Soil Biology & Biochemistry 57 (2013) 173–181

Contents lists available at SciVerse ScienceDirect

Soil Biology & Biochemistry

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

Spatial stability of a plant-feeding nematode community in relation to macro-scale soil properties

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A R T I C L E   I N F O

Article history:
Received 2 May 2012
Received in revised form
12 June 2012
Accepted 29 June 2012
Available online 27 July 2012

Keywords:
Sugarcane
Nematodes
Soil relationships
Systematic sampling
Co-inertia
STATIS-Coa

A B S T R A C T

Understanding the spatial stability of the plant-feeding nematode (PFN) community in agrosystems represents a fundamental step in the integrated control of some damaging species because modifications of soil properties in intensively managed agrosystems may allow growers to manipulate the balance between pathogenic and non-pathogenic species.

In the present study, we tested the hypothesis that a community of four PFN species (*Criconemella onoensis*, *Helicotylenchus erythrinae*, *Hemicriconemoides cocophillus*, and *Pratylenchus zeae*) in a sugarcane agrosystem is spatially structured according to macro-scale soil properties. This hypothesis was studied by using a sugarcane field in Martinique in which soil properties had been heavily modified by hillock-leveling in the 1970s, resulting in a great variation in soil properties over a small area (20.8 × 16.0 m). The goal of the study was to measure the temporal stability of the PFN community spatial structure and to identify the soil parameters associated with differences in nematode abundance. A systematic sampling design was used to collect data in the field that were analyzed using co-inertia and STATIS-Coa. The field study was complemented by a greenhouse experiment.

The field study documented the existence of a stable spatial pattern of the PFN community, a pattern that was structured in relation to macro-scale soil factors such as soil carbon, nitrogen, and phosphorus content and soil texture. The constant spatial pattern of the PFN community results from the differences in distributions among *C. onoensis* and the three other PFN species. *C. onoensis* was consistently more abundant in the deeply-leveled areas of the field, while the other PFN species were more abundant in the non-leveled areas. *H. erythrinae* was consistently more abundant in those parts of the field with higher soil pH and sodium content. These results suggested that soil properties can affect permanently the competitive balance among PFN species.

The observed relationships between PFN and these macro-scale factors were validated in a greenhouse experiment with different ratios of soil from the leveled and non-leveled areas of the field site.

Modification of some major soil properties (pH, Na^{+} content, soil organic content) by cultural practices such as hillock-leveling, fertilization, and liming, could greatly affect the balance among PFN species in agricultural fields.

1. Introduction

One aim in terrestrial ecology is to understand the spatial relationships among soil organisms and biotic and abiotic factors (Decaëns, 2010). Among these soil organisms, nematodes constitute a particularly interesting group. On the one hand, some nematode species or populations patterns are accurate bio-indicators of soil properties or vegetation status (Bongers, 1990; Ettema and Bongers, 1993; Yeates, 2003; Neher, 2010). On the other hand, the knowledge of the spatial patterns of plant-feeding nematode (PFN) community can also be very useful in the design of integrated methods for managing a damaging species (Wyse-Pester et al., 2002; Monfort et al., 2007; Mueller et al., 2010).

During nematode surveys, these spatial patterns may or may not be noticed depending on the sampling scale. According to Ferris et al. (1990), spatial patterns of a nematode community can be influenced by two kinds of factors: (i) macro-scale factors, such as cultural history and environmental parameters (e.g., soil type, drainage, and soil moisture); and (ii) micro-scale factors, such as feeding strategies, life histories, and availability of the food resources. Ettema and Wardle (2002) proposed different scales for the study of a soil organism's

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http://dx.doi.org/10.1016/j.soilbio.2012.06.019

population and community ecology. Thus, the communities can be influenced by (a) fine-scale effects due to roots, organic particles, and soil structure; (b) plot-to-field-scale effects due to burrowing animals and plant communities; and (c) large-scale gradients of texture, soil carbon, topography, and vegetation systems. Competitive interactions are also known to play a role in the spatial distribution of soil organisms (Decaëns et al., 2008; Decaëns, 2010) while being less important for plant-feeding nematodes. Finally, all these factors will act simultaneously to determine the spatial patterns of soil nematode communities. Because of the effects of a variety of factors at a variety of scales, it is often difficult to identify the key factors (including plant host, climate, and soil properties) that determine the spatial distribution of soil nematodes.

Martinique Island may be especially useful for studying factors that affect soil nematode distribution. In sugarcane fields in Martinique, hillocks were leveled in the 1970s to facilitate mechanization. This cultural practice resulted in nearby areas having soils of different origin and with very different physico-chemical properties (Chevignard et al., 1987; Barret et al., 1991). Thus, these hillock-leveled sugarcane fields enabled us to study large-scale factors, in the sense of Ettema and Wardle (2002), at a small geographic scale and without the influence of different cropping histories, cultural practices, and climatic conditions.

The aims of this work were (i) to study the influence of such macro-scale soil properties on the PFN community in a sugarcane field, (ii) to test the hypothesis that spatial differences in a PFN community are temporally stable and are related to soil properties, and (iii) to validate the inferences generated by our field data with a controlled greenhouse experiment.

2. Materials and methods

2.1. Study site

A survey was conducted in a sugarcane field (*Saccharum officinarum* cultivar B-5992, 9th ratoon) that has been cultivated for more than 200 years at the Galion farm in northeastern Martinique (14°43′ N, 60°58′ W). The climate is subtropical with a mean temperature of 25.9 °C and a mean annual rainfall of 1929 mm for the last 40 years. The "rainy season" lasts from July to late December, and the "dry season" lasts from late December to late June. The soil is an Ultisol (ferrallitic soil) developed on volcanic rocks, and partial hillock-leveling was done in the 1970's. This Ultisol is characterized by a moderately acid pH and a cation exchange capacity ranging from 8 to 20 cmol kg^{-1}. After sugarcane mechanical harvest, an experimental area was selected that included different levels of hillock-leveling, based on the color of the outcropping layer (Munsell Code) as related to carbon content (Barret et al., 1991).

2.2. Data collection

Samples were collected systematically on a large rectangular grid (20.8 × 16.0 m) that included 14 sugarcane rows. Soil samples were collected at 1.6-m intervals at an equal distance between two sugarcane rows to reduce the effect of the plant row on nematode communities (Delaville et al., 1996). For each sampling date, 130 samples were collected with a 5.5-cm-diameter coring tool (volume = 237 cm^3) from 0 to 15 cm depth. Samples were collected every 3 months during 1 year corresponding to an entire sugarcane cycle (5 sampling dates from harvest to harvest). A total of 650 samples were collected. After plant-feeding nematodes were extracted from soil samples by elutriation–sieving (Seinhorst, 1962), they were identified to species and counted with a stereomicroscope. Nematode densities were expressed as numbers of individuals by 100 g of dry soil. Among the eight species of PFN observed, the following occurred infrequently and in small number and were not included in the statistical analysis: *Xiphinema setariae* Luc, 1958b; *Paratrichodorus anthurii* Baujard and Germani, 1985; *Paratylenchus elachistus* Steiner, 1949; and *Hoplolaimus seinhorsti* Luc, 1958a. The four species frequently found in the samples were *Criconemella onoensis* Luc and Raski, 1981; *Helicotylenchus erythrinae* Golden, 1956; *Hemicriconemoides cocophillus* Chitwood and Birchfield, 1957; and *Pratylenchus zeae* Graham, 1951. The first three are ectoparasites and the last one is an endoparasite.

In addition to being used for quantification of nematodes, some samples were used for quantification of soil properties. The 130 soil samples collected on the first date were also subjected to physico-chemical analyses as indicated in Table 1. The 130 samples collected on the last date were used to measure the density of sugarcane roots in soil. The roots were separated from soil by wet sieving and elutriation and then were dried at 60 °C for 48 h. The roots were divided into two classes based on diameters (class 1: 0.2 mm < Ø < 1 mm, class 2: Ø > 1 mm), and the mass of each was expressed as weight of dry roots per 100 g of dry soil. During the last sampling, we also recorded at each of the 130 sampling points data relative to sugarcane vegetative growth and yield at harvest, i.e., sugarcane stalk weight and stalk number per 1.6 m of row. The entire database comprised 3,740,726 PFN identifications and 3080 soil parameter measurements.

The data for soil parameters, nematodes, and vegetative growth are summarized in Table 1. To facilitate data analysis and presentation, we divided the sampling area into three zones corresponding to the intensity of hillock-leveling, which affects physico-chemical parameters of the soil according to previous studies (Chevignard et al., 1987; Barret et al., 1991). To classify the field into three zones (A, B, and C), we used a hierarchical agglomerative clustering method based on soil C content (Ward, 1963). Zone A was not leveled (C content > 2%), zone B was superficially leveled (1.4% < C content < 2%), and the zone C was deeply leveled (C content <1.4%).

2.3. Greenhouse study

The effect of soil parameters on changes in the sugarcane PFN community was studied under controlled conditions in a greenhouse. Sugarcane cuttings (*S. officinarum* cultivar B-5992) were collected in the study field and were grown for 1 month in steam-sterilized soil in a greenhouse. The 1-month-old sugarcane cuttings were then replanted into 2-L pots filled with six different non-sterilized soil mixtures (8 replicates) that were obtained by mixing various quantities of soil collected from zones A and C in the following ratios: 10A/0C, 8A/2C, 6A/4C, 4A/6C, 2A/8C, and 0A/10C. The daily average greenhouse temperature ranged between 25 and 30 °C, and the pots were watered every 24 h. During 1 year, one soil sample (250 cm^3) was collected every 2 months in each pot for nematode extractions (Seinhorst, 1962). After each sampling, an equal volume of steam-sterilized soil was added to each pot to maintain the initial soil volume. Data relative to sugarcane growth and physico-chemical parameters were measured after 12 months at the end of the experiment. The soil parameters measured were carbon (C) and nitrogen (N) content, C/N, exchangeable cation content (Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}), and CEC and saturation percentage.

2.4. Data analysis

We studied the temporal stability of the spatial patterns of PFN communities using a correspondence analysis version (Coa) of the multiway table method STATIS (Lavit et al., 1994). This STATIS-Coa version, which was proposed by Gaertner et al. (1998), is a useful tool for studying the stability of spatial patterns of faunistic communities and has mostly been applied in marine ecology