of *Meloidogyne* spp. in roots were associated with sugarcane 'RB92579', 'RB93509', 'RB98710', 'SP791011' and 'SP921631' and soil aggregate mean diam. $> 0.48 \text{ mm}$, while root-zone densities were minimum in soils with $P > 28.59 \text{ mg dm}^{-3}$. This information should support further studies to investigate the effect of each variable on populations of *Pratylenchus* and *Meloidogyne*.

Keywords – Brazil, edaphic factors, nematode-soil relationships, root-knot nematodes, root-lesion nematodes, *Saccharum* spp.

Sugarcane (*Saccharum* spp.) is a strategic crop in the economy of Brazil, which is the world's largest sugarcane producer, with 616 million tons expected for the harvest period of 2018/19 (CONAB, 2018). The Brazilian northeastern region has been cultivated with sugarcane for several decades in coastal table, hillside, flatland and floodplain areas. These environments have modified the ecosystem and increased the number and ratio of plant-parasitic nematodes, especially the endoparasitic *Meloidogyne* and *Pratylenchus* (Maranhão *et al.*, 2018).

Under conditions of highly susceptible cultivars and high nematode population densities of *M. javanica*, *M. incognita* or *P. zaei*, yield losses can reach up to 50%, considering only plant cane, *i.e.*, in the first crop cycle (Dinardo-Miranda, 2005). However, damage occurring to the development of subsequent crops must also be con-

sidered. According to Bond *et al.* (2000), comparisons of plant cane and ratoon sugarcane crops showed that nematode community levels increase significantly in successive ratoon crops.

The life cycle of plant-parasitic nematodes takes place partly in the rhizosphere; therefore, their reproduction, parasitism and mobility dynamics are inevitably influenced by the soil-root interaction (Fajardo *et al.*, 2011). The host plant plays a prime role in the structuring of the nematode communities, and this can be a direct role (quantity and quality of the food resource) or an indirect role (changes in soil properties) (Kandji *et al.*, 2001). Although Bond *et al.* (2000) and Blair (2005) reported an association between soil type and prevalence of *Meloidogyne* spp. and *Pratylenchus* spp., Cadet *et al.* (2004) demonstrated the existence of spatial variability of plant-

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parasitic nematode distribution on a field scale within the same soil type and the same plant, and showed that contents of certain physical and chemical soil factors varied in the topsoil in parallel with the abundance or the relative proportions of certain nematode species.

In studies performed in sugarcane fields from the Brazilian northeastern region various aspects have been evaluated, including the relationship between soil attributes (bulk density, total porosity and soil respiration) and nematode assemblages (Cardoso *et al.*, 2015), effects of soil physical properties, such as soil mechanical resistance, water content and texture, on nematode assemblage (Cardoso *et al.*, 2016), and spatiotemporal changes in nematode abundance and diversity under different soil-climatic conditions (Maranhão *et al.*, 2018).

Considering that species of *Meloidogyne* and *Pratylenchus* are widespread in sugarcane fields and generally constitute the most damaging plant-parasitic nematodes (Ramouthar & Bhuiyan, 2018), the identification of soil properties associated with the population dynamics of these nematodes will contribute to the selection of agricultural practices that are candidates as components of an integrated management programme to control the damage caused by these pathogens on sugarcane. Thus, this study aimed to identify chemical and physical soil properties

associated with the population densities of *Meloidogyne* spp. and *Pratylenchus* spp. from the analyses of root-zone soil and the roots of sugarcane.

Materials and methods

SURVEY AREAS AND SAMPLING

During 2012, soil and root samples from sugarcane cultivars 'RB92579', 'SP813250', 'SP921631', 'RB93509', 'RB98710', 'SP791011' and 'SP753046' were collected from 20 sugarcane farm fields with records of low crop productivity and in stages 1-10 ratoon-cane cropping. These areas were located in 16 municipalities (Table 1), which represent the major sugarcane-growing areas in the Alagoas state, Brazil. The climate of these areas is considered tropical with region type classification 'Am' and 'As', characterised by rainy winters and dry summers, with an altitude of 100-200 m a.s.l. and an average annual rainfall of between 1300 and 1600 mm (Alvares *et al.*, 2013). Four samples were collected randomly from each field with an approximate distance of 20 m from each other. To collect samples, trenches were made around each clump in order to remove them as intact as possible (Fig. 1), and approximately 1 kg of soil and 100 g of roots

Table 1. Location of 20 sugarcane fields in the state of Alagoas, Brazil.

Area	Municipality	Geographic coordinates		Cultivar
		S	W	
01	Rio Largo	09°25'71"	35°48'78"	'RB92579'
02	São Miguel dos Campos	09°46'38"	36°05'10"	'SP813250'
03	Teotônio Vilela	10°00'09"	36°22'47"	'SP753046'
04	Paripueira	09°26'48"	35°35'08"	'SP921631'
05	Campo Alegre	09°48'51"	36°13'02"	'RB92579'
06	Marechal Deodoro	09°45'03"	35°57'35"	'SP813250'
07	Teotônio Vilela	09°47'35"	36°02'59"	'SP921631'
08	Penedo	10°17'38"	36°27'55"	'RB93509'
09	Anadia	09°42'34"	36°19'50"	'SP791011'
10	Novo Lino	08°56'14"	35°37'58"	'RB92579'
11	Campo Alegre	09°53'04"	36°09'27"	'RB92579'
12	Atalaia	09°29'25"	36°05'11"	'RB92579'
13	São José da Laje	08°55'36"	36°01'00"	'SP791011'
14	Teotônio Vilela	09°57'54"	36°22'48"	'RB92579'
15	Pilar	09°36'56"	35°53'22"	'RB92579'
16	Igreja Nova	10°12'41"	36°28'13"	'RB92579'
17	Maceió	09°27'07"	35°38'32"	'RB92579'
18	Matriz de Camaragibe	09°08'40"	35°30'55"	'SP813250'
19	Penedo	10°08'05"	36°26'18"	'RB98710'
20	Porto Calvo	09°00'28"	35°24'53"	'RB92579'



Fig. 1. View of the trench made for collection of soil and root samples in a sugarcane mat.

from each sample were placed in plastic bags, labelled and transported to the laboratory.

NEMATODE EXTRACTION AND IDENTIFICATION

To quantify nematode populations, soil samples were thoroughly mixed and 100 cm³ of each sample was processed by means of the centrifugal-flotation technique for 4 min at about 400 g, using 60 and 400 mesh sieves as described by Jenkins (1964). Roots were washed, surface-dried using paper tissue, cut into 2 cm pieces and thoroughly mixed. A 50 g sub-sample from each sample was macerated in water with a domestic blender at the lowest speed for 30 s. The suspension was sieved and centrifuged with kaolin. The pellet was resuspended in sucrose solution and centrifuged and the nematodes in the supernatant were collected on sieves and washed (Coolen & D'Herde, 1972). After extraction, the nematodes were killed and fixed in hot 4% formalin, and identified and counted from triplicate 1 ml aliquots with the aid of Peters counting slides under a light microscope. Root and soil

second-stage juveniles (J2) of *Meloidogyne* spp. as well as juveniles and adults of *Pratylenchus* spp. were identified to the level of genera according to the taxonomic key of Mai & Mullin (1996), and the data counted. A report from this study on the identification of nematode species has been published previously, showing a prevalence of *M. incognita* and *P. zeae* (Noronha *et al.*, 2017).

PHYSICAL AND CHEMICAL SOIL ATTRIBUTES

In order to determine the soil physical attributes, the samples were processed for analysis of the following characteristics: aggregate mean diam. (AMD), percentage of water-stable aggregates (WSA) (Arshad *et al.*, 1997), soil and particles density, micro-, macro- and total porosity, and soil texture, according to Silva (2009), as well as hydraulic conductivity in saturated soil using a Guelph permeameter (Vieira, 1998).

The soil chemical attributes assessed were: pH in water (1:2.5) by potentiometer; exchangeable aluminum (Al³⁺) extracted with 1 mol l⁻¹ KCl and quantified by titration with 0.025 mol l⁻¹ NaOH; phosphorus and potassium, extracted with Mehlich-1 and determined by the colorimetric method and flame photometry, respectively; Ca and Mg extracted with 1 mol l⁻¹ KCl and determined by atomic absorption spectrophotometry (Silva, 2009); total N was quantified in soil samples by H₂SO₄ digestion and distillation in a Kjeldahl unit (Bremner, 1996). The soil organic matter (SOM) was obtained according to Raij *et al.* (1987) and the total organic carbon was quantified by wet oxidation of organic matter, using potassium dichromate (K₂Cr₂O₇) solution in acid medium, with external heat source (Yeomans & Bremner, 1988).

STATISTICAL ANALYSES

Meloidogyne spp. and *Pratylenchus* spp. population densities, either in root-zone soil or roots, were modelled according to soil physical and chemical variables by the sum of squares univariate regression tree (SS-URT) models. This analysis described which combination of soil variables and their respective levels were associated with changes in the response variables, as well as the relative importance of each soil variable on these changes. This statistical procedure was chosen because it can deal with nonlinear relationships and high-order interactions; at the same time it is simple to understand and provides easily interpretable results. A very detailed description of SS-URT can be found in De'ath & Fabricius (2000). Briefly, the output of SS-URT are diagrammatic trees

that explain the variation of a single response variable (nematode population density in roots or soil, in our case) by repeatedly splitting the data into more homogeneous groups, using combinations of explanatory variables (soil physical and chemical variables, in our case). The tree is constructed by repeatedly splitting the response variable data, according to a simple rule based on explanatory variables. At each split, the data are partitioned into two mutually exclusive groups, each of which is as homogeneous as possible. The splitting procedure is then applied to each newly formed group separately. The objective is to partition the response into homogeneous groups, but also to keep the tree reasonably small. The size of a tree equals the number of final groups (terminal nodes). At each round of splitting, all the explanatory variables included in the analysis are tested for their relative contribution to explain data variability remaining within each data group (intermediate nodes). When a numeric explanatory variable is selected, a value of this variable is indicated at the split in the tree, which represents the value above and below which the separation of samples into two newly formed groups explains most of the variability in the response variable. From all possible splits of all the explanatory variables, the one that maximises the homogeneity of the two resulting groups is chosen. Splitting is continued until an overlarge tree is grown, which is then pruned back to the desired size.

In our study we have performed a series of 20 ten-fold cross-validations to choose the model tree size with a minimum error rate (De'ath & Fabricius, 2000), and the criterion for creation of new nodes was set at ten. A library of sum of squares univariate regression tree routines (T. Therneau, data unpubl.) was used in S-Plus 2000 (Insightful) for the SS-URT analysis. SS-URT has been successfully used in other studies to model changes in soil microbial variables to vegetation types (Mendes *et al.*, 2012) and post-wildfire vegetation response as a function of environmental conditions and pre-fire restoration treatments (Romo León *et al.*, 2012).

Results

The sugarcane cultivars, SOM and some soil chemical and physical variables such as pH, Al^{3+} , N, P, K, Mg and Ca:Mg ratios, AMD (mm) and WSA (%) were associated with *Meloidogyne* spp. and *Pratylenchus* spp. densities in the root-zone and root.

A tree with six terminal nodes originated from the combination of K, Al, Mg contents, pH and the sugarcane cul-

tivars described 60% (error: 0.40) of the total data variability among the samples, concerning *Pratylenchus* spp. population densities in sugarcane roots (Fig. 2). According to this model, K was the most important element explaining 30% of the variability observed with this nematode population in sugarcane roots. Root samples collected in soils with $\text{K} > 37.79 \text{ mmol}_c \text{ dm}^{-3}$ ($n = 62$) had smaller nematode populations (mean = 367 indiv. $(50 \text{ g root})^{-1}$) than soils with lower K contents (955 indiv. $(50 \text{ g root})^{-1}$; $n = 16$). In samples from the group with $\text{K} > 37.79 \text{ mmol}_c \text{ dm}^{-3}$, Al was further associated with *Pratylenchus* spp. populations, as samples of this group with $\text{Al} > 5.93 \text{ mmol}_c \text{ dm}^{-3}$ ($n = 14$) had higher populations (633 indiv. $(50 \text{ g root})^{-1}$) than in the group with lower Al values (289 indiv. $(50 \text{ g root})^{-1}$). In this last group, cultivars were further associated with changes in population averages, with 'RB92579', 'SP753046', 'SP813250' and 'SP92163' showing a mean of 237 indiv. $(50 \text{ g root})^{-1}$ ($n = 41$) and 'RB98710' and 'SP791011' with a mean of 594 indiv. $(50 \text{ g root})^{-1}$ ($n = 7$).

Population densities of *Pratylenchus* spp. in sugarcane roots in samples with $\text{K} < 37.79 \text{ mmol}_c \text{ dm}^{-3}$, also varied in accordance to soil pH. Samples with $\text{pH} > 5.46$ had higher *Pratylenchus* spp. populations (mean of 1420 indiv. $(50 \text{ g root})^{-1}$; $n = 5$) than those with $\text{pH} < 5.46$ (745 indiv. $(50 \text{ g root})^{-1}$, $n = 11$). The populations in this last group were also associated with Mg levels; when Mg was higher than $7.1 \text{ mmol}_c \text{ dm}^{-3}$ the population average was smaller (415 indiv. $(50 \text{ g root})^{-1}$; $n = 5$) than in samples with $\text{Mg} < 7.1 \text{ mmol}_c \text{ dm}^{-3}$ (1020 indiv. $(50 \text{ g root})^{-1}$; $n = 6$) (Fig. 2). The contents of K, Al, Mg in the soil and the pH and sugarcane cultivar, accounted for 30, 8, 7, 10 and 5%, respectively, of the data variability of *Pratylenchus* spp. population densities in sugarcane roots, these values being proportional to the fraction of the total variance.

A regression tree model with five terminal nodes, resulting from the combinations between soil factors of sum of bases (SB), Ca:Mg ratio, SOM and sugarcane cultivars, explained 68% (error: 0.32) of the total data variability of *Pratylenchus* spp. population densities in root-zone soil within the evaluated samples (Fig. 3). The five terminal nodes obtained in soil samples and their respective population means in the rhizospheric soil were: i) $\text{SB} > 1.91 \text{ mmol}_c \text{ dm}^{-3}$ (41 indiv. $(100 \text{ cm}^3 \text{ soil})^{-1}$; $n = 49$); ii) $\text{SB} < 1.91 \text{ mmol}_c \text{ dm}^{-3}$ combined with $\text{Ca:Mg ratio} < 1.2$ (47 indiv. $(100 \text{ cm}^3 \text{ soil})^{-1}$; $n = 17$); iii) $\text{SB} < 1.91 \text{ mmol}_c \text{ dm}^{-3}$ combined with $\text{Ca:Mg ratio} > 1.2$ and $\text{SOM} < 10.7 \text{ g dm}^{-3}$ (54 indiv. $(100 \text{ cm}^3 \text{ soil})^{-1}$;

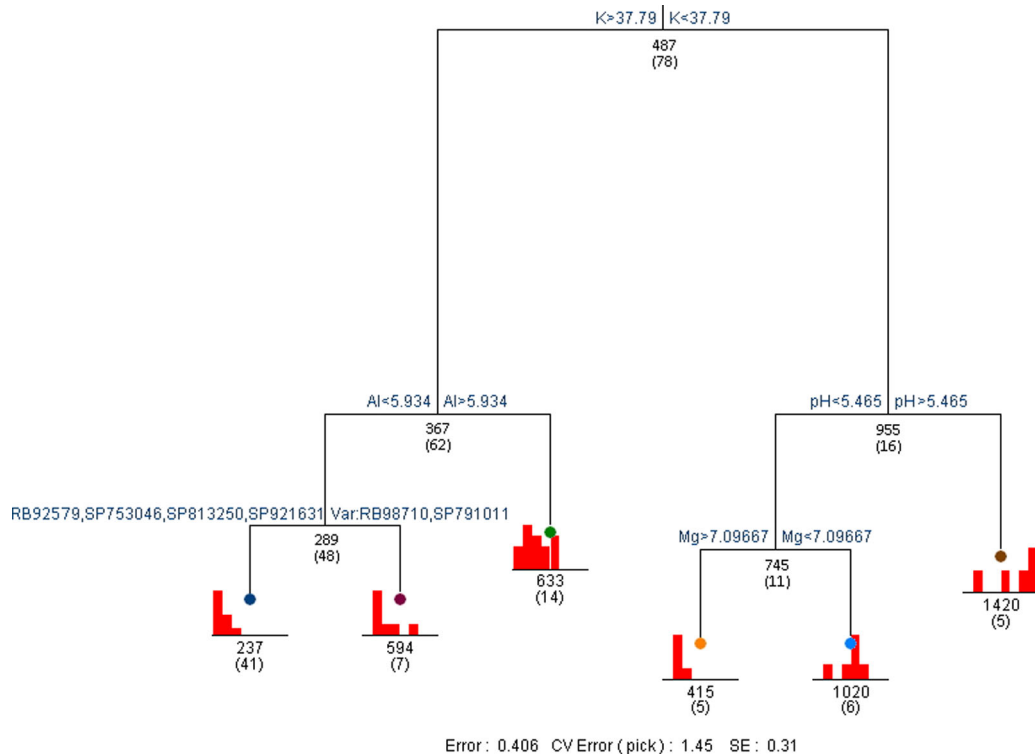


Fig. 2. Relationship between *Pratylenchus* spp. population densities in sugarcane roots and the soil factors K, Al, pH (in water), sugarcane cultivars and Mg ($\text{mmol}_c \text{dm}^{-3}$ soil), according to regression tree analysis with six terminal nodes. The lengths of the vertical tree branches are proportional to the variability explained by the explanatory variables used in each partition. Bars at the terminal nodes indicate the frequency of samples distribution in classes of increasing values of the response variable from the left to the right side of the horizontal axis. CV Error (pick) is the cross-validation error for the tree size (number of terminal nodes) selected to represent data variation of the response variables.

$n = 4$); *iv*) $\text{SB} < 1.91 \text{ mmol}_c \text{dm}^{-3}$ combined with Ca:Mg ratio > 1.2 and $\text{SOM} > 10.7 \text{ g dm}^{-3}$ and ‘SP791011’ and ‘SP921631’ ($119 \text{ indiv. (100 cm}^3 \text{ soil)}^{-1}$; $n = 4$); *v*) the same chemical conditions as in (*iv*) with ‘RB92579’ ($371 \text{ indiv. (100 cm}^3 \text{ soil)}^{-1}$; $n = 4$).

Considering the total variance of 68% explained by the explanatory variables, the contributions of soil and cultivar factors to explain the variability of *Pratylenchus* spp. population densities in the root-zone soil decreased according to the order: Ca:Mg ratio (20%) = cultivars (20%) > SOM (16%) > SB (12%).

Population densities of *Meloidogyne* spp. in sugarcane roots were associated with cultivars, AMD, WSA and content of Mg, according to the regression analysis on a tree with five terminal nodes, which explained 68% (error: 0.32) of the total data variability (Fig. 4). ‘RB92579’, ‘RB93509’, ‘RB98710’, ‘SP791011’ and ‘SP921631’ ($n = 62$) were associated with a smaller population aver-

age ($96.6 \text{ indiv. (50 g root)}^{-1}$; $n = 62$) than ‘SP753046’ and ‘SP813250’, which had a mean of $363 \text{ indiv. (50 g root)}^{-1}$ ($n = 16$). For the first group of cultivars, changes in *Meloidogyne* spp. populations in roots were associated with AMD, with lower populations being observed in samples with $\text{AMD} > 0.48 \text{ mm}$ ($89.1 \text{ indiv. (50 g root)}^{-1}$; $n = 59$) than in those with $\text{AMD} < 0.48 \text{ mm}$ ($245 \text{ indiv. (50 g root)}^{-1}$; $n = 3$).

For the second group of cultivars, another physical variable, WSA, was further associated with the populations of *Meloidogyne* spp. in roots. In this case, highest populations were found in samples with $\text{WSA} > 39.61\%$ ($596 \text{ indiv. (50 g root)}^{-1}$; $n = 5$), compared with samples with $\text{WSA} < 39.61\%$ ($256 \text{ indiv. (50 g root)}^{-1}$; $n = 11$). In this last, samples with $\text{Mg} < 10.6 \text{ mmol}_c \text{dm}^{-3}$ had a mean of $153 \text{ indiv. (50 g root)}^{-1}$; ($n = 7$), whereas the corresponding value for samples with $\text{Mg} > 10.6 \text{ mmol}_c \text{dm}^{-3}$ was $438 \text{ indiv. (50 g root)}^{-1}$; ($n = 4$) (Fig. 4). The order of

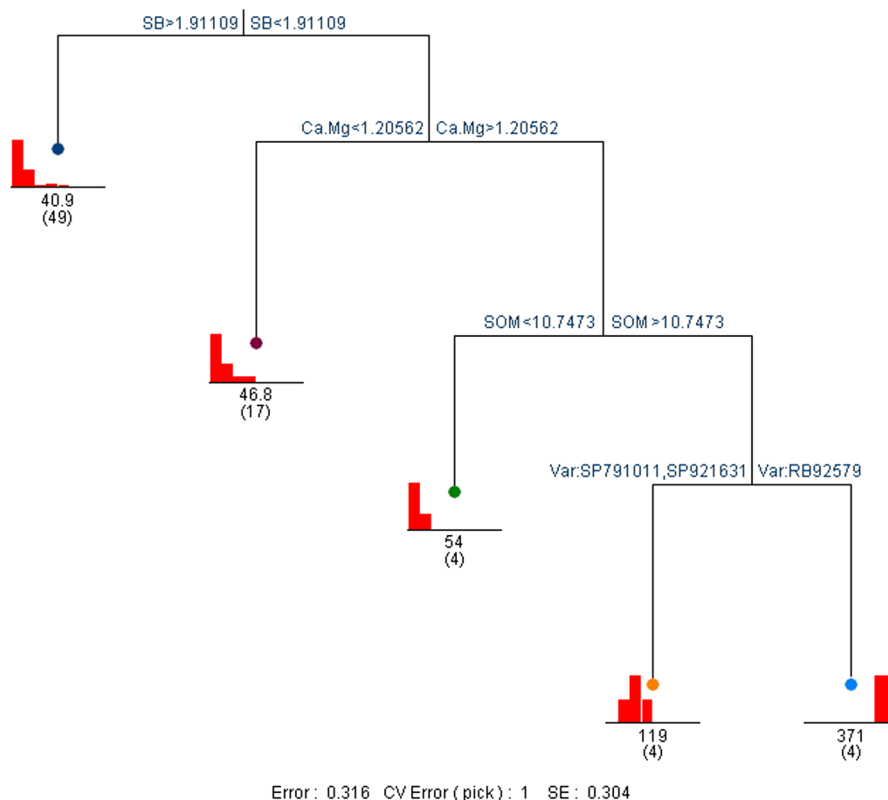


Fig. 3. Relationship between *Pratylenchus* spp. population densities in sugarcane root-zone soil and the soil factors sum of bases (SB, $\text{mmol}_c \text{dm}^{-3}$ soil), Ca:Mg ratio (mg dm^{-3} soil), SOM (g dm^{-3}) and sugarcane cultivars according to regression tree analysis with five terminal nodes. The lengths of the vertical tree branches are proportional to the variability explained by the explanatory variables used in each partition. Bars at the terminal nodes indicate the frequency of samples distribution in classes of increasing values of the response variable from the left to the right side of the horizontal axis. CV Error (pick) is the cross-validation error for the tree size (number of terminal nodes) selected to represent data variation of the response variables.

importance of the soil chemical variables and cultivars to explain the model, considering the total variance (68%), decreased according to the sequence: sugarcane cultivars (38%) > WSA (16%) > Mg (10%) > AMD (4%).

A regression tree with five terminal nodes, resulting from the combination of the factors P content, soil pH, N and Ca:Mg ratio, explained 59% (error: 0.41) of the total data variability of *Meloidogyne* spp. population in sugarcane root-zone soil (Fig. 5). Soils from sugarcane crops with P content > 28.59 mg dm^{-3} (n = 52) showed a smaller mean number of nematodes (8.15 indiv. $(100 \text{ cm}^3 \text{ soil})^{-1}$) than samples with a lower P content (23.0 indiv. $(100 \text{ cm}^3 \text{ soil})^{-1}$, n = 25). Samples with P < 28.59 mg dm^{-3} (n = 23), associated with pH < 5.0 (n = 15), had a mean population of 11.7 indiv. $(100 \text{ cm}^3 \text{ soil})^{-1}$ (n = 15), whereas the corresponding value for those

with pH > 5.0 was 40 indiv. $(100 \text{ cm}^3 \text{ soil})^{-1}$ (n = 10). The group of samples combining P < 28.59 mg dm^{-3} and pH < 5.0, soil N content < 0.91 g dm^{-3} were associated with lower populations (6.1 indiv. $(100 \text{ cm}^3 \text{ soil})^{-1}$; n = 12) than samples with higher N content (34 indiv. $(100 \text{ cm}^3 \text{ soil})^{-1}$; n = 3). In the group of samples with P < 28.59 mg dm^{-3} and pH > 5.0, Ca:Mg ratio was associated with changes in nematode populations, as samples with values > 1.51 for this ratio had mean populations of 19.4 indiv. $(100 \text{ cm}^3 \text{ soil})^{-1}$ (n = 5), whereas the corresponding value for samples with ratio < 1.51 was 60 indiv. $(100 \text{ cm}^3 \text{ soil})^{-1}$ (n = 5). Contribution of soil variables to explain the total variability (59%) of populations of *Meloidogyne* spp. in sugarcane root-zone soil decreased as follows: pH (18%) > Ca:Mg ratio (17%) > P (15%) > N (8%).

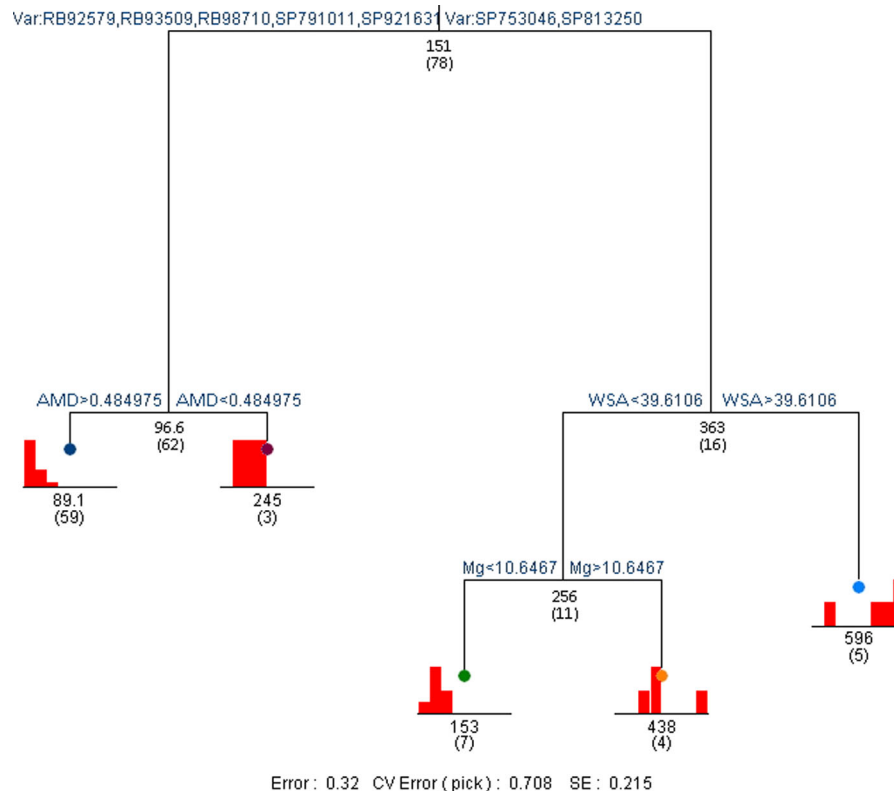


Fig. 4. Relationship between *Meloidogyne* spp. population densities in sugarcane roots and cultivars, soil factors, AMD (mm), WSA (%) and contents of Mg ($\text{mmol}_c \text{dm}^{-3}$ soil), according to regression tree analysis with five terminal nodes. The lengths of the vertical tree branches are proportional to the variability explained by the explanatory variables used in each partition. Bars at the terminal nodes indicate the frequency of samples distribution in classes of increasing values of the response variable from the left to the right side of the horizontal axis. CV Error (pick) is the cross-validation error for the tree size (number of terminal nodes) selected to represent data variation of the response variables.

Discussion

This study verified associations between *Meloidogyne* and *Pratylenchus* population densities and some abiotic soil factors in sugarcane fields. The implemented model showed that the influence of each soil variable on nematode population densities was associated with the content of each element, as well as the sugarcane cultivar. The selected statistical models showed that nematode population densities were associated with a combination of variables related to soil fertility, soil physical structure and/or sugarcane cultivar. Although no direct inference can be drawn whether changes in nematode densities are due to these soil and cultivar variables, the selected variables are potential candidates to be modified by soil and crop management as part of integrated strategies to control nematodes in sugarcane.

In relation to K (content > $37.79 \text{ mmol}_c \text{dm}^{-3}$) and *Pratylenchus* spp. in sugarcane roots, a lower nematode population was observed; data are in line with information from Delaville *et al.* (1996) and Cadet *et al.* (2002), who observed a negative relationship with soil K content and *P. zeae* populations on this crop.

Potassium is the most important nutrient in sugarcane development, acting as an enzyme activator in the plant metabolism, such as in photosynthesis, protein synthesis and translocation of sucrose from leaves to the stalk storage tissues (Medina *et al.*, 2013). Low K levels in soil contribute to reduce the longevity of sugarcane fields (Schultz *et al.*, 2010). In addition to the effects on crop yield, it is possible that K fulfils another role that may be associated with the management of *Pratylenchus* spp. in sugarcane. This assumption has been observed in studies that demonstrated the activation of various

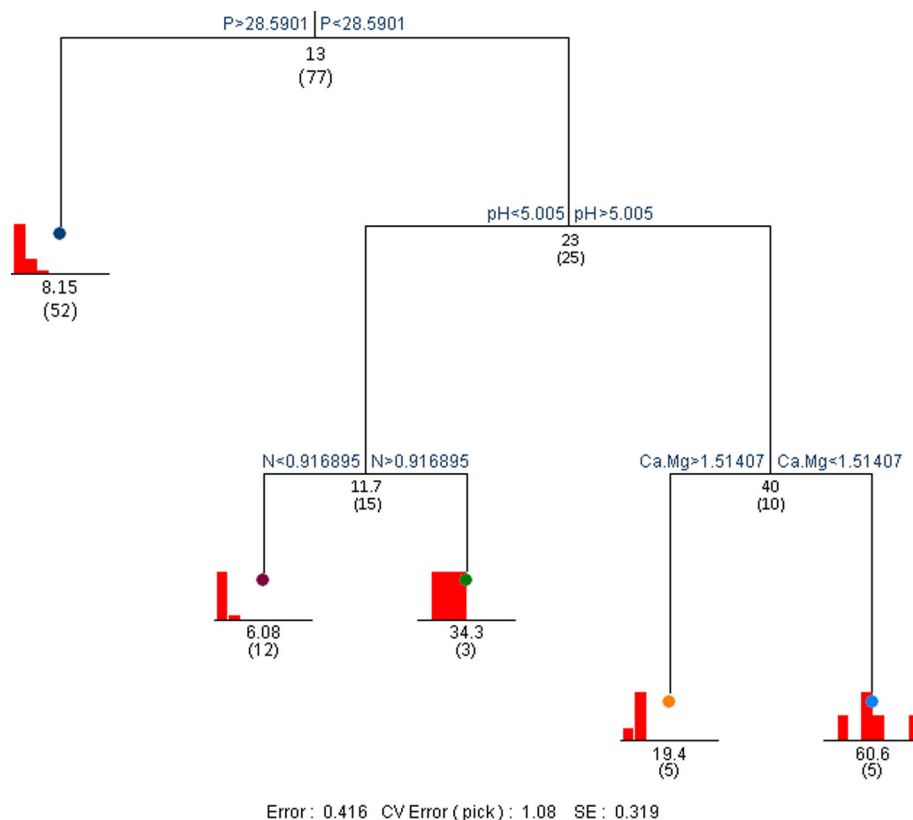


Fig. 5. Relationship between *Meloidogyne* spp. in sugarcane root-zone soil and the soil factors P content (mg dm^{-3} soil), pH (in water), N (g dm^{-3}) and Ca:Mg ratio (mg dm^{-3} soil), according to regression tree analysis with five terminal nodes. The lengths of the vertical tree branches are proportional to the variability explained by the explanatory variables used in each partition. Bars at the terminal nodes indicate the frequency of samples distribution in classes of increasing values of the response variable from the left to the right side of the horizontal axis. CV Error (pick) is the cross-validation error for the tree size (number of terminal nodes) selected to represent data variation of the response variables.

enzymes with K application to improve resistance against plant-parasitic nematodes such as *Heterodera glycines* (Gao *et al.*, 2018) and *M. incognita* (Zhao *et al.*, 2016). Additional possible mechanisms of the action of K relate to stabilising cell structure, thickening cell wall and preventing the expansion of intracellular space (Li *et al.*, 2010). The imbalance of this nutrient can affect the secondary metabolism of the crop, influencing the nematode population.

An association between the increase of both SOM and the population densities of *Pratylenchus* spp. was observed in the present study. A similar result was also observed by Mutala'liah *et al.* (2017), who noted a positive correlation between organic matter and population abundance of *Pratylenchus* sp. On the other hand, Rimé *et al.* (2003) recorded a decrease in *P. zaeae* populations

in sugarcane with an increase of SOM. Studies reporting the increase of *Pratylenchus* spp. population densities with the increase of SOM attributed these responses to the increased fecundity of nematodes feeding on nutrient-enriched roots, increased root growth providing more feeding sites and even suppression of natural biological control agents (Forge *et al.*, 2005; Villenave *et al.*, 2010) and to the better environmental conditions for nematode survival and reproduction, due the increase in water retention, modulation of soil temperature and better plant development (Franchini *et al.*, 2018). Thus, it is possible that some of these mechanisms lead to an increase of *Pratylenchus* population densities in the present study.

The sugarcane cultivars were associated with high or low nematode population densities. However, it is not possible to make statements in relation to resistance or

susceptibility of these genotypes to *Pratylenchus* spp. and *Meloidogyne* spp., because 'RB92579' was grouped with the cultivars with lower *Meloidogyne* spp. population densities. However, this cultivar is considered by some authors (Silva *et al.*, 2012, 2016) to be susceptible to *M. incognita* and *M. javanica*. On the other hand, 'SP791011', which was included among the cultivars with lower *Pratylenchus* spp. population densities in roots and root-zone soil, showed a reproduction factor greater than 1.1 according to Barros *et al.* (2005), thus being classed as susceptible.

Regarding the soil physical variables, AMD less than 0.48 mm diam. and the percentage of WSA greater than 39.61 were associated with an increase in the population of *Meloidogyne* spp. This diameter corresponds to a sandy soil (0.2-2.0 mm), whilst WSA lower than 50% is related to the formation of macro-aggregates; both variables are related to macro-porosity, which is characterised by increased soil aeration and water infiltration, but to a lower water retention (Salton *et al.*, 2008; Kabir *et al.*, 2017). Thus, considering that AMD < 0.48 mm and percentage of WSA > 39.61 reduce the nematode population, it is probable that a more structured soil with higher clay content favours *Meloidogyne* spp.

Fajardo *et al.* (2011) showed that populations of *Meloidogyne* spp. were inversely related to the sand content and positively related to a more structured soil, suggesting that these results may be related to the loamy texture soils that showed a higher total porosity, with predominance of storage pores, indicating higher water retention available for roots and the creation of water transport-films that allow nematode movement through the soil. According to Otobe *et al.* (2004) the ability of *Meloidogyne* J2 to migrate in soil depends on the pore distribution. These data indicate that soil physical properties should be important for mobility of *Meloidogyne* spp., and thus to infection efficiency.

Phosphorus (value higher than 28.59 mg dm⁻³) was the element that most influenced *Meloidogyne* spp. populations in root-zone soil since it explained 59% of total data variability, according to the model. This element is essential for cell division and enhances photosynthetic activity. It also regulates synthesis of sugar and storage. It helps in root development, which leads to greater absorption of nutrients and results in higher number of tillers and millable canes, thereby resulting in a higher sugarcane yield (Devi *et al.*, 2012). The biochemical changes resulting from using P, such as the increase in plant oils, phenolics, peroxidases and ammonia, are not favourable to plant-

parasitic nematodes, reducing the fecundity of the nematodes (Zambolim & Ventura, 2012). Studies that evaluated the efficiency of phosphate fertilisers on *M. javanica* and *M. incognita* showed hatching inhibition and J2 mortality, probably due to the type of ingredients and the major changes in the acidity of the reaction medium (Habash & Al-Banna, 2011; Hemmati & Saedizadeh, 2019). Considering the observations of this study and the promising results with the use of P-based compounds, it is expected that its application can be efficient in reducing *Meloidogyne* populations in sugarcane.

Regarding the variable SB, values higher than 1.91 were associated with lower *Pratylenchus* population densities. These findings are in line with Galbieri *et al.* (2016), who observed that the increase of SB showed some effect in the reduction of the initial population of nematodes such as *P. brachyurus* in cotton. As this variable includes the sum of Ca, Mg and K, it is important to focus in the adjustment of these elements.

Soil pH higher than 5.5 and 5.0 was associated with an increase of *Pratylenchus* and *Meloidogyne* populations, respectively. Melakeberhan *et al.* (2004) also observed that pH values of 5.9 and 4.6 significantly favoured more pre-adult and adult stages of *M. incognita* than pH 4.3 in soybean roots, whilst *P. zae* was negatively correlated with soil pH 5.57-6.98 in cereal fields (Talwana *et al.*, 2008). Soil pH can be considered a key variable due to its influence on soil properties and processes affecting plant growth and microorganism activity, as well as nutrient solubility and availability (Gentili *et al.*, 2018).

The soil profiles from the Alagoas coastal table have acid pH (Lima Neto *et al.*, 2009), including the soils sampled in this study, whose pH > 6.0 occurred only in four sampling points. According to Melakeberhan *et al.* (2000) soil levels of P, K, Mg and Ca decreased with decreasing pH, showing that nutrient imbalance and deficiencies may be induced at low pH, and this condition probably favoured infections by *Pratylenchus* spp. and *Meloidogyne* spp. populations in sugarcane roots. Thus, it is important to focus on balanced plant nutrition rather than on soil pH.

High nitrogen content was only associated with *Meloidogyne* spp. population density in sugarcane root-zone soil, being an essential element for plant growth and yield. A similar condition was also found by Assif *et al.* (2015) and Ngeno *et al.* (2019) who positively correlated *Meloidogyne* spp. populations with nitrogen in tomato. An abundance of nitrogen results in the production of new tissues and saps, and can extend the vegetative state and

increase the number of feeding sites in the roots, encouraging nematode attack (Santana-Gomes *et al.*, 2013). Furthermore, this element is the second most absorbed macronutrient by sugarcane (Lira *et al.*, 2019).

Although the data suggest a positive association between N levels and populations of *Meloidogyne* spp., the efficiency of nitrogen fertilisers to control this nematode was previously reported (Karajeh & Al-Nasir, 2012, 2014; Wei *et al.*, 2012; Patil *et al.*, 2013). Probably the effect of N on nematodes will depend on the source from where it is available in the soil (Sánchez-Moreno & Ferris, 2018). On this basis this element can minimise or have no effect on the impact of nematodes on the crop.

In the current study, increasing Ca:Mg ratios were associated with further increases in *Pratylenchus* spp. densities in the root-zone soil, the opposite being true for *Meloidogyne* spp. densities. Calcium is an essential regulator for growth and development in plants and plays a key role in cross-linking acidic pectin residues in the cell wall; it is also important in the cellular membrane system (Hepler, 2005), whereas Mg plays a fundamental role in photosynthesis and influences plant growth and vigour (Huber & Jones, 2013). Considering only the effect of Mg, our results showed a contrast between *Meloidogyne* spp. and *Pratylenchus* spp. populations. However, studies that correlate Ca:Mg ratios on nematode populations were not found, but the individual effect of each element on plant-parasitic nematodes has been documented, showing that positive or negative relationships may occur (Trevathan *et al.*, 1985; Kandji *et al.*, 2001; Freitas *et al.*, 2017; Almeida *et al.*, 2018; Ngeno *et al.*, 2019). The reason for this difference may be related to different soil types and crops and to the field scale of the sampling.

Associations showed in this study between the primary (N, P and K) and secondary (Ca and Mg) macronutrients and nematode population densities can be a consequence of the interactions of the three main nutrient contents with secondary macronutrients. The cationic antagonism between these three nutrients, K, Ca and Mg, has been reported in sugarcane, suggesting that K may reduce Ca and Mg uptake far more strongly than *vice versa* (Rhodes *et al.*, 2018). In addition to these interactions, Ca plays an important role in nitrogen metabolism, and Mg is needed for phosphorus transport in the plant (Thangavelu & Rao, 2004).

This exploratory study from sugarcane fields showed that, in general, among the evaluated components, K, P, N, Ca, Mg, pH and soil organic matter are more strongly linked with *Pratylenchus* and/or *Meloidogyne* popula-

tion densities. Variables altered by liming (Ca and Mg contents, pH) and by fertilisation with primary nutrients (P and K) were observed as strongly associated with the density of both nematodes; therefore, practices that improve soil fertility are potential candidates to compose an integrated strategy for controlling sugarcane nematodes. Although it was not possible in this study to classify the sugarcane cultivars in relation to their resistance or susceptibility to these pathogens, it is important to consider the reaction of some genotypes reported in previous studies in sugarcane renovation areas.

The data from this study must be validated in further research in order to understand responses of sugarcane crops to some physical and chemical components of the soil environment as a viable option for the management of *Pratylenchus* and *Meloidogyne* populations.

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