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Cover crops alter the soil nematode food web in banana agroecosystems

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A B S T R A C T

Cover crops are increasingly being used in agriculture, primarily for weed or erosion management. The addition of cover crops increases the primary productivity of the system and diversifies basal resources for higher trophic levels. How increases in the quality and quantity of basal resources affect bottom-up and top-down control remains a key question in soil food web ecology. We evaluated the response of the nematode community to the introduction of cover crops between rows of a banana plantation. We measured changes in nematode food web structure and inferred the prevalence of bottom-up and top-down effects on the abundance of phytophagous nematodes (i.e., plant-feeding and root-hair-feeding species) 1.5 years after plots with cover crops (Poaceae or Fabaceae species) or bare soil were established. The addition of a cover crop greatly affected the structure and the abundance of the soil nematode community 1.5 years after planting. The abundance of all trophic groups except for plant-feeding nematodes tended to increase with the addition of cover crops. The Shannon–Weaver diversity index and the enrichment index increased with the addition of cover crops, indicating that opportunistic, bacterivorous and fungivorous nematodes benefited from the added resources. Plant-feeding nematodes were least abundant in plots with Poaceae cover crops, while bacterivorous, omnivorous, and root-hair-feeding nematodes were more abundant with Fabaceae cover crops than with bare soil, indicating that cover crop identity or quality greatly affected soil food web structure. Bottom-up effects on all trophic groups other than plant-feeding nematodes were evident with Poaceae cover crops, suggesting an top-down control of plant-feeding nematodes by omnivorous nematodes. Conversely, plant-feeding nematodes were evidently not suppressed in Fabaceae cover crops, perhaps because bottom-up effects on omnivorous nematodes were weaker (hence, top-down control by omnivorous nematodes was weaker), and because Fabaceae cover crops probably served as good hosts for some plant-feeding nematodes.

1. Introduction

The enhancement of biodiversity in agricultural systems is receiving increasing attention because increased biodiversity is associated with pest suppression, reduced chemical inputs, and the closing of biogeochemical cycles (Altieri, 1999; Tilman et al., 2002). One practical way to enhance biodiversity is by the planting of cover crops (Teasdale, 1996), which are also frequently used for weed management (Moonen and Barberi, 2008). While cover crops directly provide several services, e.g., they reduce soil erosion (Derpsch et al., 1986), increase soil carbon and nitrogen content, and increase microbial activity (Ramos et al., 2010), they also have the potential to decrease the use of chemical pesticides by promoting natural enemies. Adding a cover crop typically increases the quantity of primary resource for herbivorous species and therefore for the predators that consume herbivores. One risk of adding cover plants in agroecosystems is that this new resource may increase the numbers of one or more herbivorous pest species to damaging levels. However, when the entire community, including predators and other species that suppress herbivorous populations, benefits from this new resource and their numbers are increased, peaks in pest populations may be controlled by top-down effects (Chen and Wise, 1999). Cover crops can also directly affect pests through chemical components; exudates from *Tagetes* spp., for example, suppress plant-parasitic nematodes (Hooks et al., 2010). Cover crops should be selected that do not aggressively compete with the cultivated plant for resources (Tixier et al., 2011) and that do not increase populations of the pests including those of plant-feeding nematodes.

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As noted, the addition of cover crops typically increases primary productivity of the system and diversifies the basal resources used by higher trophic levels. Theoretical approaches predict that ecosystems with high primary productivity should have food webs with greater structure and longer food chains than ecosystems with low productivity (Lindeman, 1942; Post, 2002). From a functional point of view, increasing the quantity and diversity of basal resources alters trophic links. A key question in food web ecology is whether food webs are bottom-up controlled, top-down controlled, or both (Bardgett and Wardle, 2010; Neher, 2010). Bottom-up effects are relatively straightforward; when a new resource is added, it can modify consumer populations at various levels of the food web (Birkhofer et al., 2008; Scherber et al., 2010; Aguilar-Fenollosa et al., 2011). In contrast, responses of top-down effects to basal resources can be complex. Addition of a basal resource may enhance top-down effects by supporting longer food chains, e.g., by supporting an increased abundance of predators that can control plant-feeding species (including plant-parasitic and root-hair-feeders), or by modifying food web structure, e.g., by providing alternative prey that increase predator abundance (Wise et al., 2006; Barberi et al., 2010). In this paper, we investigated how bottom-up and top-down effects on herbivores (plant-parasitic nematodes) are altered by addition of a basal resource (a cover crop) to an ecosystem.

Because of their relatively simple food webs, agroecosystems, including banana plantations, can be useful biological models for studying how the addition of a new basal food source affects top-down suppression of herbivores. Until now, most of the dessert bananas (*Musa* spp., AAA group, cv. Cavendish Grande Naine) grown for export, whether from Martinique or other countries, have been intensively cultivated in monocultures on bare soil. Several candidate species, which belong to the Fabaceae and Poaceae (legumes and true grasses, respectively), are being studied as cover crops in bananas (Blazy et al., 2009). The selection of the most appropriate species depends on their agronomical compatibility, e.g., how they compete with banana for resources and how well they control weeds (Tixier et al., 2011), and on their effect on pest populations. In most tropical countries including the entire Caribbean region, the most damaging pests in banana ecosystems are plant-parasitic nematodes (Quénéhervé, 2009). In Martinique, the nematode community parasitizing bananas comprises migratory endoparasites and sedentary endoparasites. The migratory endoparasites include the burrowing nematode *Radopholus similis* (Cobb, 1893) Thorne, 1949; the lesion nematode *Pratylenchus coffeae* Goodey, 1951; the spiral nematode *Helicotylenchus multicinctus* (Cobb, 1893) Sher, 1961; and the lance nematode *Hoplolaimus seinhorsti* Luc, 1958. The sedentary endoparasites include the root-knot nematodes *Meloidogyne* spp. and the reniform nematode *Rotylenchulus reniformis* Linford & Oliviera, 1940. By attacking primary and lateral roots, these plant-parasitic nematodes reduce plant nutrition, root anchorage, plantation life, and yield (Quénéhervé, 1993).

Although Duyck et al. (2011a) showed that the addition of a cover crop (signal grass, *Brachiaria decumbens*, Poaceae) alters the food web of macrofauna in soil litter and may help control the banana weevil, *Cosmopolites sordidus*, the impact of cover crops on the nematode community in banana plantations remains unclear. Cover crops can affect plant-parasitic nematodes by acting as a food resource (a bottom-up effect) and by enhancing predators of nematodes (a top-down effect). In addition to abiotic factors that structure the nematode community (Duyck et al., 2011b), the quality of the cover crop (species identity) can affect the entire soil food web. For example, the composition of the plant community affected the structure of a plant-feeding nematode community (Duyck et al., 2009), and complementarity in resource quality and the identity of plants explained the diversity of primary consumers and higher trophic groups (De Deyn et al., 2004).

Soil nematodes are important components of soil systems, and they have been widely used as indicators of soil food web structure and soil health (Bongers and Bongers, 1998; Ferris and Bongers, 2006). Soil nematodes include the following tropic groups: phytophages (plant-feeding and root-hair-feeding nematodes), bacterivores, fungivores, omnivores, and predators. Nematodes may be particularly relevant for the study of resource-driven effects on trophic composition because they are involved in an array of ecosystem functions: i) consumption of plants (by phytophagous nematodes), ii) decomposition and nutrient mineralization (by bacterivorous and fungivorous nematodes) (Djigal et al., 2010), and iii) control of plant-feeding nematodes (by predacious and omnivorous nematodes) (Yeates and Wardle, 1996). The relative proportions of nematode tropic groups have been used to generate enrichment and structure indices, which are indicators of soil health (Ferris et al., 2001; Pattison et al., 2008), and a maturity index, which is an indicator of system resilience (Bongers, 1990).

The objective of this study was to evaluate the response of the nematode community to the introduction of cover crops in banana plantations. We attempted to answer two questions: Is nematode food web structure differentially altered by the addition of different cover crops? Is the abundance of phytophageous nematodes more affected by bottom-up effects than top-down effects when a cover crop is added to the ecosystem?

2. Materials and methods

2.1. Site, experimental design, and treatments

The experiment was conducted in a banana plantation at the Rivière Lézarde CIRAD Research station in the center of Martinique (14°40′21.38″N; 60°59′50.07″W). The experimental site was a former banana plantation; after 1 year of fallow, a duration that is sufficient to considerably reduce the abundance of root-feeding nematodes (Chabrier et al., 2010), banana and cover crops were planted. The soil was a nitisol derived from volcanic ash (andesitic basalt) with 73% clay. This type of soil is characteristic of the lowlands in central Martinique. Before the start of the experiment, herbicides had been applied every 3 months during the fallow period but no nematicide or insecticide had been applied for at least 5 years. The experiment had six cover crop treatments. These included a control without cover crop, which was maintained by herbicide application every 2 months; a “spontaneous” cover crop (composed exclusively of Poaceae species that were not planted); and four cover crop that where planted. The cover crops planted were *Paspalum notatum* cv. Common, *Neonotonia wightii*, *Pueraria phaseoloides*, and *Stylosanthes guyanensis*. *P. notatum* is a perennial grass in the Poaceae, and the latter three cover crop species are legumes (Fabaceae). The experimental design included three replicates of the six treatments, giving 18 plots that were randomly distributed over the experimental field. Each plot occupied 75 m^2 and was separated from adjacent plots by a 2 m-wide alley.

2.2. Soil and root sampling

Soil samples were collected in October 2010 and February 2011 (16 and 20 months after the plots were established), corresponding to the rainy and dry season, respectively. From each of the 18 plots, four monoliths of soil ($25 \times 25 \times 15$ cm) were collected in the banana inter-row and mixed thoroughly to form a composite sample; banana roots were removed from soil and were analyzed separately. Thirty-six composite soil samples (two sampling dates) and 18 banana root samples (first sampling date) were collected.