Applied Soil Ecology 49 (2011) 40–45

Contents lists available at ScienceDirect

Applied Soil Ecology

journal homepage: www.elsevier.com/locate/apsoil

Effect of banana crop mixtures on the plant-feeding nematode community

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ARTICLE INFO

Article history:
Received 19 May 2011
Received in revised form 5 July 2011
Accepted 7 July 2011

Keywords:
Community structure
Crop mixture
Nematode
Musa
Martinique
Radopholus similis

ABSTRACT

Varietal mixture is a cultural technique in which the genetic and functional diversities of varieties are used to manage pests and diseases. This strategy is commonly used on grass crops such as rice, barley, maize, and wheat to mitigate some windborne and soilborne pathogens. The effects of varietal mixtures on the number and community structure of pests, including plant-feeding nematodes (PFNs), however, have rarely been studied. In experiments conducted in Martinique, we evaluated the effect of varietal mixtures of bananas on PFN communities. A growth chamber experiment was used to measure the susceptibility of three banana cultivars dessert banana cv. 902 (*Musa* AAA, Cavendish subgroup); a new synthetic hybrid cv. FB924 (*Musa* AAA); and a plantain cv. Creole blanche (*Musa* AAB, French Horn) to the two major PFNs. The multiplication rates of *Radopholus similis* and *Pratylenchus coffeae* were substantially different on the three varieties; for example, the multiplication rate was up to 10 times greater on plantain cv. Creole blanche than on hybrid cv. FB924. In a field experiment, we planted the three varieties in pairs that included all six possible combinations. Banana varietal mixtures significantly affected both PFN densities and community composition. Differences in community composition among the pairs involved a shifting equilibrium among nematode species and an interspecific competition for food resources. The relative abundance of the spiral nematode *Helicotylenchus multicinctus* increased while that of the burrowing nematode *R. similis*, which is the most damaging species on bananas, decreased. The use of a varietal mixture in which one variety supports a low PFN multiplication rate appears to have practical relevance, especially in systems based on very susceptible cultivars such as plantains. The use of varietal mixtures should not create management problems, especially for plantations that produce bananas for local markets.

1. Introduction

Genetic uniformity of monocultures is well known to predispose crops to outbreaks of plant diseases and pests (Meung et al., 2003). Because the introduction of plant diversity increases the number of individual functional traits and potential ecosystem services (Hajjar et al., 2008; Malezieux et al., 2009), an agroecological strategy for disease control is to grow a mixture of plants differing in their susceptibility to pathogens (Smithson and Lenné, 1996; Wolfe, 1985). This strategy, which has mainly been used to control fungal diseases on grain crops, is promising because varieties are well selected toward complementary functional traits (Mundt, 2002). Effective disease management based on plant diversity requires that the mixed plants have complementary levels of resistance/susceptibility. Varietal mixtures can reduce pathogen selective pressure providing hosts that differ in their sensitivity and comprise variable sources resistance. Varietal mixtures have been used to suppress rice blast (Wolfe, 2000), powdery mildew of barley and wheat, and rust on barley, wheat, maize, and common bean (Smithson and Lenné, 1996).

The effect of varietal mixtures have been rarely studied on pests, including plant-feeding nematode (PFN), for which only one study investigate this effect on sugarcane (Cadet et al., 2007). Nematodes are one of the most damaging pests of bananas and plantains, which are mostly cultivated in intensive monocultures (Quénéhervé, 2009). Because communities of PFNs in banana agroecosystems are structured by host plants (Duyck et al., 2009; Quénéhervé et al., 2006b), a mixture of banana cultivars could alter the structure of

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doi:10.1016/j.apsoil.2011.07.003

the nematode community, and not only act as a dilution process of the pest as for diseases.

In banana plantations, two species of PFNs are particularly prevalent and damaging: the burrowing nematode *Radopholus similis* Cobb and the lesion nematode *Pratylenchus coffeae* Zimmerman (Gowen et al., 2005). Both are migratory endoparasites that feed inside the root cells; they cause necrosis and lesions which may attract other opportunistic pathogens, reduce root biomass, and eventually cause the plants to topple over. While the burrowing nematode is mostly found in commercial plantations of Cavendish varieties, the lesion nematode *P. coffeae* is mostly associated with plantains (Quénéhervé et al., 2009b) or in cropping systems based on crop rotation with sugarcane (Tixier et al., 2006). Other harmful PFNs in banana plantations include the spiral nematode *Helicotylenchus multicinctus* Cobb, the root-knot nematode *Meloidogyne* spp., and the reniform nematode *Rotylenchulus reniformis* Linford and Oliveira. Bananas infected with PFN are less able to take up water and nutrients, resulting in stunting, delayed maturation, and reduced bunch size. The damage can vary from a slight lengthening of the vegetative period to the ultimate symptom of attack by lesion nematodes, which is the toppling over of banana plants. The effect of a community of PFN on crop damages depends on the geographical location (Quénéhervé, 2009).

As with the damage caused by any other pest or parasite, damage caused by PFNs depends on environmental conditions, susceptibility of the host, and pathogenicity of the nematode considered. In the last 50 years, nematologists have collected substantial data concerning these factors, and they have also studied a range of nematode management practices on bananas. Several complementary approaches are now used to reduce both nematode damage and nematicide applications in commercial banana plantations. These include the planting of clean seed material combined with crop rotation or fallowing; the planting of cover crops; and the use of resistant varieties (Chabrier and Queneherve, 2003). Nevertheless, PFNs remain a major pest problem for the cultivation of bananas worldwide (Quénéhervé, 2009). These pests are an important cause in the limitation of the production, both in export and local market systems, which represent 16 and 90 million tons of fruits per year, respectively. In export systems, the control of PFNs rely mainly on pesticides and rotations, while in smallholder systems the control is based on re-plantation of older and most damaged fields. Varietal mixtures represent a promising way to control PFNs in both export and smallholder systems. The organization of smallholder systems makes the use of varietal mixtures a relevant option because in these systems, fields usually encompass many cultivars of banana.

In this study, we evaluated how the PFN community is altered by varietal mixtures in banana plantations. First, we characterized under controlled conditions the multiplication rates of the burrowing nematode *R. similis* and the lesion nematode *P. coffeae* on three varieties of banana. In a field experiment, we then measured the effect of associating two varieties of banana on the PFN community. We measured the nematode densities and nematode composition for all the possible pairs of three varieties of banana. Finally, we discuss the applicability of using a mixture of varieties for cultivation of bananas for the local market and for export.

2. Materials and methods

2.1. Plant materials

We selected three cultivars of banana that are genetically distant from each other: the hybrid cv. FB924 (*Musa* AAA, a new synthetic hybrid from CIRAD, Centre de coopération internationale en recherche agronomique pour le Développement; A) was chosen for its resistance to nematodes (Quénéhervé et al., 2009a). The plantain cv. Creole blanche (*Musa* AAB, French Horn; B), and the dessert banana cv. 902 (*Musa* AAA, Cavendish subgroup; C) were chosen because they are the most prevalent plantains and dessert bananas cultivated in the French West Indies.

2.2. Growth chamber experiment

The screenings were conducted with an experiments in a growth chamber with controlled conditions. The complete screening method has been described (Quénéhervé et al., 2006a), and all cultivars were separately challenged with the burrowing nematode *R. similis* and the lesion nematode *P. coffeae*. The plant material was propagated on Murashige and Skoog (MS) medium, maintained in the dark in a cooled incubator at $22 \pm 0.5\,^{\circ}C$ and regenerated as needed in test tubes on modified MS medium including active charcoal in a culture incubator at $25 \pm 0.5\,^{\circ}C$ with continuous light for 6–8 weeks. Plantlets were then transferred to PVC culture tubes (4.5 cm in diameter; 17.5 cm in length), placed in a growth chamber ($24–28 \pm 1\,^{\circ}C$, with 14 h of light). The culture tubes were filled with steam-sterilized Andosol (1 h at $100\,^{\circ}C$; pH 6.2, organic matter content 7.3%, CEC 10.3 mequiv./100 g soil). Plants were watered every three days with a nutrient solution (Mairol® 14:12:15 + oligo-elements, GmbH & Co, Germany). In addition to three cultivars and two nematodes, the experiments also included three culture times (plants were destructively sampled 30, 45, and 60 days after they were inoculated with nematodes). The 18 treatment combinations (3 cultivars, 2 nematode species, and 3 culture times) were replicated 5 times. Both nematode species were originally isolated from banana plants in Martinique. *R. similis* was maintained on the susceptible banana cv. Grande Naine (*Musa* AAA, Cavendish subgroup), while *P. coffeae* was maintained on the susceptible plantain cv. Popoulou (*Musa* AAB). Nematodes were extracted from the roots in a mist chamber (Seinhorst, 1950) over a 48-h period to prepare the inoculum, which consisted of 400 females per plant for *R. similis* or *P. coffeae*. At each measure, 30, 45, and 60 days after inoculation with the nematodes, the entire root system was carefully collected and weighed separately before nematodes were extracted. All the roots were placed in a mist chamber for a 2-week period of extraction (Seinhorst, 1950). Nematodes were counted in a 5-ml aliquot of a homogenized suspension with a stereomicroscope and expressed as number of nematodes per gram of fresh roots. The multiplication rate was calculated as the ratio of the final nematode population divided by the inoculum.

2.3. Field experiment

The experiment was set up in October 2008 in an area previously occupied by a 6-year-old dessert banana plantation at the Rivière Lézarde research station in the centre of Martinique; the banana plants had been removed, and weeds invaded the area. The soil was a nitisol derived from volcanic ash (andesitic basalt) with 73% clay. This type of soil is mostly found in the lowlands in central Martinique. The experimental design was a randomized complete-block with 16 replicates or blocks. All blocks ($235.2\,m^2$ per block) consisted of six pairs of banana plants (AA, BB, CC, AB, BC, and AC). A pair of banana consist of two plants separated by 80 cm, this limited distance between plants facilitate their biological interactions. Pairs were planted 6-m apart from other pairs to avoid root interference between two distinct pairs. Irrigation and fertilization were conducted according to standard recommendations in dessert banana plantations (Lassoudière, 2007). All banana and plantain materials for planting originated from micropropagation, and they were therefore free of nematodes before planting.

Before the bananas were planted, the abundance of PFN in the soil was assessed at each location where banana pairs were

Table 1
Abundance of nematodes (mean ± SE) and relative abundance in the field experiment measured before planting (October 2008) in 96 soil samples.

Variable	*Radopholus similis*	*Helicotylenchus multicinctus*	*Rotylenchulus reniformis*	*Hoplolaimus seinhorsti*
Nematode abundance (number per 250 cm^3 of soil)	8 ± 2	29 ± 6	3605 ± 287	11 ± 3
Relative abundance (%)	0.20%	0.80%	98.70%	0.30%

planted. Nematodes were extracted from 96 soil samples (six per block) by elutriation (Seinhorst, 1962). The PFN community in the experimental plot comprised the five most common species in the banana–nematode complex (Table 1). Reniform nematodes *R. reniformis* were most abundant and represented 98.7% of the PFNs. Other, less abundant species included spiral nematodes *H. multicinctus* (0.8%), lance nematodes *Hoplolaimus seinhorsti* (0.3%), burrowing nematodes *R. similis* (0.2%), and a few barely detectable *P. coffeae*. This PFN specific composition is usually found in banana monoculture. For each species of PFN, we calculated their relative abundance that is for a given species its proportion among the total PFN population.

The bananas were planted in October 2008, and banana roots were collected between banana pairs in February, June, and November 2009 and in July 2010. The banana root samples (about 500 g fresh mass per sample) were washed, sliced, and homogenized in the laboratory. A subsample of 50 g was placed in a mist chamber, and nematodes were collected for 2 weeks (Seinhorst, 1950). Nematodes were identified to species, counted, and expressed as the number of nematodes per gram of fresh roots.

2.4. Statistical analysis

For the growth chamber experiment, multiplication rates of nematodes were analysed using a generalized linear model (GLM) with Poisson error as a function of nematode species, culture time, banana cultivar, and interactions among these factors. For the field experiment, densities of the different nematode species were analysed by a GLM with Poisson error as a function of time, nematode species, initial abundance of nematodes in soil, and genotypes of banana pairs. We used standard model simplification procedures to eliminate non-significant terms of the model. The significance of each term was assessed through the change in deviance between models with and without that term. Overdispersion was accounted for using Quasi-Poisson instead of Poisson models in R (O'Hara and Kotze, 2010). We started from the most complex model (including all interactions and quadratic terms for continuous variables) and kept eliminating higher order terms as long as they remained insignificant (Crawley, 1993). All models were fitted using R (R Development Core Team, 2009).

3. Results

3.1. R. similis and P. coffeae multiplication rates in the growth chamber experiment

Multiplication rates of the nematode species differed among the three banana cultivars (ΔDev = 7111.9; df = 2, 96; $P < 0.001$). The multiplication rate on plantain cv. Creole blanche was significantly affected by nematode species (ΔDev = 1141.4; df = 1, 32; $P < 0.001$), culture time (ΔDev = 5365.5; df = 2, 30; $P < 0.001$), and the interaction between these two factors (ΔDev = 228.8; df = 2, 28; $P < 0.001$). In other words, nematode multiplications of *R. similis* and *P. coffeae* differed over time for this cultivar. The plantain cv. Creole blanche was significantly more susceptible to nematodes than the other varieties (Fig. 1). Sixty days after inoculation, the multiplication rate was 644 for *P. coffeae* and 187 for *R. similis*, and the plantain cv. Creole blanche was the only cultivar exhibiting a higher multiplication rate for *P. coffeae* than *R. similis* (Table 2).

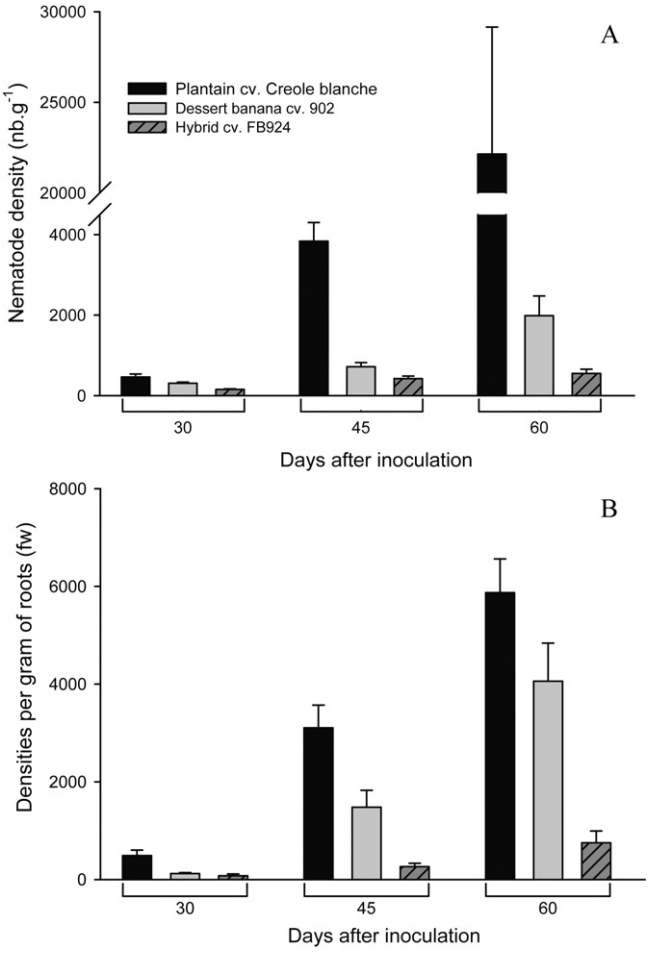

Fig. 1. Nematode densities (individuals per gram of fresh root, mean ± SE) of *R. similis* (A) and *P. coffeae* at 30, 45, and 60 days after inoculation for three banana cultivars in the growth chamber experiment.

On the dessert banana cv. 902, only culture time (ΔDev = 968.41; df = 2, 30; $P < 0.001$) and the nematode species (ΔDev = 124.81; df = 1, 32; $P < 0.001$) affected the final numbers of nematodes. The susceptibility of the dessert banana cv. 902 was intermediate for

Table 2
Fresh root weight (FRW) and multiplication rates (MR) of *R. similis* and *P. coffeae* at 30, 45, and 60 days after inoculation (DAI) for three banana cultivars in the growth chamber experiment.

DAI	*Radopholus similis*			*Pratylenchus coffeae*		
	30	45	60	30	45	60
FRW (g)						
A	10.7	15.4	14.9	11.3	13.6	14.1
B	9.9	11.9	14.5	8.3	11.8	12.9
C	8.2	9.7	11.7	7.7	9.3	11.0
MR						
A	1.3	5.6	17.8	2.8	8.7	14.0
B	11.8	94.5	187.2	11.1	132.1	643.6
C	2.2	42.1	113.8	6.7	18.7	60.9

With A the Hybrid cv. FB924, B the Plantain cv. Creole blanche, and C the Dessert banana cv. 902.

Table 3
Nematode densities (mean ± SE) and relative abundances in the field experiment measured 6 months after planting (February 2009) in 96 samples.

Variable	*Radopholus similis*	*Helicotylenchus multicinctus*	*Meloidogyne* spp.	*Rotylenchulus reniformis*	*Hoplolaimus seinhorsti*
Nematode density (numbers per gram of root)	21 ± 5	55 ± 13	11 ± 3	5 ± 1	0.3 ± 0.08
Relative abundance (%)	22.8%	59.4%	11.8%	5.7%	0.3%

both nematode species. The multiplication rate was 61 for *P. coffeae* and 114 for *R. similis* (10.5 and 1.6 times less, respectively, than those on plantain cv. Creole blanche).

On the hybrid cv. FB924, only culture time significantly influenced nematode multiplication (ΔDev = 124.517; df = 2, 30; $P < 0.001$). Of the three cultivars, the hybrid cv. FB924 was the least susceptible to both nematode species. At the end of the experiment, there were 550 *P. coffeae* per gram of fresh roots, corresponding to a multiplication rate of 14, a rate that was 45 times lower than that with the plantain cv. Creole blanche.

3.2. PFN community composition and population dynamics in banana roots in the field experiment

Six months after planting (February 2009), six species of PFN were detected in root samples of all pairs of banana. The PFNs detected in the roots included four species identified in soil samples at planting (*R. reniformis*, *H. multicinctus*, *H. seinhorsti*, *R. similis*) and one species, *Meloidogyne* spp., that was not detected in the soil (Table 3). No *P. coffeae* was detected at the first sampling but a few individuals were detected in subsequent samples (data not shown). The community was dominated by *H. multicinctus* and *R. similis* (59.4% and 22.8%, respectively). Between February 2009 and July 2010, PFN densities increased sharply, and this increase was significantly associated with time after planting and nematode species (Table 4). The percentage of the field community represented by *H. multicinctus* increased from 58% in February 2009 to 83% in July 2010, while that represented by *R. similis* decreased from 22 to 13% for the same sample times. The densities of combined PFN increased with time from 92 per gram root at the first sampling to 648 per gram root at the final sampling.

3.3. Factors affecting the nematode community in the field experiment: banana genotype combinations and time

The genotypes of bananas had a major impact on the densities of nematodes (Table 4). The comparison of all possible pairs of banana varieties on *R. similis* and *H. multicinctus*, which are the two of the most damaging to roots, shows that numbers of these nematodes were increased by genotype B but decreased by genotype A (Fig. 2). PFN densities were highest with the BB pair (plantain cv. Creole blanche); almost 2 years after planting, PFN infestations on the BB pair had increased to 1081 nematodes per gram of fresh roots. When genotype B (plantain cv. Creole blanche) was associated with genotype A (hybrid cv. FB924) or C (dessert banana cv.

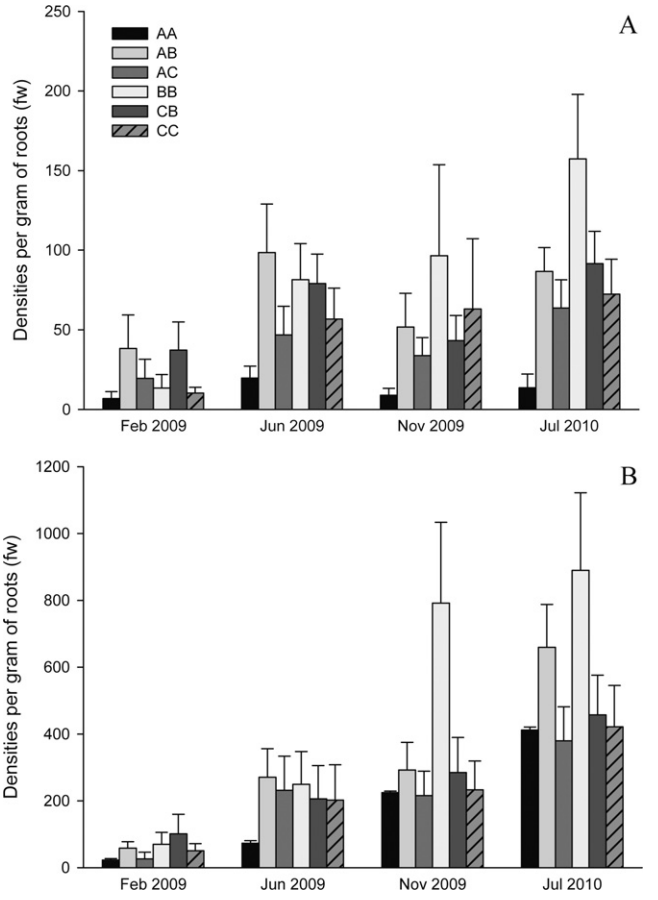

Fig. 2. Densities (mean ± standard errors) of *R. similis* and *H. multicinctus* in root samples from paired plantings as affected by sampling time and genotypes of the pairs. Species refer to nematode species, genotype pair refers to AA, BB, CC, AB, AC, and BC (with A the hybrid cv. FB924, B the plantain cv. Creole blanche, and C the dessert banana cv. 902).

Table 4
Results of the analysis of deviance on nematode densities in roots in the field experiment using a GLM with Quasi Poisson error.

Source of deviance	df	Residual df	Deviance	Residual deviance	*P*-value
Sample	1	2302	592 760	108	ns
Species	5	2297	286 918	305 841	<0.0001
Genotype pair	5	2292	272 877	14 041	<0.0001
Time	1	2291	230 565	42 312	<0.0001
Abundance in soil	1	2290	230 110	455	ns
Species × Genotype pair	25	2265	225 417	4693	ns
Species × Time	5	2260	220 001	5416	<0.0001
Species × Abundance in soil	4	2256	212 604	7397	<0.0001
Species × Genotype pair × Time	30	2226	210 029	2575	ns
Species × Time × Abundance in soil	5	2221	205 942	4087	<0.0001

df: degree of freedom.
Species refers to nematode species, Genotype pair refers to AA, BB, CC, AB, AC, and BC (with A the hybrid cv. FB924, B the plantain cv. Creole blanche, and C the dessert banana *cv.* 902).
Time refers to time of sampling.
Abundance in soil refers to the abundance of nematodes in soil at the start of the experiment.

902), the densities of PFN were lower (760 and 589 nematodes per gram of fresh root for AB and CB, respectively) than in the pure stand pairs (BB). The composition of the community was similar for BB and CB pairs and showed less *R. similis* infestation for AB combinations (11% opposite to 16% for BB combination). In contrast, the AA pair supported the lowest densities of *R. similis* and of all PFNs.

4. Discussion

The growth chamber experiment showed that, of the three varieties tested, the plantain cv. Creole blanche is by far the most susceptible to nematodes. The high multiplication rate for *P. coffeae* on this variety is consistent with the work of Speijer et al. (2001) and confirms that monoculture of this plantain cultivar (like monoculture of many other plantain cultivars) should lead to a fast increase of the most damaging PFN species and to the overall unsustainability of the cropping system (Coyne et al., 2005). The dessert banana cv. 902 showed an intermediate level of susceptibility for both inoculated nematode species, and the hybrid cv. FB924 showed the lowest level of susceptibility. These results confirm that the tested varieties have a wide range of multiplication rates for at least two damaging PFN species (Quénéhervé et al., 2009a,b).

At planting in the field experiment, the soil nematode community was dominated by the reniform nematode, *R. reniformis*, which was present in large numbers in all samples. Other nematode species, including *R. similis*, *H. multicinctus*, *H. seinhorsti*, and *P. coffeae*, were present but with irregular and sparse distributions. This diverse PFN community is typical of banana monoculture, i.e. when banana fields are replanted shortly after the previous banana crops have been destroyed. In our case, the experiment was started just after weeds invaded this old banana plantation. Weeds affect the structure of the PFN community (Duyck et al., 2009; Quénéhervé et al., 2006a). The six pairs of genotypes showed markedly different PFN communities and PFN densities at the end of the field experiment. The pairing of the plantain cv. Creole blanche with itself (BB) supported the highest numbers of PFNs, and the next highest numbers were supported by the pairing of plantain and the hybrid cv. FB924 (AB). In contrast, the pairing of Cavendish and hybrid cv. FB924 (AC) supported the lowest PFN densities. Comparison of these pairs indicates that the genotype of the plantain cv. Creole blanche is not only the most susceptible but is also the largest reservoir of PFNs. The pairing of the hybrid cv. FB924 with itself (AA) supported the lowest proportions and densities of *R. similis* throughout the experiment. Two years after planting, AA and BB exhibited the lowest and highest PFN densities, respectively. All other pairing had intermediate numbers of PFN. We can conclude that the depressive effect due to the most resistant variety of the pair is moderated. However, the pairing of the most susceptible variety with one of the other two varieties (pair AB or BC) appears to be sufficient to decrease the PFN densities to a level similar to the ones observed for pair CC, which supported an intermediate densities of PFNs. PFNs have different levels of pathogenicity and affect differently the growth of bananas. Although *H. multicinctus* was dominating the community, it is not the most damaging on banana (effect on bunch weight) as shown by Moens et al. (2006).

In contrast to Cadet et al. (2007), we show an effect of crop mixture not only on the PFN densities but also on PFN community structure. In our study, the changes in community composition among the genotype combinations mainly involve a balance between nematode species and interspecific competition for food resources. The use of mixtures caused the relative abundance of *H. multicinctus* to increase while that of *R. similis* to decrease slightly, which was consistent with results, obtained with new banana hybrids by Tixier et al. (2008). This can be explained by the differences in the PFN multiplication rates supported by the tested genotypes. The banana root dynamics can also alter the ratio of *H. multicinctus* to *R. similis*. Indeed, the proportion of old roots increased in older banana plants, which are a potential resource for *H. multicinctus* but not for *R. similis*, which prefer younger banana roots (Quénéhervé, 1990). This difference in resource preference probably contributed to the succession that we observed in the PFN community.

From a practical point of view, the introduction of hybrid FB924 in a former monoculture composed of plantain or Cavendish would be beneficial for PFN control. In addition, this hybrid is also resistant to black Sigatoka disease, e.g., the black Sigatoka caused by the fungus *Mycosphaerella fijiensis* (Abadie et al., 2009). Conversely, the introduction of dessert banana or plantain into a cropping system solely based on hybrid cv. FB924 would tend to dilute the existing resistance and therefore increase the global infestation of nematodes. The main reason for the limited use of varietal mixtures is that modern agriculture generally requires uniformity in cultural practices and harvest. In the case of banana, however, monocultivar plantations already contain unsynchronized populations of banana plants (Tixier et al., 2004), leading to heterogeneous cultural practices after only two cropping cycles. In such conditions, it seems possible that farmers would be able to manage a complex plant population that includes more than one cultivar. Because harvest of banana is always manual, it appears reasonable to organize separate harvests for two or more cultivars, which allow the targeting of different markets with fruits harvested within the same plot, e.g., local market and export. Such innovative systems are also important to address environmental and health issues (pesticide residues) that are particularly important when banana plant population is unsynchronized, as commonly found in smallholder plots (Tixier et al., 2007). For smallholders, the use of crop mixtures provides an interesting perspective, especially when no rotation, fallows, or chemical treatments are possible. Nevertheless, for being efficient, crop mixture systems need to include at least highly tolerant cultivar against the targeted pest. These systems may help to grow the most favourite cultivars in mitigated levels of pests. In production areas where other diseases are hampering the production of banana, the use of a varietal mixture (including tolerant varieties) may limit the risk of emergence of pesticide-resistant strains. Such strategies should be managed from the field scale to the landscape scale, as is the case with rice (Wolfe, 2000).

By altering the composition of the PFN community so that there is a reduced density of the most damaging species, varietal mixtures combining several resistances could be a useful strategy for improved management of PFNs on bananas. This strategy appears to be particularly appropriate with extremely susceptible cultivars of such plantains. In such systems, special attention has to be paid in the choice of varieties in the plant mixture in order not only to introduce genetic diversity but also to increase the functional diversity with respect to pest resistance (Mundt, 2002). Attention should also be paid to the spatio-temporal pattern of PFNs, especially on the capacity of varietal mixtures to suppress nematode dissemination. Recognizing the effect of varietal mixtures on multiple pests and diseases is also a key to the design of innovative and efficient cropping systems based on crop mixtures.

Acknowledgments

This work was supported by CIRAD and IRD funds, by the SYBAN project from the French Ministry of Ecology, Sustainable Development (grant CV070000779), and by the “sustainable cropping systems design” project from E.U. ERDF (grant PRESAGE 30411).

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