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Population Dynamics of Phytoparasitic Nematodes in Pineapple (*Ananas comosus* cv MD-2)

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In a long-term commercial pineapple farm (*Ananas comosus* cv MD-2) with more than 10 planting cycles, the root content and nematode population dynamics was determined on the crop. In the plant crop, 10 terraces with 16 beds were selected, each with plants of 2, 4, 6, 8 and 13 (at fruit harvest) months after planting for root sampling on both Inceptisol and Ultisol soils. In areas of first ratoon crop, 10 terraces also with 16 beds with 4 and 8 months after selection of the sucker and 10 terraces at fruit harvest, were sampled on both Inceptisol, and Ultisol soils. In each terrace, a composited root sample was taken from roots of 5 plants distributed diagonally along the terrace in beds:4, 6, 8, 10 and 12 (one plant per sampled bed). Plants were extracted in each of the 10 terraces and each growing age with a shovel, all the roots were cut off and collected, placed in identified plastic bags, and sent in coolers to the CORBANA nematology laboratory for nematode extraction. The results revealed an increase in root weight up to 180 (Inceptisol) and 120 (Ultisol) days after planting. Then there was a slight decrease that was aggravated at fruit harvest of the plant crop, which was extended until the first ratoon, with differences ($P< 0.0001$) between crop ages in both soils. The nematode frequency was 78% in the Inceptisol, and 96% in the Ultisol soil. In both soils, the predominant nematode was *Pratylenchus* spp. with more than 91% of the total nematode population, and the rest was *Helicotylenchus*. An increase in the population of *Helicotylenchus* spp. ($P< 0.0001$), *Pratylenchus* spp. ($P< 0.0001$) and total nematodes ($P< 0.0001$) was observed with the age of the crop until 8 months of sowing, in both soils. According to the nematode thresholds established for the crop, the populations found deserve control to prevent losses in production.

Introduction

Among the biotic factors that affect pineapple production, nematodes, which are very small microorganisms, invisible to the naked eye, which can only be observed under a microscope, parasitize the pineapple roots. More than 100 nematode species are reported in pineapple (Caswell *et al.*, 1990; Petty *et al.*, 2002; Sipes *et al.*, 2005).

Nematodes are considered the second most important parasitological problem of the crop

(Rebolledo *et al.*, 1998). Four genera, *Meloidogyne* spp., *Pratylenchus* spp., *Helicotylenchus* spp. and *Rotylenchulus reniformis* are frequent in pineapple (Caswell *et al.*, 1990; Stirling *et al.*, 1998; Rohrbach and Johnson, 2003; Sipes *et al.*, 2005; Rabie, 2017; Sipes and Chinnasri, 2018). They are common in all fruit-producing countries such as Costa Rica (López and Salazar, 1981; Figueroa, 1984; Jiménez, 1999; Quesada, 2013; Guzmán, *et al.*, 2014; Araya, 2019), Panamá (Organismo Internacional Regional de Sanidad Agropecuaria-OIRSA 1999), Puerto Rico (Ayala *et al.*, 1967; Román, 1978), Cuba (Hernández, 1998), Jamaica (Hutton, 1975, 1978), Perú (Julca and Carbonell, 2004; Vera *et al.*, 2017), Venezuela (Montilla de Bravo *et al.*, 1997; Jiménez *et al.*, 2001), Colombia (Redondo and Varon de Agudelo, 1993), Ecuador (Saráuz, 2015), México (Rebolledo *et al.*, 1998, 2011; Reyes *et al.*, 2005), Brazil (Manica, 2000; De Ferreira and Moreira, 2015; Pires de Matos, 2019), Canary Islands (Galan and Cabrera sf), Australia (Stirling and Nikulin, 1993; Stirling, 1993; Stirling *et al.*, 1998), South Africa (Keetch, 1982), Nigeria (Daramola and Afolami, 2014, Daramola *et al.*, 2013), Uganda (Bafokuzara, 1982), Ivory Coast (Guerout, 1975; Sarah, 1986), Philippines (Bondad *et al.*, 1979; Benzonan *et al.*, 2021), Hawaii (Caswell *et al.*, 1990; Sipes, 1994, 1996).

In Costa Rica, it is common to find *Pratylenchus brachyurus*, *Pratylenchus* spp. (Fernández *et al.*, sf.; López and Salazar, 1981; Figueroa, 1984; León, 2007; Carvajal, 2009; Barrantes, 2010; Quesada, 2013; Guzmán *et al.*, 2014; Araya, 2019), *Helicotylenchus* spp. (Fernández *et al.*, sf.; López and Salazar, 1981; Figueroa, 1984; León, 2007; Carvajal, 2009; Barrantes, 2010; Guzmán *et al.*, 2014; Araya, 2019), *Meloidogyne* spp. (Fernández *et al.*, sf.; León, 2007; Carvajal, 2009; Barrantes, 2010; Guzmán *et al.*, 2014; Araya, 2019) and *Rotylenchulus* spp. (Leon, 2007). Nematodes affect the functioning and number of roots, which do not regenerate in the pineapple crop (Rohrbach and Apt, 1986; Petty *et al.*, 2002; Rohrback and Johnson, 2003; Umble *et al.*, 2006; Paull and Duarte, 2011; Nurfadhilah *et al.*, 2012; Rabie, 2017) which leads to reducing the absorption of water, nutrients, photosynthesis, and production of the plant. Therefore, the plant parasitic nematode population dynamics throughout a crop cycle was determined to define possible vegetative states in which its control maybe be required that could contribute to adapt management practices for promoting yield.

Materials and Methods

In a long-term (more than 10 planting cycles) commercial pineapple plantation (2000 ha) located in Río Cuarto, Alajuela-Costa Rica at an elevation of 60-130 masl, a nematode monitoring was done at different ages of the plant crop and first ratoon crop planted on an Inceptisol and Ultisol soil. Farm management practices were applied uniformly. The field soil was cleaned free of plant residues and weeds, ripped to 80 cm depth, and later cross ploughed to a depth of 40-50 cm and finished with a disc harrow. Beds were formed one month prior to planting. The Inceptisol soil was clay loam (44% sand, 21% silt and 35% clay), with 1.8% organic matter content and a pH of 4.7and the Ultisol was a well aggregated clay (12% sand, 27% silt, 61% clay), with 2% organic matter content and a pH of 4.5. A system of primary, secondary, and tertiary drains was provided to remove excess rainfall water and avoid water logging conditions during heavy rains.

Manual planting was done with suckers of *Ananas comosus* cv. MD-2 at a plant density of 72,000 plants ha^{-1}. Annual rainfall for 2020 and 2021 was 2217 and 2456 mm, respectively, evenly distributed. The driest months were from December to April with rainfall lower than 100 mm. Mean daily maximum/minimum temperatures varied between 25.4 and 29.7 °C and between 16.8 and 19.8 °C. Custom made fertilizer 25-8-5-1.5-0.2-0.5-1.5-0.5(N-P_2O_5-K_2O-MgO-B-Ca-S-Zn) was applied at 8 g per sucker 30 days after planting. Thereafter, every two weeks a mix of nutrients in 1,800 L of water were foliar applied with a spray boom at a rate adapted to the soil and crop requirements to complete 700 kg N, 117 kg P_2O_5, 800 kg K_2O, 100 kg MgO, 1 kg Cu and 2 kg Zn per hectare for the crop cycle. Diseases were controlled with spray applications of systemic and protectant fungicides. Weeds were controlled pre-planting with oxyfluorfen, and post planting with a mixture of diuron, ametrineand clethodim and sometimes manually.

The plantation layout was in terraces of 16 beds wide and 10-15 m long with about 1200 - 1700 plants. In the plant crop, 10 terraces with 16 beds were selected, each with plants of 2, 4, 6, 8 and 13 (at fruit harvest) months after planting for root sampling on both Inceptisol and Ultisol soils. In areas of the first ratoon crop, 10 terraces also with 16 beds with 4 and 8 months after the sucker selection and 10 terraces at fruit harvest, were sampled on both Inceptisol and Ultisol soils. In each terrace, a composited root sample was taken from roots of 5 plants distributed diagonally along the terrace in beds: 4, 6, 8, 10 and 12 (one plant per sampled bed). In total, 10 samples were taken in both Inceptisol and Ultisol soils at each plant age for the plant crop and first ratoon crop. This resulted in 50 samples for the plant crop and 30 for the first ratoon crop in each soil type.

With a shovel, the 5 plants were extracted in each of the 10 terraces of each plant growth age, all the roots were collected, placed in an identified plastic bag, and sent to the CORBANA nematology laboratory at La Rita, Guápiles for nematode extraction. The total of 160 samples (80 Inceptisol soil and 80 Ultisol soil) were taken on two consecutive days. Nematodes were extracted from 25 g of fresh roots or the total available, which were macerated in a kitchen blender (Araya, 2002) for 10 sec at low and 10 sec at high speed, and nematode recovered in 0.025 mm (No 500) sieve. The nematodes were identified at the genus and species level, when possible, based on the morphological characteristics under a light microscope, following the key of Siddiqi (2000). The population densities of all plant-parasitic root nematodes present were recorded, and the values were converted to numbers per 100 g of roots. The nematode population composition was determined for each soil. Root weights by crop age were subjected to ANOVA by Proc GLM of SAS and nematode data by crop age was analyzed with generalized linear models, using the log transformation as link function and negative binomial distribution of the errors, and the absolute frequency (number of samples containing nematodes / number of samples analyzed * 100) was estimated (Barker, 1985) by soil type.

Results and Discussion

In the root content per plant, an increase was observed up to 180 and 120 days after sowing in the Inceptisol (Figure 1A) and Ultisol soil (Figure 2A), respectively, with differences (P< 0.0001) between plant ages in both soil types. Subsequently, there was a slight decrease that was aggravated at harvest of the plant crop and extended until the harvest of first ratoon crop. This decrease in the root weight after 180 and 120 days is not so real, because the distribution and depth of the root system beyond that plant age, makes that, when extracting the plants from the soil, root mass remained in the soil and was not collected.

Of the 80 samples taken from the Inceptisol soil, 18 were found free of phytoparasitic nematodes, which means that 78% of the samples had nematodes. In the Ultisol soil, of the 80 samples taken, only 3 were free of nematodes, which means that 96% had plant parasitic nematodes. In the phytoparasitic nematode community it was found in both types of soil, a predominance of *Pratylenchus* spp. with 91.9% in the Inceptisol and 92.3% in the Ultisol soil and 8.1 and 7.7% of *Helicotylenchus* spp., respectively (Figure 3).

In both soil types, an increase in the population of *Helicotylenchus* spp. (Figure 1B, Figure 2B), *Pratylenchus* spp. (Figure 1C, Figure 2C) and the total number of nematodes (Figure 1D, Figure 2D), which was the sum of both genera, was observed as the vegetative cycle of the plant crop progresses until 8 months after sowing. Differences (P< 0.0001) in the number of nematodes between plant ages were found in the Inceptisol and Ultisol soil. Subsequently, the populations of these nematodes decreased gradually in the Inceptisol soil and sharply at the harvest of the plant crop in the Ultisol soil, which remained very similar throughout the harvest of the first ratoon crop.

The root content by plant age was low and its trend was like that found by Hernández and Tello (2011) and Cruz (2012) also in pineapples in Costa Rican conditions. The average root content of the plant at 6-8 months of age was 22 g (Inceptisol) and 23.5 g (Ultisol) per plant. If we calculate the proportion of roots with the plant at forced weight (8 months old) of 2.5 to 3 kg, it would be that the roots represent 0.8 and 0.9% of the total plant weight, not including the fruit. In other local studies, Hernández and Tello (2011) reported at harvest of the plant crop, based on fresh weight, 0.6% of roots with respect to the total plant weight including the fruit, and Cruz (2012) found also at harvest of the plant crop, on two different farms 1.36 and 1.65% of roots with respect to the total plant weight.

According to Godfrey (1936) the pineapple root system consists of 100 main-primary roots, very uniform in size. From each primary root, a system of lateral roots (secondary and tertiary roots) develops, the latter being progressively thinner and shorter. When roots emerge higher above the soil, they wrap around the stem becoming in axillary roots. Main, lateral, and axillary roots have roots hairs. According to Py *et al.,* (1987), the total root mass can reach 350 g and represent 6.7% of the total plant. So, what the crop has the least are roots, and the anchoring of the plant, the absorption of water and nutrients depends on it. Therefore, potentialize the maximum genetic expression of the root system in pineapple as well as to keep its health and conservation is essential, since, in this crop, the roots do not regenerate.

The two nematode genera detected are widely reported pests in pineapple roots (Guerout, 1975; Hutton, 1978; Rohrbach and Apt, 1986; Py *et al.,* 1987; Caswell *et al.,* 1990; Petty *et al.,* 2002; Julca and Carbonell, 2004; Sipes *et al.,* 2005; Rabie, 2017; Sipes and Chinnasri, 2018). The nematodes found in this population dynamic are consistent with those previously reported in Costa Rica and other pineapple producing countries as mentioned earlier in the introduction.

The increase in the *Pratylenchus* spp. population with the age of the crop in its vegetative phase agreed with that reported by León (2007) and Carvajal (2009) in Costa Rica, where the maximum population was found 8 and 7 months after sowing, respectively. This behavior is reasonable since the propagules used as planting material are free of nematodes, since they are slips, stem shoots or crowns without roots, which become infected in the soil when root emission begins 15-22 days after sowing. Once the plants are infected, the nematode reproduction begins, whose growth rate is affected by the availability and health of the root system (food) and the application of control measures. Dinardo *et al.,* (1997) in Brasil also found a similar behaved, where *Pratylenchus brachyurus* augmented the population progressively with the plant growth, reaching the maximum 7-8 months after sowing, and they attributed the nematode built up to the higher soil water content and rain fall.

The high *Pratylenchus* spp. population is favored by the pineapple monoculture and coincides with other local studies (López and Salazar, 1981; León, 2007; Carvajal, 2009; Barrantes, 2010) and with studies from Australia (Stirling and Nikulin, 1993) and Ivory Coast (Sarah, 1987; Sarah *et al.,* 1991). Lack of information by farmers on the damage of this pest and its biology could have contributed to the high infections. Additionally, the high reproductive capacity and short life cycle of the nematode result in high populations. *Pratylenchus brachyurus* reproduces by parthenogenesis and the life cycle is completed in 28 days at 30-35 ^{o}C (Corbett, 1976) and females from pineapple roots lay two to three eggs per day for one week (Guerout, 1975). In the case of *H. multicinctus*, mating is required for reproduction (Karakas 2007) and the life cycle lasted 42 days at 28 ^{o}C in *Arabidopsis thaliana*, adult females laid 4 eggs per day for a period of 10-12 days (Orion and Bar-Eyal, 1995).

The different parasitic habits of the nematode genera found, migratory endoparasite: *Pratylenchus* and ecto-endoparasite, *Helicotylenchus*, which feed on subsurface root tissue are likely to exacerbate root damage, because lesions can develop through the root, which favors the invasion of soil pathogens (Viglierchio, 1991; Manzanilla-López and Starr, 2009).

There is scientific information on the damage caused by nematodes in pineapple. In Peru, Julca and Carbonell (2004) found that *Pratylenchus*, *Helicotylenchus* and *Meloidogyne* diminished the length and weight of the D leaf, reduced the weight of the fruit and its diameter, and drop the % of fruit brix. Guerout (1969) inoculating *Pratylenchus brachyurus* in pineapple plants, found a 26% decline in area of the D-leaf, 64% drop in root mass and 35% reduction in fruit weight compared to control plants.

Later, the same Guerout (1975) reported a 35-40% reduction in plant growth, leaf emission and leaf weight. In Colombia, *Pratylenchus* neglectus reduced the fresh plant weight by 54% and, reduced the root mass and the thickness and size of the leaves (Redondo and Varon de Agudelo 1993).

In Hawaii, *Meloidogyne*-infected plants showed 16.4% less total fresh weight, 26.5% less roots, 15% reduction on leaf weight, and a 47.5% drop in fruit weight (Goodfrey and Hagan 1934). Furthermore, in Hawaii, Godfrey (1936) found that root elongation is 8 to 8.1 mm per day in the absence of infection by *Meloidogyne* ssp., but in plants inoculated with 100 larvae it was 2.14 to 2, 88 mm per day, when infected with 250 larvae per plant, was 1.34 to 1.79 mm and in plants inoculated with 1000 larvae, the elongation of the roots was only 1 mm per day.

In the case of *Rotylenchulus reniformis*, losses of up to 26.8% in marketable fruit (Sipes, 1994) in the plant crop and up to 50% in ratoon crop are reported in Hawaii (Sipes, 1996). Nematode losses in Mexico ranged from 15 to 45% (Rebolledo *et al.*, 1998) and more recently from 15 to 60% (Rebolledo *et al.*, 2011). Román (1978) in Puerto Rico, found in soils infested with nematodes a reduction in fruit weight of 47.5%. Hutton (1978) in Jamaica, comparing the control of *Helicotylenchus multicinctus* and *Pratylenchus* spp. before and after planting with untreated plants, reported an increase in fruit weight of 79% for Red Spanish, 146% for Smoth Cayenne, and 94% for Sugar loaf.

There are economic thresholds for some of the nematodes that cause damage to the pineapple root system. Sarah (1986) in Ivory Coast suggested a tolerance threshold of 1 to 2 *Pratylenchus brachyurus* per liter of soil. In Mexico, Rebolledo *et al.*, (1998) proposed a threshold of 1 *Meloidogyne* or 1 *Pratylenchus* spp. per gram of soil. In Australia, Stirling *et al.*, (1998) considered 0.5 *Meloidogyne*; 0.5 *Pratylenchus* or 0.5 *Rotylenchulus* per gram of soil as harmful level and then Stirling and Kopittke (2000) mentioned a population of 0.02 of any of these nematodes per gram of soil as tolerance limit.

In the roots, Keetch (1982) reported that 1 *Meloidogyne*, 1 *Pratylenchus* or 1 *Rotylenchulus* in the root system was sufficient to cause yield losses, and Sarah (1986) recommended less than 5 nematodes per gram of roots during the growing cycle.

These economic thresholds consider individual nematodes such as *Pratylenchus*, *Meloidogyne* and *Rotylenchulus*, however, there is scientific knowledge that *H. multicinctus* also damages pineapple roots and reduces their growth and yield (Hutton, 1978; Hernández, 1998; Julca and Corbonell, 2004; Ferreira *et al.*, 2014). Therefore, to decide on pineapple nematode management it would be convenient to consider the total phytonematode population, since the four genera damage the pineapple root system and reduce yield.

Fig.1 A-D. Root weight per plant and number of nematodes per 100 g of roots per plant according to the age of the plant crop and first ratoon crop of pineapple (*Ananas comosus* cv. MD-2) established in an Inceptisol soil. Each bar is the mean ± standard error of 10 repetitions. In each repetition the samples consisted of the roots of 5 plants. All samples were taken within two consecutive days.

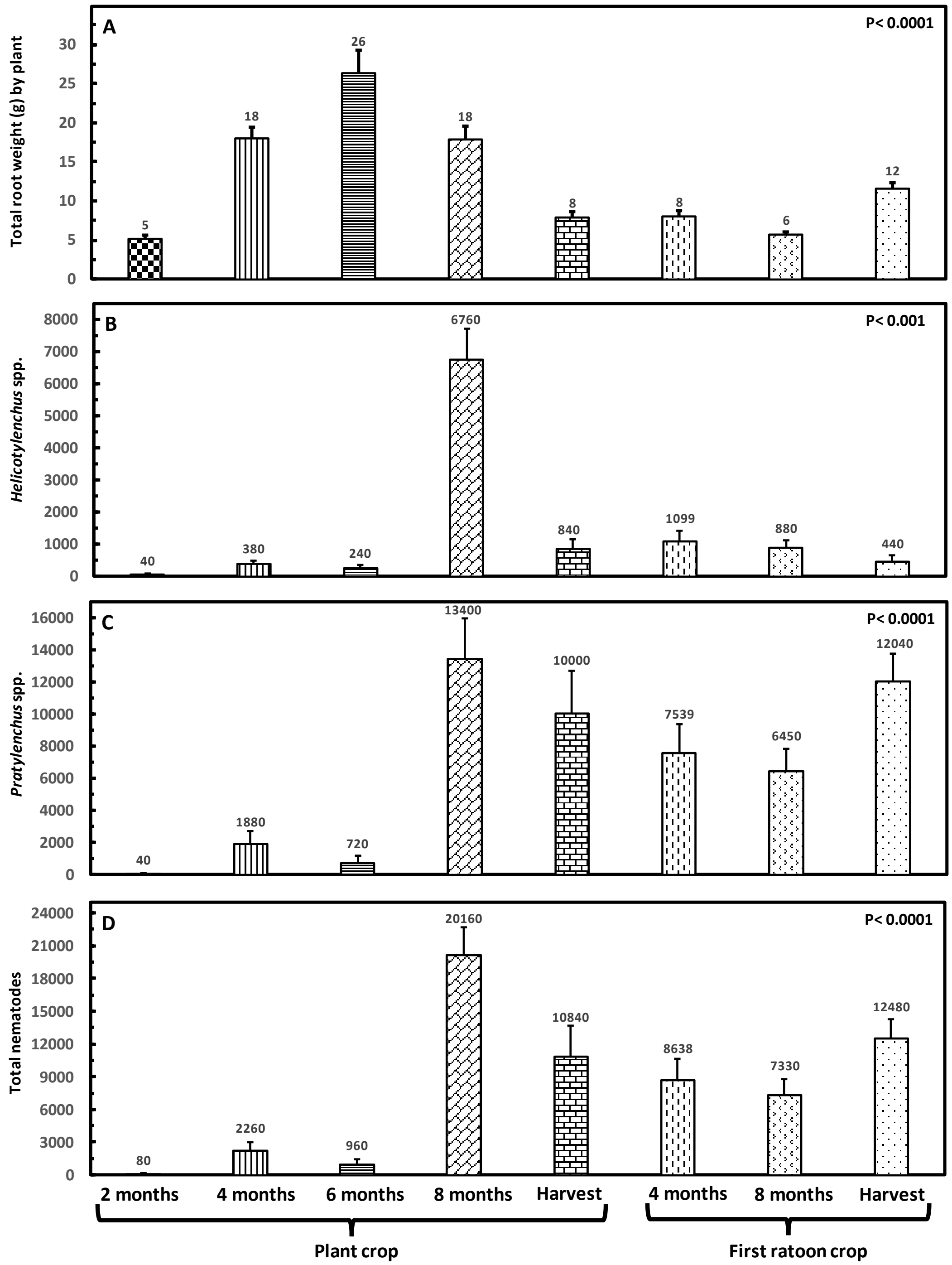


Fig.2 A-D. Root weight (g) by plant and number of nematodes per 100 g of roots per plant according to the plant crop and first ratoon crop of pineapple (*Ananas comosus* cv. MD-2) established in an Ultisol soil. Each bar is the mean ± standard error of 10 repetitions. In each repetition the sample consisted of the roots of 5 plants. All samples were taken within two consecutive days.

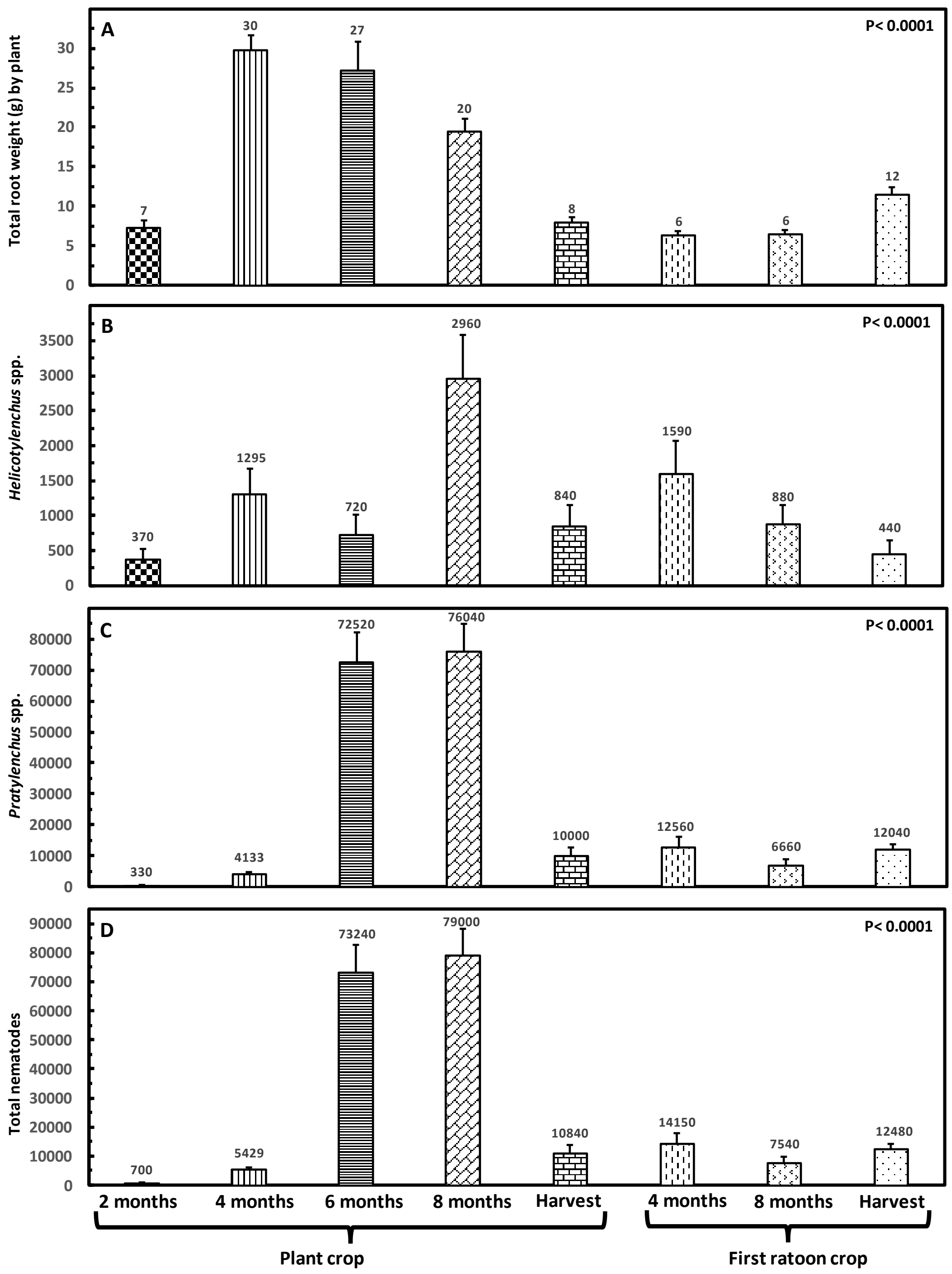
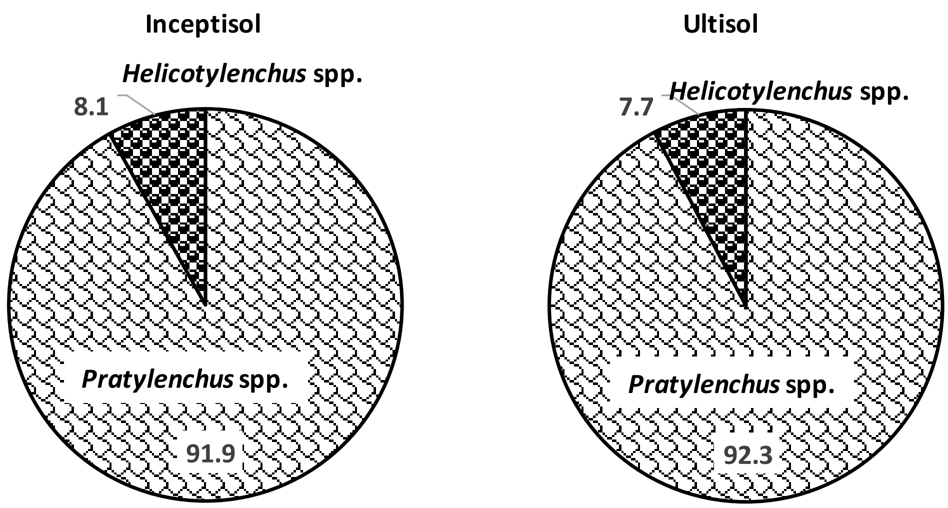


Fig.3 Distribution of the plant parasitic nematode community (*Helicotylenchus* spp. and *Pratylenchus* spp.) by soil type from samples of pineapple roots (*Ananas comosus*cv. MD-2) taken at different plant ages in two consecutive days. N = 80 in each soil type.



In South Africa, where *Meloidogyne* and *Helicotylenchus* are serious pests of pineapple, pre-seeding dipping in a solution with systemic nematicide followed by post-seeding treatment at monthly intervals for 12 months, increased crop yield by 916 boxes (12 kg) per hectare (Paull and Duarte, 2011). In Puerto Rico, Ayala and Sequeira (1974) found an increase in yield of 1350 boxes per hectare and Roman (1978) up to 2166 boxes per hectare when controlling pineapple nematodes. Hutton (1978) found a yield improvement of up to 1058 boxes per hectare when controlling nematodes in Jamaica. López and Salazar (1981) in Costa Rica reported increases in fruit weight up to 205 g, which multiplied by 55,000 fruits (85% of marketable fruits) per hectare would result in 11.2 Tm (939 boxes) more per hectare with the control of nematodes. In Hawaii, Apt (1981) and Apt and Caswell (1988) found increases in yield of 50 tm (4166 boxes) and 36.9 tm (3075 boxes) more per hectare, respectively, with the control of nematodes in pineapple. Then to prevent the nematode population to build up, it is recommended to monitor the nematode population periodically (pre-planting and vegetative growth) to make timely decisions about their control options.

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