



Short communication

Bottom-up control of fertilization on soil nematode communities differs between crop management regimes



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ABSTRACT

We evaluated how fertilization impacted nematode trophic groups via changes in trophic resources (soil microbes, plant roots) and the soil environment in a 3-year fertilization experiment in a double-cropped paddy rice and upland wheat agroecosystem. Fertilization exerted a strong influence on bacterial- and fungal-feeding nematodes by changing soil microbes and the soil environment in both phases, whereas plant- and root-associated fungal-feeding nematodes were bottom-up controlled by plant roots in the upland wheat phase only. Also, fertilization-induced linkages between bacteria phyla and bacterial-feeding nematode genera were inconsistent across crop phases. Although fertilization results in bottom-up control of nematode feeding groups in well-drained soils, our findings suggest environmental filtering due to water management and crop species can be responsible for the abundance of dominant nematode genera.

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Soil nematode community responses to fertilization are expected to be due to bottom-up control resulting from a change in food resources (Bardgett and Wardle, 2010). For example, organic fertilizers increase microbial abundance (Metting, 1992; Esperschütz et al., 2007), the food supply for microbial-feeding nematodes (i.e. bacterial-feeding, fungal-feeding and omnivorous nematodes). Fertilization also increases root biomass and rhizodeposition, which could be food resources for nematodes that feed directly on roots (plant-feeding nematodes), on the root-associated microorganisms (fungal-feeding nematodes) or on these trophic groups and plant-derived substrates (omnivorous nematodes) (Ge et al., 2015). Besides, fertilization-induced changes in physico-chemical properties such as soil pH and moisture content can act as environmental filters in modulating the soil nematode community, especially the abundance of microbial feeders (Chen et al., 2015).

The prey–predator relationship between bacteria and bacterial-feeding nematode is important because they are the most abundant and diverse microbe and microbial feeding groups in agroecosystems (Okada et al., 2011; Jiang et al., 2013). Since such

prey–predator relationships have mostly been studied in controlled experiments (Venette and Ferris, 1998; Carta, 2000; Djigal et al., 2004; Salinas et al., 2007), they may be valid for a limited number of specialist bacterial-feeding genera rather than generalist predators (Djigal et al., 2004). In agroecosystems, we postulate the prey–predator relationship should be responsive to fluctuations in field conditions and management regimes (e.g. soil moisture content, crop species).

To understand how fertilization impacts soil nematode communities through bottom-up control of food resources (soil microbes, plant roots) and environmental filtering by modulating the soil environment (moisture content and pH), we conducted a 3-year fertilization experiment in a double-cropped paddy rice (*Oryza sativa* L.) and upland wheat (*Triticum aestivum* L.) agroecosystem. We hypothesized that (i) fertilization will affect the abundance of microbial-feeding nematodes through bottom-up control (soil microbes) and environmental filtering (soil environment), whereas fertilizer greatly impacts the plant- and fungal-feeding nematodes through bottom-up control (plant roots), and (ii) the prey–predator relationships between bacterial phyla and bacterial-feeding nematode genera will differ among crop management regimes (i.e. paddy rice vs. upland wheat).

The fertilization experiment in Jiangsu Province, China (31°39'N, 119°28'E) was established in October 2010 as a completely randomized block experiment with six fertilizer treatments replicated

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four times (=24 plots). Fertilizer treatments were: (i) no fertilizer; (ii) chemical fertilizer; (iii) manure + chemical fertilizer; (iv) straw + chemical fertilizer; (v) manure + straw + chemical fertilizer; (vi) compound pig manure-chemical fertilizer. Details of the research site, experiment layout, crop rotations and fertilizer applications were reported by Liu et al. (2015) and Zhao et al. (2014).

Soil samples and plant roots were taken in summer (June 2013) after wheat harvest, and in winter (October 2013) after rice harvest. Eight soil cores (2.5 cm in diameter) were randomly collected at least 10 cm away from the taproot system from soil plough layer (0–10 cm) and divided into four subsamples to analysis soil properties (moisture content and pH), abundance of soil nematode feeding groups and genera (methods of analysis described by Liu et al., 2015), bacterial communities by 454 pyrosequencing (Zhao et al., 2014), and microbial communities by phospholipid fatty acid analysis (Buyer and Sasser, 2012). Sixteen plants per plot were excavated (20 cm depth) to evaluate root length, surface area and volume using a root scanner (EPSON expression 1640 XL, Japan), with root dry biomass, root carbon and nitrogen contents subsequently determined.

Structural equation modeling (SEM) was performed to analyze hypothetical pathways that may explain how fertilization impacted the soil nematode community (Grace, 2006). Prior to the SEM procedure, we performed Principal Component Analysis (PCA) using raw data on soil organic carbon, available nitrogen, phosphorus and potassium as soil nutrients that were influenced by fertilizer treatments (Veen et al., 2010). The most significant principal components were used in the subsequent SEM analysis to represent fertilization. The *a priori* model evaluated relationships among: soil microbes (bacteria, fungi, AM fungi and actinomycetes), plant roots (dry biomass, surface area, volume, carbon and nitrogen content), soil environment (moisture content and pH) and nematode communities at the trophic group level. Because the rice phase had a greater abundance of algae-feeding nematodes but wheat phase had higher abundance of bacterial-feeding nematodes, we used algae-feeding nematodes to perform SEM in the rice

phase, while bacterial-feeding nematodes were used in the SEM for the wheat phase. Linkages between the abundance of bacteria phyla and bacterial-feeding nematode genera were tested with SEM. The SEM was performed with the *lavaan* package (Rosseel, 2012) of R 3.0.0 programme (Team, 2014) using maximum likelihood estimation procedures. Model fit was assessed by a χ^2 -test, the comparative fit index and root square mean error of approximation.

Fertilization directly altered soil microbes, plant roots and soil environment, based on the significant standardized path coefficients (Fig. 1). Fungal-feeding nematodes were responsive to soil microbes and soil environment in both crop phases, with stronger associations in the wheat phase than in the rice phase (Fig. 1). Plant roots significantly affected the abundance of fungal-feeding, plant-feeding and omnivorous nematodes in the wheat phase only (Fig. 1). Bacterial-feeding nematode abundance was affected by soil environment, followed by soil microbes, in the wheat phase (Fig. 1B). The SEM models suggested that relationships between bacteria phyla and bacterial-feeding nematode genera were inconsistent in the two crop phases (Fig. 2). *Eucephalobus* correlated with most of the bacterial phyla in both phases, including *Acidobacteria* (subgroups 3, 4, 6 and 7), *Proteobacteria* (β , δ and γ) and *Chloroflexi*, while *Cephalobus* correlated with most bacterial phyla in wheat phase but correlated with few of them in rice phase (Fig. 2). *Panagrolaimus* correlated with many bacterial phyla in the wheat phase but only one group of bacteria in the rice phase, while *Tylopharynx* showed the opposite result (Fig. 2).

Hypothesis (i) was partially supported since microbial-feeding nematodes and omnivorous nematodes responded to the bottom-up control (change in soil microbes) and environmental filtering (change in soil environment) induced by fertilization. However, plant- and fungal-feeding nematodes had a stronger relationship with plant roots when fertilizer was applied to upland wheat than in the paddy rice phase. Upland wheat exhibits spatial heterogeneity between the root-associated and bulk soils, but paddy rice is more homogeneous due to the uniform soil moisture condition in

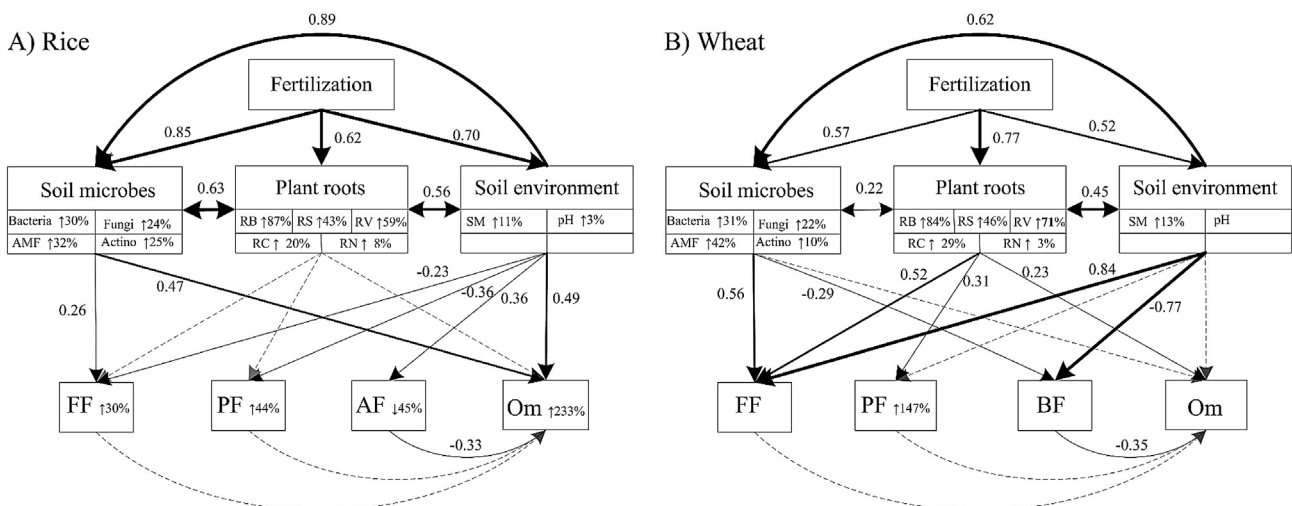


Fig. 1. Structural equation modeling (SEM) analysis of the fertilization effects on soil nematode communities as a result of fertilizer-induced changes in soil microbes, plant roots and the soil environment. Results of the optimal model fitting [A] Rice: Chi-square (χ^2) = 87.66, degree of freedom (df) = 54, comparative fit index (CFI) = 0.886, root square mean error of approximation (RMSEA) = 0.106; B) Wheat: Chi-square (χ^2) = 105.708, degree of freedom (df) = 54, comparative fit index (CFI) = 0.822, root square mean error of approximation (RMSEA) = 0.201. Square boxes denote variables included in the models. The following soil nematode trophic groups were analyzed: bacterial-feeding nematodes (BF), fungal-feeding nematodes (FF), plant-feeding nematodes (PF), algae-feeding nematodes (AF) and omnivorous nematodes (Om). Soil microbes include bacteria, fungi, arbuscular mycorrhizal fungi (AMF) and actinomycetes. Plant root variables include root dry biomass (RB), root surface area (RS), root volume (RV), root carbon content (RC) and root nitrogen content (RN). Soil environment variables include soil moisture (SM) and soil pH. Values (as a percentage) associated with symbols \uparrow or \downarrow within each box indicate an increase or decrease of the mean value in response to fertilization compared to the unfertilized control. Values associated with solid arrows represent standardized path coefficients. Solid arrows denote the directions and effects that were significant ($P < 0.05$) and the thickness represents the magnitude of the path coefficients. Dashed arrows represent the directions and effects that were non-significant ($P > 0.05$).

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