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Title

Competitive interactions in plant-parasitic nematode communities affecting organic vegetable cropping systems.

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ABSTRACT

Plant-parasitic nematodes (PPN) are detected everywhere as mixed-species communities. Most non-chemical control strategies of PPN only target some species, thus raising questions about the consequences that this specificity may have on the residual community. In this respect, the long-term ecological sustainability of such strategies is challenged. In order to evaluate the impacts of agronomical practices on PPN communities, two four-year experiments that differed by the presence or absence of root-knot nematodes (RKN - *Meloidogyne* spp.) were carried out under cold shelters in the south of France, under native field conditions of vegetable cropping systems that included a nematicidal sorghum green manure and a pepper variety carrying a RKN resistance gene. At the site with RKN, RKN populations developed on susceptible vegetables. But they were controlled by the green manure but not by the R-pepper, and were also vulnerable to low soil temperatures. At the site without RKN, Paratylenchidae populations developed on susceptible vegetables, but were controlled by both the green manure and the R-pepper, and not by low temperatures. At each site, populations of Telotylenchidae exhibited dynamics suggesting competition with RKN or Paratylenchidae. Hypotheses about competition models are discussed according to the specific life traits of the PPN involved, including ecto- vs. endoparasitism and sedentary vs. free-living behaviour, and to the antagonist mechanisms of the cover and resistant crops that must be introduced in vegetable cropping systems.

Keywords: Community; Green manure; Plant-parasitic nematode; Plant resistance; Species competition; Vegetables.

1. Introduction

Plant parasitic nematodes (PPNs) are responsible for great yield losses estimated at US$100 billion annually worldwide (Abd-Elgawad and Askary, 2015). Chemical nematicides used for the management of plant-parasitic nematodes (PPNs) can have broad and unintended effects. They act not only on PPNs, but also on all free-living nematode species (Chitwood, 2003). Moreover, they are able to kill a wide range of other soil-borne organisms and may negatively impact soil biodiversity (Rich et al., 2004). On the other hand, the natural plant-protection alternatives against PPNs, such as service plants, plant resistance and biocontrol agents, are more species-specific, and better preserve soil functions involved in soil health and plant production (Doran and Zeiss, 2000; Timper, 2014).

In Mediterranean regions, RKN are most destructive to vegetable farms (Djian-Caporalino, 2012). Despite the promising results obtained with these alternatives for controlling RKN populations in vegetable cropping systems, questions arise concerning the effect of such strategies on the entire PPN community (including RKNs) and, more precisely, the effects that these strategies may have on other members of the PPN community, especially competing one. Indeed, all natural control alternatives developed in agriculture focus on a few target species compared to the whole PPN diversity encountered in specific sites (Jones et al., 2013). As an example, most developed methods on vegetable crops concern only a few RKN species (Nyczepir and Thomas, 2009). Thus, when bearing in mind that PPNs occur everywhere as mixed-species communities, most natural plant protection alternatives would induce long-term richness erosion, community rearrangements, increased development of minor species, etc. (Mateille et al., 2008). Furthermore, the sustainability of soil suppressiveness (i.e. capacity of soils to suppress plant diseases even in the presence of a virulent soil-borne pest and a susceptible host) should not only be considered in terms of success over time in relation to emblematic crop-specific nematode species, but in terms of biodiversity and long-term soil health. In that sense, a promising option is the combination of control methods targeted against the main pathogenic species plus non-specific cropping practices aimed at promoting suppressiveness such as by organic amendments (Evans et al., 1993; Luc et al., 2005).

PPN community assemblages are subjected to various types of constraints: nematode evolution, intra- and interspecific interactions, climate, plant diversity and attractiveness, soil characteristics and functions, land-use changes and cropping practices, etc. (Hodda et al., 2009). In that way, PPN community assemblages would be shifted when applying control alternatives in cropping systems (Wang et al., 2016). Previous works have been shown that some sorghum species and varieties are able to reduce PPN populations such as RKNs, *Helicotylenchus dihystera*, *Pratylenchus penetrans* and *Rotylenchus reniformis* (La Mondia et al., 2002; Wang et al., 2004; Asmus et al., 2008; Stapleton et al., 2010; Navarrete et al., 2016). However, the same sorghum species can lead to an increase of other taxa such as *Belonolaimus longicaudatus*, *Mesocriconema* sp., *Paratrichodorus minor*, *Pratylenchus* spp. and *Tylenchorhynchus* spp. (Rhoades, 1983; McSorley and Dickson, 1995; Crow et al., 2001; Bhan et al., 2010; Villenave et al., 2010; Fraedrich et al., 2012). In southeast France, RKNs occur now over 40% of the vegetable production area since the ban of methyl bromide in Europe (Djian-Caporalino, 2012). As soon as alternative strategies were implemented to control RKNs in this area, especially using Sudan grass as green manure, the expansion of *Paratylenchus* spp. infestations was observed (Mateille and Tavoillot, 2019), even leading to worrisome crop damage in some cases as seen elsewhere (Faulkner, 1964; Wang et al., 2016).

Usually, because PPN species utilize the same trophic source, they are under competition either by exploitation (use of the same resource in limited quantities) or by interference (reciprocal disturbances generated by the search for this resource when it is not in limited quantities) (Begon et al., 2006). Thus, exploitation produces the elimination of species, either by direct exclusion or by moving or reducing their niche until coexistence becomes possible (Connell, 1980). The coexistence between PPN species depends partly on their different life traits: (*i*) they exhibit all reproduction modalities (amphimixis, mitotic and meiotic parthenogenesis, hermaphroditism), and different modalities can be found among the same genus, such as RKN or *Pratylenchus* (Chitwood and Perry, 2006); (*ii*) they exhibit different parasitism strategies (Bird and Bird, 2001): PPN may feed on plant tissues from outside the plant (i.e., ectoparasites) or inside the tissues (i.e., endoparasites) and they can move through plant tissues (migratory species) or can become swollen and permanently immobile (sedentary species).

Therefore, considering the PPN diversity associated with vegetable cropping systems, this study focused on the unbalanced development of PPN populations in communities subjected to management techniques targeting RKNs especially. Moreover, two sites differing by the presence/absence of RKNs were chosen in order to better understand how PPN species compete.

2. Materials and methods

2.1. Field survey designs

Two field trials were performed each on two separate commercial organic farms located in southern France, with Mediterranean climate, from 2012 to 2016. The trials were carried out under 40 m x 8 m x 3.5 m plastic cover plots that were previously cropped with RKN susceptible vegetables (salad and melon) since several seasons. One trial was performed near Lambesc (43.65N, 5.21E). The sandy-silty soil (37.5% sand, 22.3% silt, 10.7% clay, 3.5% organic matter, pH 8.4) was heavily infested with RKN. During the study period, the soil temperature at a depth of 15 cm varied from 5°C in winter to 30°C in summer. In order to explore deeper interactions between species, the other trial was performed on a site free of RKNs, located at the INRA Experimental Centre near Alénya (42.64N, 2.97E). The soil was sandy-silty (33.7% sand, 48.1% silt, 18.1% clay, 1.8% organic matter, pH 7.5) and its temperature reported at a depth of 10 cm varied from 4.7°C in winter to 26°C in summer.

In both sites, a nematicidal green manure (hybrid sorghum '270911' = three-way hybrid from *S. bicolor* spp. *bicolor* x Sudan grass cvs. 'Almuden', 'Bihar', 'Magno' and 'Artis' cross developed by UPL France SAS™) was used for biofumigation. Four weeks after sowing, the plants were cut, and then grounded and rotavated. The soil was rolled and left uncovered for one month to allow biofumigation (Goillon et al., 2019). Moreover, a resistant pepper crop (*Me-3* DLL R-pepper) was cultivated in spring and summer. This resistant pepper is *Capsicum annuum* sweet pepper grafted on a resistant pepper rootstock carrying the major *Meloidogyne* R-gene *Me-3* in the susceptible genetic background Doux-Long-des-Landes (BC1-S1 [(DH149 × DLL) × DLL]). The rootstock was provided by the Genetic Resources Centre for Vegetable Species (CRB-Leg) at INRA Montfavet, and the sweet pepper variety was grafted by Scea Meffre Plants™.

The green manure and the resistant crops were included into crop sequences that alternated RKN-susceptible vegetables such as melon (*Cucumis melo*) in spring, and lettuce (*Lactuca sativa*) or Swiss chard (*Beta vulgaris* subsp. *vulgaris*) in winter.

2.2. Nematode analyses

Soil samples (eight random replicates in each plot at each sampling date) were collected from the top 20 cm soil layer (500 ml for each replicate) at before the experiment and after each susceptible crop was terminated. The samples were systematically taken from the same core site, to minimize the effects of heterogeneity in the distribution of nematodes over the plot. PPNs were extracted from a 250-ml aliquot of each soil replicate using the elutriation procedure (Seinhorst, 1962). They were identified first to genus (Mai and Mullin, 1996) and counted in 5 mL aliquots sampled from 25 mL suspensions under a stereomicroscope at 60x magnification (Merny and Luc, 1969). Then, nematode suspensions were fixed (De Grisse, 1969) and one hundred PPN specimens at least were mounted onto slides and morphologically identified to species level according to specific keys (Van

Bezooijen, 2006). PPN levels were expressed as the number of individuals per dm^3 of fresh soil. RKN populations were identified using the SCAR-PCR procedure (Zijlstra, 2000; Zijlstra et al., 2000) and their avirulence was assessed on *Mi-1*-tomato and *Me3*-peppers in controlled conditions (Djian-Caporalino et al., 2011).

2.3. Data analyses

In each site, population dynamics were monitored for each taxa. Mean population levels were analysed and compared between taxa (ANOVA and Wilcoxon-Mann-Whitney test with $P<0.05$) at each sampling date. In order to analyse competitions between PPN taxa, the whole PPN data (individuals from each family /100mL of soil) gathered during the experiment were analysed with normalized Principal Component Analyses (PCA). The PCA were performed by using the *ade-4* package provided in R software (Chessel et al., 2004; R Core Team, 2016). Then we monitored the regression kinetics of pairs of taxa adapted from the Lotka-Volterra model (Begon et al., 2006) by displaying the population levels of each pair of taxa at each sampling date.

3. Results

3.1. Dynamics of plant-parasitic nematodes in communities

3.1.1. At the 'Lambesc' site

The PPN taxa detected were *Ditylenchus acutus, Nothotylenchus acutus* and *N. thornei* (Anguinidae), *Helicotylenchus canadensis* (Hoplolaimidae), *Meloidogyne arenaria, M. incognita* (Meloidogynidae), *Mesocriconema* spp. (Criconematidae), *Paratylenchus nanus* (Paratylenchidae), *Pratylenchus thornei* (Pratylenchidae), *Histotylenchus* sp., *Merlinius microdorus* and *Tylenchorhynchus clarus* (Telotylenchidae), *Xiphinema pachtaicum* (Longidoridae), and Tylenchidae species (*Basiria tumida, Boleodorus thylactus, Filenchus hamatus, F. misellus, Ottolenchus facultativus, Psilenchus aestuarius, P. hilarulus*). *M.*

arenaria and *M. incognita* populations were identified as *Mi-1* and *Me-3* avirulent.

Only nematode families with a total abundance > 1% were considered for dynamics: Hoplolaimidae, Meloidogynidae, Telotylenchidae and Tylenchidae. The Hoplolaimidae and Tylenchidae nematodes remained in low abundance throughout the experiment and were not impacted by either the green manure or by the R-pepper (Fig. 1). Meloidogynidae (98% *M. arenaria* and 2% *M. incognita*) were the most dominant with 1,883 ± 398 individuals/100 mL of soil at the beginning of the experiment. The Meloidogynidae abundance was strongly reduced after the sorghum green manure (-94.4% in 2012 and -81.8% in 2014). At the same time, the Telotylenchidae population (73.5% *T. clarus*) was enhanced (+81.9% in 2012 and +57.5% in 2014), respectively. Unexpectedly, the Meloidogynidae population increased on the resistant pepper crop (+99.8% in 2013 and +91.6% in 2015), while the Telotylenchidae population decreased in 2013 (-44.3%) and increased in 2015 (+7.5%). Furthermore, Meloidogynidae decreased on susceptible vegetables when cultivated in winter (-99% on Swiss chard in 2012; -77.9% on lettuce in 2014 and -92.4% in 2015; -70.1% on lettuce in 2016). In contrast, the dynamics of Telotylenchidae depended on the crop succession: populations declined on Swiss chard (-51.9% in 2013) and on lettuce (-48.8% in 2015) following the green manure. On the other hand, they increased on lettuce following resistant pepper (+17.9% in 2014 and +64.9% in 2016). The melon crop multiplied both Meloidogynidae and Telotylenchidae populations increased on the melon following lettuce in 2014 (+85.7% and +32.3%, respectively). From the beginning to the end of the experiment, the alternation of sorghum green manure and resistant pepper resulted in an overall 11.7% reduction of the Meloidogynidae population, and an overall 8.7% increase of the Telotylenchidae populations.

3.1.2. At the 'Alénya' site

The PPN taxa detected were *N. acutus* and *N. geraerti* (Anguinidae), *Lelenchus* *leptosoma* (Ecphyadophoridae), *P. nanus* (Paratylenchidae), *P. thornei* (Pratylenchidae), *Histotylenchus* sp. and *T. clarus* (Telotylenchidae), and Tylenchidae species (*B. tumida, F. hamatus, O. facultativus, P. aestuarius*).

As indicated above, only the most representative nematode families were considered (total abundance > 1%): Paratylenchidae, Telotylenchidae and Tylenchidae. The Tylenchidae populations were the most abundant at this site at the beginning of the experiment (Fig. 2), but they decreased just after the first lettuce crop and remained at a very low level throughout the experiment. The two applications of green manure in 2013 and 2015 did not prevent the Telotylenchidae populations (73% *T. clarus*) from increasing on lettuce and melon (+88.6% and +48.6%, respectively). In the same time, the Paratylenchidae populations decreased (-46.4% and -89.5%, respectively). Both Telotylenchidae and Paratylenchidae populations were able to multiply on all vegetables, except when lettuce was cultivated after a four-month bare period (2013), but they declined on the resistant pepper crop in 2014 (-49.7% and -94.4%, respectively). Nevertheless, from the beginning to the end of the experiment, the alternation of sorghum green manure and resistant pepper resulted in an overall increase of the Telotylenchidae and Paratylenchidae populations (+5.4% and +28.9%, respectively).

3.2. Interactions between nematode taxa

When modelling the correspondence between all the nematode families by using the whole PPN data gathered during the experiment at the ‘Lambesc’ site, the PCA analysis revealed the major contribution of the Meloidogynidae (Me) and the Telotylenchidae (Te) variables, and their opposite position on the first PCA axis (Fig. 3A). Moreover, when modelling the kinetic regression between RKN and Telotylenchidae populations throughout the experiment, we observed, with few exceptions, that Meloidogynidae populations decreased when Telotylenchidae populations increased, and vice versa (Fig. 4A). In addition, there was a constant increase of the Telotylenchidae at the expense of the Meloidogynidae because the regression kinetic moved as a spiral according to a long-term reversal of the Meloidogynidae /Telotylenchidae ratios in favour of Telotylenchidae nematodes.

The PCA analysis modelled on all of the nematode family data at the ‘Alénya’ site revealed the major contribution of Paratylenchidae (Pa) and Telotylenchidae (Te) variables and their opposite position on the first PCA axis (Fig. 3B). The regression modelled between these two families showed a cyclic kinetic, meaning that populations of Telotylenchidae decreased when populations of Paratylenchidae increased, and vice versa (Fig. 4B), but with a long-term increase of both PPN families until the end of the experiment.

4. Discussion

Since RKN are usually dominant in vegetable soils, the resort to the two sites, one highly infested with RKN and one free of RKN, should make it possible to analyse contrasted communities and their dynamics when submitted to similar cropping systems. We have chosen two different sites because RKN infestation and non-infestation conditions cannot be found on the same site. Therefore, the strict comparison of the two sites cannot be performed “all other factors being equal” (with/without RKN, crop sequence, climatic conditions, etc.) and the interpretation should take into consideration all the different agro-environmental conditions. In addition, we deliberately conducted this study under native farm conditions, i.e. on large enough plots to manage all practices as in real conditions, even if it makes the analysis more difficult. Therefore, replicate plots within each site could not be designed, and the individual sampling points were considered as replicates.

4.1. Response of PPN populations to seasons

Looking at vegetable cropping periods, low soil temperatures that occurred during each winter (5 to 10°C) decreased Meloidogynidae populations at the ‘Lambesc’ site, although they were able to infest lettuces that are highly susceptible. *Meloidogyne arenaria* and *M. incognita* can survive poorly in soils below 10°C (Evans and Perry, 2009). Low temperatures are known to affect several functions. They reduce the mobility of free RKN juveniles in the soil, which impacts their penetration into the roots, hence their survival. Juveniles that have infested roots fail to reproduce and the embryogenesis is slowed down by curbing eggs in tardicultus states (Evans and Perry, 2009). At the 'Alénya' site, winter periods did not affect the development of *Paratylenchus nanus* that increased on winter lettuce, except when the lettuce followed the 4 month-bare period in 2013. In fact, *Paratylenchus* species are widespread under all types of climates and *P. nanus* is able to develop at high altitudes and in cold countries (Talavera and Navas, 2002; Ryss et al., 2005). That could explain why *P. nanus* was not disturbed by cold periods. Telotylenchidae nematodes that were dominated by *Tylenchorhynchus clarus* exhibited contrasted behaviours. Their populations declined during the winter periods at the 'Lambesc' site, except in 2015, whereas they were enhanced or maintained at the 'Alénya' site, except after the bare period in 2013. Like the other Telotylenchidae, *T. clarus* is cosmopolitan and is not that sensitive to temperature (Noel and Lownsbery, 1978). Consequently, Meloidogynidae species were obviously susceptible to low temperatures while Paratylenchidae nematodes were tolerant, and Telotylenchidae were indifferently affected or not. On the other hand, the Meloidogynidae, Paratylenchidae and Telotylenchidae nematodes reproduced during hot periods (spring and summer), especially on melon, while it is well known that RKN are very aggressive on Cucurbitaceae, and Paratylenchidae and Telotylenchidae have been shown to cause damage to several vegetables (Potter and Olthof, 1993; Faske, 2013).

4.2. Response of PPN populations to R-pepper

Looking at the R-pepper crop that was introduced in spring and summer (soil temperature up to 28°C), the low efficiency of the resistance of the *Me3*-DLL variety towards RKN was confirmed at the 'Lambesc' site. The *Me-3* gene induces early root-cell necrosis around the second stage juveniles in the upper root layers (epidermis and cortex), preventing many of the juveniles from reaching their feeding site on the vascular cylinder and continuing their life cycle and reproducing. This gene is weakened because it is introgressed by backcross in a highly susceptible genetic background, which favours the development of RKN when submitted to a high-inoculation pressure (Barbary et al., 2014). At the 'Alénya' site, the *P. nanus* populations strongly decreased during the R-pepper crop, whereas this crop was installed during a hot period. Therefore, it is hypothesized that either *Capsicum annuum* sweet pepper is not a good host plant for *P. nanus*, or that the *Me-3* gene may have some effect on the reproduction of a nematode species other than RKN. The Telotylenchidae populations were either reduced ('Lambesc' 2013 and 'Alénya' 2014) or enhanced ('Lambesc' 2015), meaning that population dynamics would be under outer drivers (soil, climate, etc.) and then that this pepper is probably also a host plant for this nematode family (Santos et al., 2005).

4.3. Response of PPN populations to sorghum

RKN populations were significantly reduced by the sorghum hybrid '270911'. *P. nanus* was also reduced but to a lesser extent, despite the fact that sorghum is a good host for Paratylenchidae (Siddiqi et al., 1993). On the other hand, Telotylenchidae populations reproduced at both experimental sites. Sorghum is a good host for *Tylenchorhynchus* species (Fraedrich et al., 2012). However, this nematicidal hybrid did not affect them. It is therefore surprising that the three nematode families did not react in the same way to sorghum '270911'. The same observations were previously made with other sorghum varieties: in PPN communities, ring (*Mesocriconema* spp.) and lesion (*Pratylenchus* spp.) nematodes multiplied, whereas root-knot nematodes (*M. incognita*) were controlled (Bhan et al., 2010); Sudan grass growth was reduced by *B. longicaudatus,* whereas the abundance of *M. incognita* was kept constant (Crow et al., 2001). Considering that no PPN species should be immune to the HCN released after burial of Sudan grass, it was postulated (i) that HCN activity would be very short-lived, or (ii) that HCN would not be uniformly distributed in roots and soil (McGuidwin and Layne, 1995). We suspect that the effectiveness of the sorghum ‘270911’ depends on the parasitic behaviour of each nematode group. Second-stage *Meloidogyne* juveniles are free in the soil, but they immediately infest roots after hatching, and the next stages concerning the females are endoparasite and sedentary. *Paratylenchus* species are ectoparasites, but they become sedentary when feeding on cortical root cells with their long stylet. Telotylenchidae are ectoparasites, feeding on epidermal cells and root hairs. Thus, since only the species exhibiting a sedentary behaviour (RKN and *Paratylenchus*) were reduced with sorghum ‘270911’ and not the free species in the soil (*T. clarus*), we hypothesize that the deep feeding of sedentary species in toxic roots of living sorghum plants would be more efficient than the toxicity on the nematode free-living stages of the HCN released in the soil after sorghum incorporation. This hypothesis is supported by another experiment done at ‘Lambesc’ and ‘Alenya’ with the Sudan grass ‘Piper’, commonly used as green manure in France and with low leaf dhurrin content (compared to root content), thus less HCN release. The same results as those obtained with sorghum ‘270911’ were described in the field, and an additional experiment in controlled conditions showed that both sorghums were very poor RKN hosts, not supporting reproduction of RKNs (Djian-Caporalino et al., 2019).

4.4. Competitive interactions

Consequently, the response of the different PPN towards the practices introduced into complex vegetable cropping systems depends on their species diversity, but the plant-nematode interaction is not the only interaction involved. Indeed, as an example, the Telotylenchidae populations once increased and again decreased on the same crop (e.g., on lettuce and R-pepper) while the soil sample replicates were removed from the same core places avoiding possible bias due to the aggregated distribution of PPN. This probably means that other interactions occurred, such as PPN-PPN competition. It is known that the intensity of interspecific competition is directly related to the overlap level of the ecological niches of species (Pianka, 1978). We observed that Paratylenchidae populations were not able to develop when Meloidogynidae were present, as observed at the ‘Lambesc’ site. In this case, the almost total exclusion of *P. nanus* would be due to RKN juveniles, perhaps because they occupy the same cortical parenchyma niche, at least temporarily, either by moving between cortical cells before reaching their feeding site on the vascular cylinder (for RKN) or by feeding on the cortical cells (for *P. nanus*). Moreover, the strong opposition between Telotylenchidae and either Meloidogynidae (‘Lambesc’ site) or Paratylenchidae (‘Alénya’ site) revealed by PCA and time regression analyses confirmed competition in PPN communities. However, the competition differed according to the species involved. At the ‘Lambesc’ site, the cropping system that is targeted for controlling Meloidogynidae led to the long-term replacement of RKN by Telotylenchidae. This would mean that when a crop succession is susceptible to RKN, the Telotylenchidae are excluded by competition. On the contrary, in a crop sequence that reduces Meloidogynidae, the competition is lessened in favour of the Telotylenchidae. Thus, the replacement of Meloidogynidae by Telotylenchidae would be due to the long-term control of the Meloidogynidae. At the ‘Alénya’ site, the competition between Paratylenchidae and Telotylenchidae seems to be more cyclic with a long-term increase of both PPN families, meaning less dependence on the cropping system. The cyclic competition between Paratylenchidae and Telotylenchidae would be due to their ectoparasitic behaviour (i.e., competition for root surface). It seems that competition between Telotylenchidae and RKN, on one hand, and Telotylenchidae and Paratylenchidae, on the other, would correspond to hierarchic and cyclic models, respectively (Daly et al., 2015). Nevertheless, more research should be conducted in order to (i) understand how competition occurs between PPN species and contributes in up and down kinetics (microcosm experiments), and (ii) predict how changing cropping practices would regulate PPN diversity with competition (Groselj et al., 2015).

5. Conclusion

From an agronomic point of view, these competitive interactions raise the question of the risk due to a residual PPN community, once a target species (e.g., RKN) is controlled (Ferris et al., 2004; De Araujo Filho et al., 2016). Even if some cropping strategies have been shown to control RKN populations, Paratylenchidae and Telotylenchidae are known to be pathogenic on vegetables (Khan et al., 1986; Potter and Olthof, 1993). In these experiments, the replacement of RKN by Telotylenchidae nematodes and the extensive development of Paratylenchidae nematodes raise questions about the sustainable reduction of the global pathogenicity of the PPN community. It is therefore necessary to reconsider long-term unfailing soil suppressiveness strategies such as managing the diversity of the PPN communities rather than focusing on controlling targeted species. This requires a more holistic approach associating several scientific disciplines such as soil ecology, nematology, breeding and agronomy.

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Legends for figures and tables

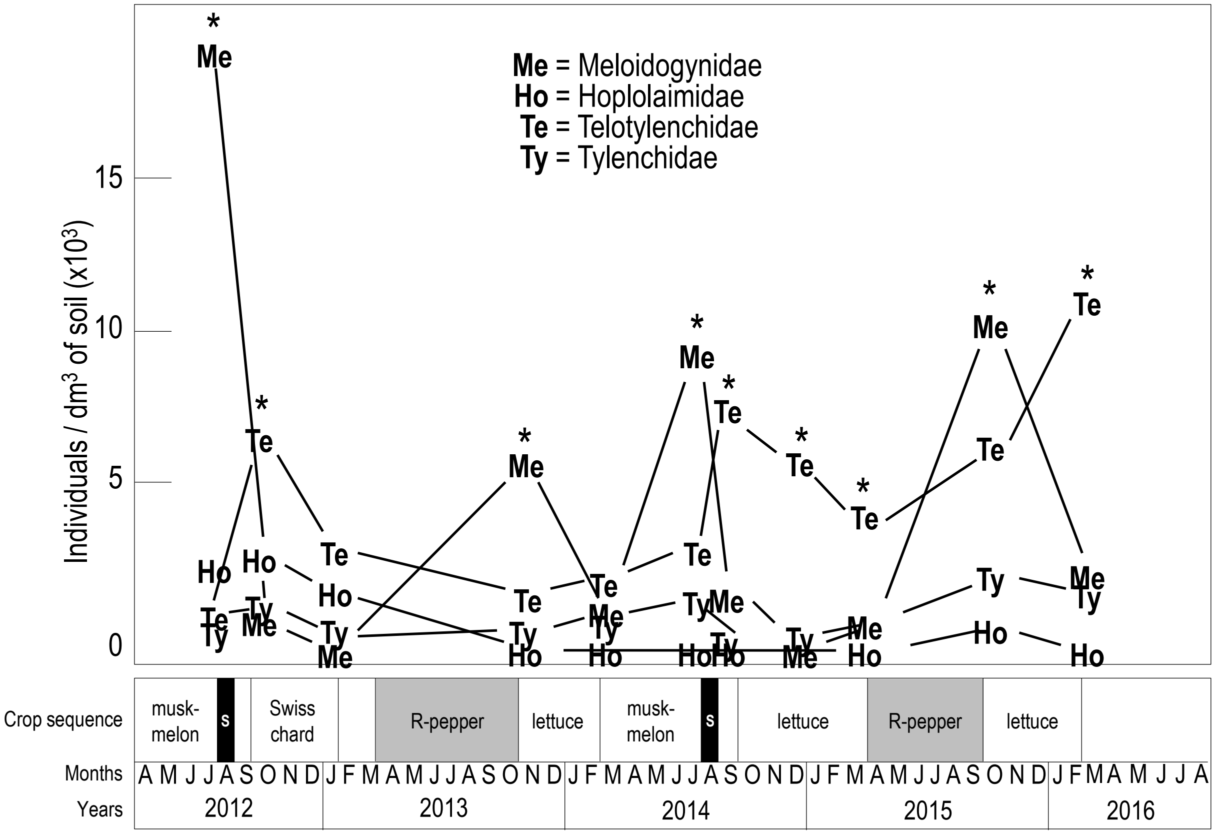
Figure 1. Kinetics of plant-parasitic nematode populations all along the cropping schedule assayed at the 'Lambesc' site. S = nematicidal *Sorghum* hybrid '270911'; R pepper = *Capsicum annuum* rootstock *Me3* DLL. Unnamed periods = bare periods. Stars indicate significant differences between population levels at each sampling date ($P<0.05$).

Figure 2. Kinetics of plant-parasitic nematode populations all along the cropping schedule assayed at the 'Alénya' site. S = nematicidal *Sorghum* hybrid '270911'; R pepper = *Capsicum annuum* rootstock *Me3* DLL. Unnamed periods = bare periods. Stars indicate significant differences between population levels at each sampling date ($P<0.05$).

Figure 3. Covariation among taxa in plant-parasitic nematode communities at the 'Lambesc' (A) and 'Alénya' (B) sites. Normalized PCA loading plot of the plant-parasitic nematode families (Ho = Hoplolaimidae; Me = Meloidogynidae; Pa = Paratylenchidae; Te = Telotylenchidae; Ty = Tylenchidae).

Figure 4. Covariation among taxa in plant-parasitic nematode communities at the 'Lambesc' (A) and 'Alénya' (B) sites. Time regression between nematode families (1 to 11 = sampling dates; dotted lines = tendency line).

Figure 1



Me = Meloidogynidae
Ho = Hoplolaimidae
Te = Telotylenchidae
Ty = Tylenchidae
Individuals / dm^3 of soil (x10^3)
0
5
10
15
Crop sequence
musk-melon
s
Swiss chard
R-pepper
lettuce
musk-melon
s
lettuce
R-pepper
lettuce
Months
A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A
Years
2012
2013
2014
2015
2016

Figure 2

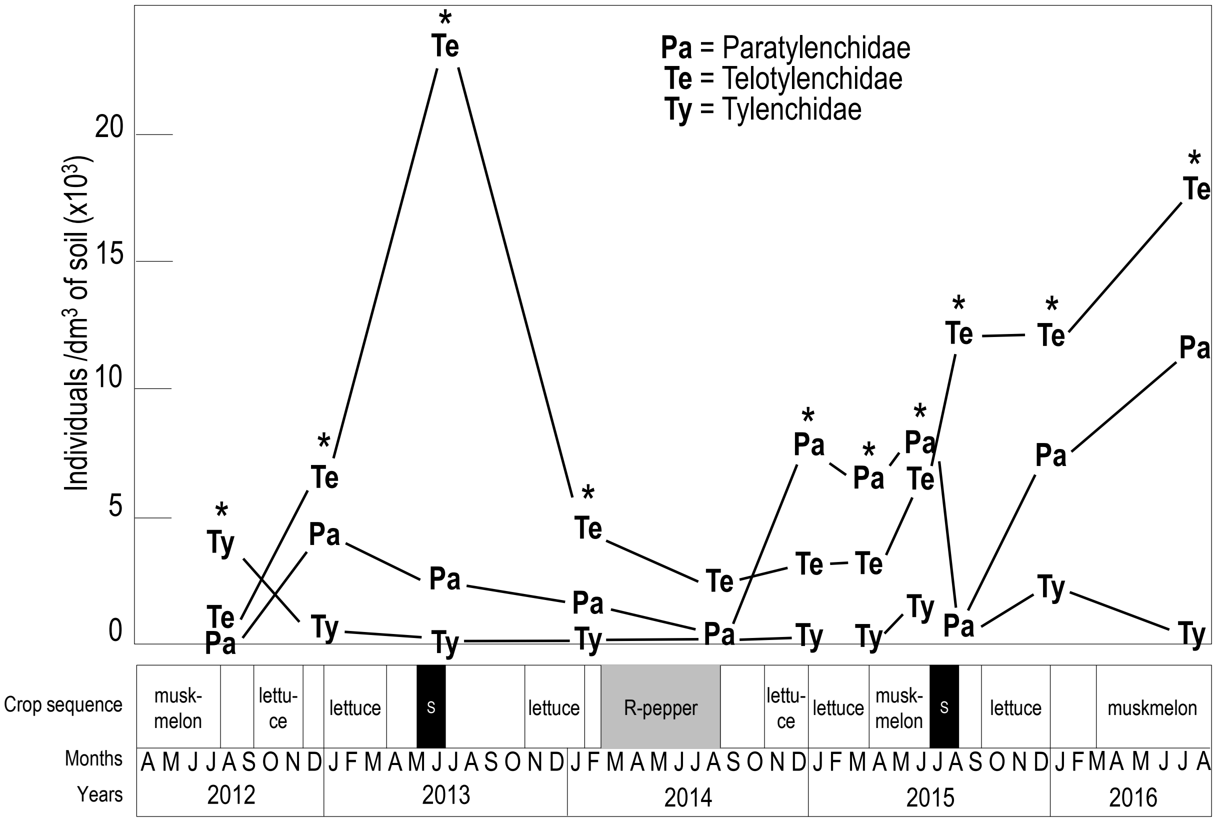

Pa = Paratylenchidae
Te = Telotylenchidae
Ty = Tylenchidae
Individuals /dm³ of soil (x10³)
0
5
10
15
20
Pa
Te
Ty
*
Crop sequence
musk-melon
lettu-ce
lettuce
S
lettuce
R-pepper
lettu-ce
lettuce
musk-melon
S
lettuce
muskmelon
Months
A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A
Years
2012
2013
2014
2015
2016

Figure 3

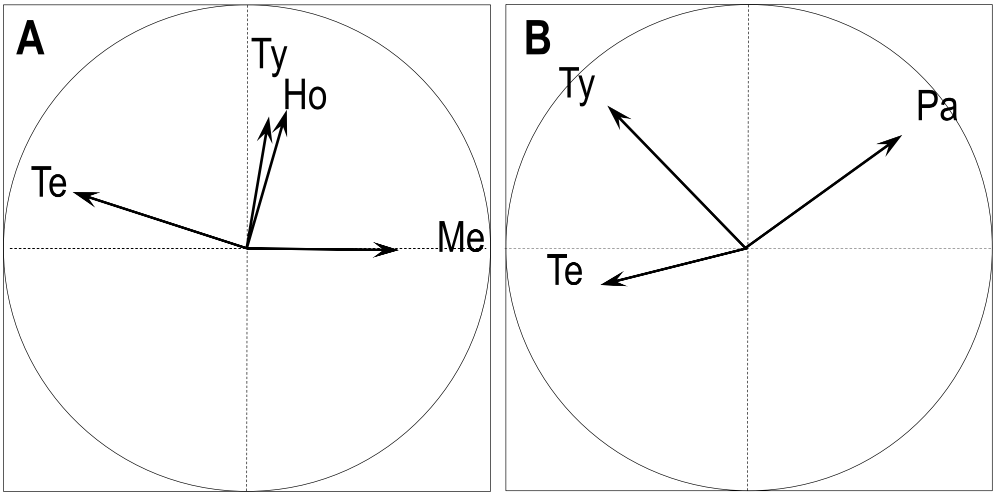
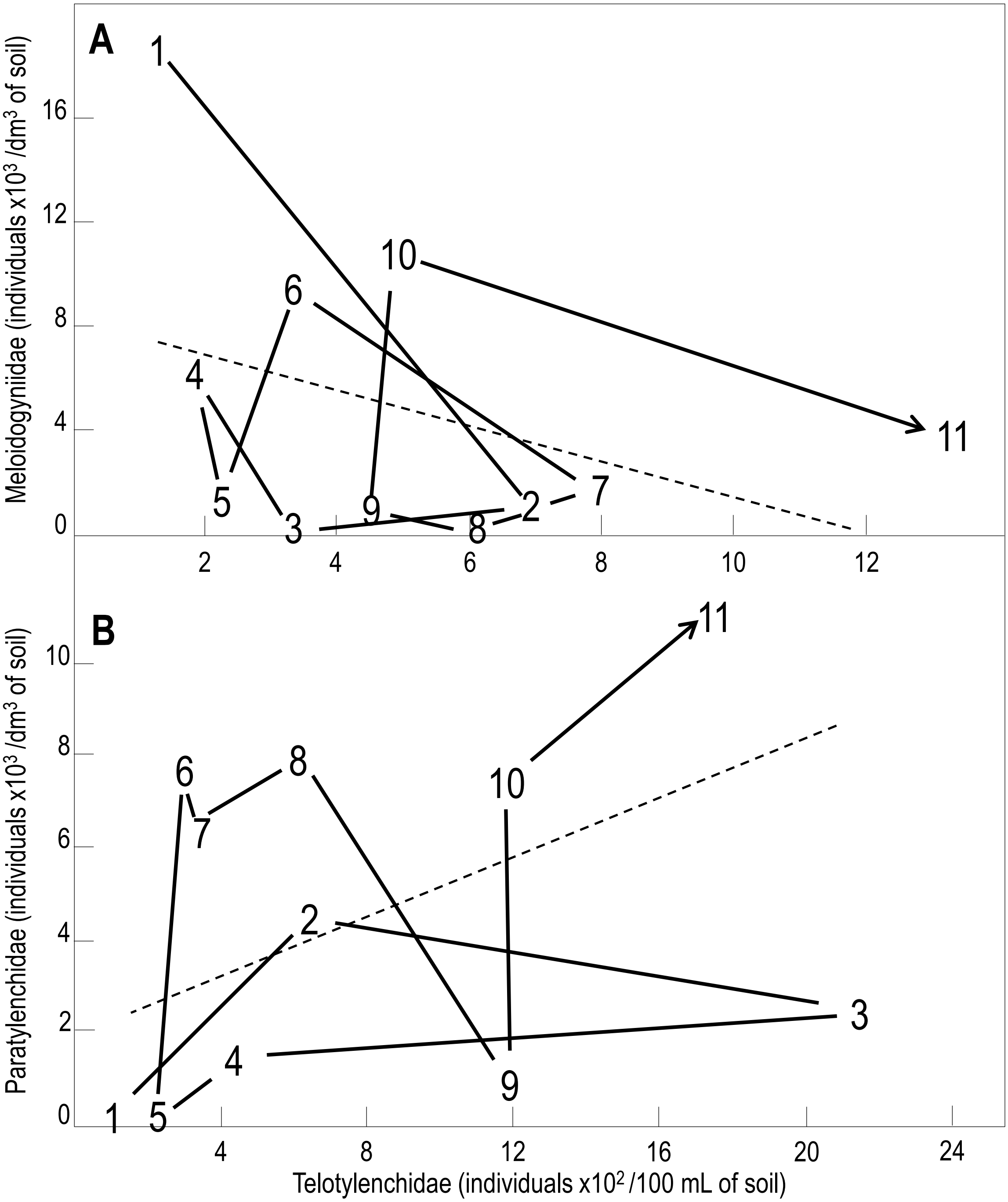


Figure 4


A
B
Meloidogyniidae (individuals x10^3 /dm^3 of soil)
Paratylenchidae (individuals x10^3 /dm^3 of soil)
Telotylenchidae (individuals x10^2 /100 mL of soil)
0
4
8
12
16
2
4
6
8
10
12
0
2
4
6
8
10
4
8
12
16
20
24
1
2
3
4
5
6
7
8
9
10
11