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Original article

Increase in soil nematode abundance due to fertilization was consistent across moisture regimes in a paddy rice–upland wheat system

Ting Liu [a, b], Joann K. Whalen [b, *], Qirong Shen [a], Huixin Li [a, **]

[a] College of Resources and Environmental Sciences, Nanjing Agricultural University, Nanjing, 210095, PR China
[b] Department of Natural Resource Sciences, McGill University, Montréal, Québec, H9X 3V9, Canada

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A B S T R A C T

Nematodes exert top-down control on the microbially-mediated processes of decomposition and nutrient cycling due to their position in the soil food web. Fertilization of agricultural soils can increase substrates for nematode populations, but whether the nematode community response to fertilization is consistent under anaerobic and aerobic soil conditions is not known. Our study investigated how soil nematode abundance and community structure responded to fertilization of a double-cropping system with paddy rice, representing anaerobic soil conditions due to flooding, followed an upland wheat phase that was rainfed and predominantly aerobic. We examined nematode communities twice a year from 2011 to 2013 at the ripening stage of rice (October) or wheat (June). Five fertilizer treatments were compared, including control (CK), chemical fertilizer (CF), compound pig manure-chemical fertilizer (MCF), straw plus chemical fertilizer (SCF) and pig manure plus straw plus chemical fertilizer (MSCF). Total nematode abundance increased by fertilization consistently in the rice and wheat cropping phases, and straw addition (i.e. SCF and MSCF) showed higher increment than manure addition (i.e. MCF) and CF treatments. However, dominant nematode genera respond to fertilization differently, depending on the crop phase. This is because dominant genera in the anaerobic soils of the rice phase were the plant-feeding nematode *Hirschmanniella* and algae-feeding nematode *Rhabdolaimus*, whereas dominant genera in the aerobic soils of the wheat phase were the fungal-feeding nematode *Filenchus* and bacterial-feeding nematodes *Cephalobus*, *Eucephalobus* and *Acrobeloides*. The manure addition (i.e. MCF) significantly raised *Hirschmanniella* abundance (by 133–616%) but sharply reduced the *Rhabdolaimus* population by 115–774% in the rice phase. In addition, straw addition (i.e. SCF and MSCF) increased *Filenchus* numbers (18–118%) but decreased the *Acrobeloides* population (49–145%) in the wheat phase. Since the MCF, SCF and MSCF fertilizers supply organic substrates for microbes and nutrients for plants, both of which are consumed by nematodes, this implies that food resources are the key determinant of total nematode abundance, the population size of all trophic levels. Our findings show that the nematode community structure is distinctive for each crop grown under a particular soil moisture regime, and that food resources derived from fertilizer inputs act as a bottom-up modulator of nematode population size in paddy rice–upland wheat systems.

1. Introduction

Occupying a central position in the soil food web, nematodes are considered an integrative bioindicator of soil ecological functions [1,2]. Nematodes modulate nutrient cycling and energy flow through the soil food web by feeding on plants and microbes, and are in turn consumed by predators from higher trophic groups (e.g. arthropods and earthworms). They respond positively when food resources are in greater supply, and larger population sizes are expected when nematode growth and reproduction are not limited by soil environmental conditions or biotic factors.

Agricultural soils possess ample food resources for nematodes,

* Corresponding author.
** Corresponding author.
E-mail addresses: joann.whalen@mcgill.ca (J.K. Whalen), huixinli@njau.edu.cn (H. Li).

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which may be enhanced by adding fertilizer. Organic fertilizers (e.g. animal manures, crop residuals, green manure and composts) not only supply nutrients for crop production and soil fertility improvement, but they also promote soil biodiversity [3,4]. However, the response of nematode trophic groups to organic fertilizers tends to be controlled by the quality of the organic material [5]. Swine manure addition significantly increased the plant-feeding nematodes compared to the control or crop residue amendment, whereas crop residue greatly raised the abundance of fungal-feeding nematodes [6]. Nematode populations are 30–120% larger when manure is applied because of the greater supply of organic matter for microbial growth than with chemical fertilizer [6–8]. Still, chemical fertilizers may promote total nematode abundance by 15–90% relative to control plots that receive no fertilizer, probably due to the beneficial effect of fertilizer on crop growth, leading to more rhizodeposits or residues that serve as substrates for microorganisms and nematodes [8]. Organic fertilizers are often combined with chemical fertilizers to enhance crop yield and improve soil quality [9], and this combination was found to significantly increase the abundance of soil microbes and nematodes that feed on microbes [6,7,10].

Fertilizers are necessary for profitable crop production, particularly in regions where two crops are grown per year on the same field. An example of this double-cropping system is an annual summer rice–winter wheat rotation, the dominant farming system on 60% of the paddy fields in southeast China [11]. During the year, the soil moisture regime shifts from anaerobic to aerobic, resulting in diverse soil food web structure in the rice and wheat phases [12,13]. During the rice growing season, the field is flooded and under anaerobic conditions for 3–4 months, then drained [14]. Under paddy rice, soil microbial communities are dominated by strictly anaerobic fungi, bacteria (e.g. *Colstridium* spp., *Streptococcus* spp., *Staphylococcus* spp.) and archaea (e.g. methanogens) [15]. Bacterial populations are generally larger than fungal populations, but the soil organic matter decomposition rate is slow due to the low oxygen content [16]. The nematode community will include species that prefer anaerobic environments such as the plant-feeding nematode *Hirschmanniella* [17]. In contrast, upland wheat is rainfed and soils drain between rainfall events, providing an aerobic environment that is suitable for the activity and growth of most bacteria and fungi, e.g. carbon mineralization was ~10 times faster under aerobic than anaerobic conditions [18]. This is expected to provide ample food resources for bacterial-feeding and fungal-feeding nematodes, including the fungal-feeding nematode *Filenchus* whose population was larger in soils having an elevated O_2 concentration, i.e., 200 ppm greater than the ambient O_2 level [17].

The objective of this study was to determine if the soil nematode community responded to fertilization consistently in both phases of a paddy rice–upland wheat system. We hypothesized that (1) more bacterial- and fungal-feeding nematodes will exist in the upland wheat phase than paddy rice phase, and (2) straw addition will support greater abundance of fungal-feeding nematodes, whereas manure addition will favor more plant-feeding nematodes. These hypothesis were evaluated for five fertilizer treatments during a three year period (2011–2013) in a paddy rice–upland wheat system in southeast China.

2. Materials and methods

2.1. Site and experimental design

We conducted the study at Jintan, Jiangsu Province, China (31°39′N, 119°28′E), where double-cropping of summer rice (*Oryza sativa* L.) and winter wheat (*Triticum aestivum* L.) is a common agricultural practice on 80% of farms. This region has a humid subtropical climate (Köppen climate classification) with average annual precipitation is of 1063.6 mm. The mean summer temperature of 25 °C, ranging from 18 to 30 °C, occurs during the rice growing season and the mean winter temperature during wheat growing season is 9 °C, with a range of 2–20 °C. Water regime management is obviously different between the two phases. During the rice growing season, the field is flooded and under anaerobic conditions for about 130 days, then drained for 5–10 days. The upland wheat planted in the same field is rainfed and under aerobic conditions during the wheat growing season (about 140 days). Soil in the experimental field is classified as clay loam texture (USDA soil classification). Initial soil analysis was 13.5 g organic C kg^{-1}, 1.6 g total N kg^{-1}, 18.0 mg available P kg^{-1}, 56.4 mg available K kg^{-1} and pH of 7.3.

The fertilization experiment was established in November 2010. We set up twenty plots (5m × 8 m per plot) and randomly assigned five fertilizer treatments in four blocks (=four replicates per treatment). Every plot was separated by 0.15 m concrete buffers on both sides and there was a 1.5 m lane between blocks. Five fertilization treatments were: no fertilizer (CK), chemical fertilizer (CF), compound pig manure-chemical fertilizer (MCF), straw + chemical fertilizer (SCF), and pig manure + straw + 50% chemical fertilizer (MSCF). The CF and SCF treatments received 240 kg N ha^{-1} from urea, 120 kg P_2O_5 ha^{-1} from triple superphosphate and 100 kg K_2O ha^{-1} from muriate of potash, while the MSCF treatment received 120 kg N ha^{-1} from urea, 60 kg P_2O_5 ha^{-1} from triple superphosphate and 50 kg K_2O ha^{-1} from muriate of potash, as summarized in Table 1. The compound fertilizer used for the MCF treatment contained 12.2% N, 2% P and 2% K with 16.1% organic matter and moisture content of 19.3%. As MCF was applied at a rate of 240 kg MCF ha^{-1} (wet weight basis), this resulted in an input of 27 kg N ha^{-1}, 10 kg P_2O_5 ha^{-1} and 5.2 kg K_2O ha^{-1} as well as 35 kg organic matter ha^{-1} (Table 1). Straw in the SCF and MSCF treatments either contained 0.63% N, 0.11% P, 0.85% K, 78.6% organic matter and 33.1% moisture when applied as 18 t rice straw ha^{-1} (wet weight basis) in the wheat phase, while wheat straw with 0.52% N, 0.11% P, 1.07% K, 82.6% organic matter and 30.7% moisture was applied at 11 t wheat straw ha^{-1} (wet weight basis) in the rice phase. Thus, the SCF and MSCF treatments received an additional NPK input of 76 kg N ha^{-1}, 30 kg P_2O_5 ha^{-1} and 123 kg K_2O ha^{-1} plus 943 kg organic matter ha^{-1} in the wheat phase, while received an additional NPK input of 40 kg N ha^{-1}, 19 kg P_2O_5 ha^{-1} and 98 kg K_2O ha^{-1} plus 628 kg organic matter ha^{-1} in the rice phase. In the MSCF treatment, pig manure containing 2.3% N, 1.3% P, 1.0% K and 45.4% organic matter with moisture content of 29.1% was applied at 400 kg pig manure ha^{-1} (wet weight basis). Thus, the MSCF treatment received an additional NPK input of 6.5 kg N ha^{-1}, 8.5 kg P_2O_5 ha^{-1} and 3.4 kg K_2O ha^{-1} plus 128.8 kg organic matter ha^{-1}. Total NPK fertilizer and organic matter inputs applied in two phases are summarized in Table 1.

Fertilizer treatments were applied in both rice and wheat growing seasons. The P_2O_5, K_2O, straw and pig manure were applied as basal fertilizers 3–5 d before planting summer rice in June (harvested in late October) and 3–5 d before planting winter wheat in November (harvested in late May). The total rice straw was returned to soil before planting wheat, while total wheat straw was returned to soil before planting rice. After broadcasting the basal fertilizers uniformly across the plot area, they were incorporated to a depth of 15–20 cm with a tilling machine within 24 h of application. The urea-N fertilizer application was split into three equal amounts and applied before planting (broadcast and incorporated with the basal fertilizers), at the tillering stage (broadcast uniformly across the plot area) and at the panicle stage (broadcast uniformly across the plot area).

Table 1
Application rate of NPK fertilizers and organic matter in fertilizer treatments spread on rice and wheat phases of a double-cropping system from 2011 to 2013.

Fertilizer		Rice phase (inputs in kg ha^{-1})				Wheat phase (inputs in kg ha^{-1})			
Treatment		N	P_2O_5	K_2O	Organic matter	N	P_2O_5	K_2O	Organic matter
CK	Organic	0	0	0	0	0	0	0	0
	Inorganic	0	0	0	0	0	0	0	0
CF	Organic	0	0	0	0	0	0	0	0
	Inorganic	240	120	100	0	240	120	100	0
MCF	Organic	27	10	5.2	35	27	10	5.2	35
	Inorganic	0	0	0	0	0	0	0	0
SCF	Organic	40	19	98	628	76	30	123	943
	Inorganic	240	120	100	0	240	120	100	0
MSCF	Organic	47	17	102	757	83	39	127	1072
	Inorganic	120	60	50	0	120	60	50	0

Fertilizer treatments were: CK, no fertilizer. CF, chemical fertilizer. MCF, compound pig manure-chemical fertilizer. SCF, straw + chemical fertilizer. MSCF, pig manure + straw +50% chemical fertilizer.

2.2. Soil sampling and analysis

We collected soil samples at the ripening stage of wheat (May) and rice (October) in 2011, 2012 and 2013. In each plot, eight soil cores (2.5 cm in diameter) from the soil plough layer (0–10 cm) were collected randomly at least 10 cm away from the taproot system and mixed together to generate one composite sample per plot. Samples were stored at 4 °C until nematode populations and soil properties were analyzed.

Soil nematodes were extracted from 50.0 g field-moist soil in three years (2011, 2012 and 2013) by a modified Baermann method [19]. After counting the total nematode abundance, about 150 specimens per sample were selected and identified to genera under an Olympus BX50 microscope at 400-1000 × magnification [20].

Soil properties were measured in 2012 only. This included measuring soil pH by a glass electrode in slurries (1:2.5 soil: deionized water) and gravimetric moisture content was determined by drying 10.0 g field-moist soil at 105 °C for 24 h. Organic C was measured by Walkley-Black procedure [21]. Total N and available N were measured using the semi-Kjeldahl method [22]. Microbial biomass C and microbial biomass N were determined using the chloroform-fumigation direct extraction method with correlation factors of $K_{EC} = 0.45$ [23] and $K_{EN} = 0.54$ [24]. The percentage of water-filled pore space (%WFPS) was calculated from the gravimetric moisture content and used as an indicator of the soil oxygen content [25].

2.3. Statistical analysis

Due to the difference in crop species, agronomic practices, soil moisture regimes and climate conditions during the rice and wheat phases, it is appropriate to analyze the effect of fertilization on soil nematode communities separately for each crop phase. To account for repeated fertilizer applications to the plots in 2011, 2012 and 2013, we used a repeated-measures (in time), one-way ANOVA to analyze the effect of fertilizer treatments on total nematode abundance and dominant nematode genera for the rice and wheat phases separately, after the assumption of normality and homogeneity of variance were tested by the Shapiro–Wilk test and Levene's test, respectively. Post-hoc comparisons between fertilizer treatments (between-subject effects) and of fertilizer treatment × year (within-subject effects) were evaluated with LSD test.

Since soil properties were measured in 2012 only, we used generalized canonical discriminant and correlation analyses (gCCA) with linear model (multiple response variables ~ year/fertilization) to visualize the relationships between soil properties and dominant nematode genera in the rice and wheat phases.

All statistics and figures were generated with R software version 3.0.1 [26]. The generalized linear-mixed model was conducted under the *lme4* package [27], and gCCA was performed under the *candisc* package [28].

3. Results

Total nematode abundance was affected significantly by fertilization in the rice phase ($F(4,8) = 14.2$, $P < 0.001$) and the wheat phase ($F(4,8) = 15.5$, $P < 0.001$) of the double-cropping system during the three years of this study (Fig. 1). MSCF treatment significantly ($P < 0.001$, LSD test) increased total nematode abundance compared to CF and CK treatments, which had 80–89% more in the rice phase and 28–250% more in the wheat phase than CF and CK treatments (Fig. 1). The SCF treatment also significantly ($P = 0.006$, LSD test) increased total nematode abundance by 5–80% in the rice phase and 14–186% in the wheat phase compared to CK treatment, except that there was no difference between SCF and CK treatments in the rice phase of 2011 and in the wheat phase of 2013 (Fig. 1). There was no difference in nematode abundance among MCF, CF and CK treatments, although there was greater nematode abundance in the MCF than CK plots in the wheat phase of 2012 ($P = 0.003$, LSD test).

We identified 48 nematode genera in this field (Table S1) and as expected, the dominant genera differed between the two crop

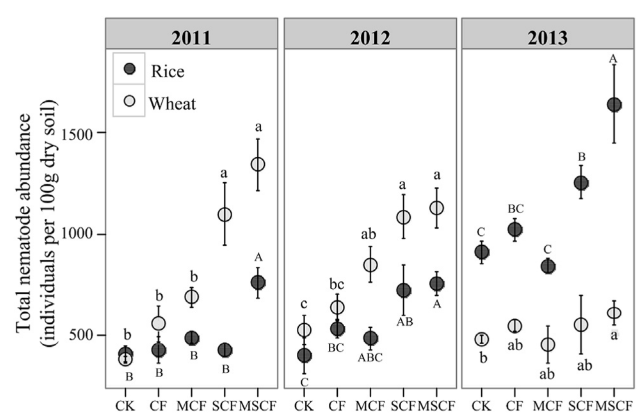

Fig. 1. Response of total nematode abundance to fertilization in rice and wheat phases of a double-cropping system from 2011 to 2013. Lowercase letters indicate significant ($P < 0.05$) difference among fertilizer treatments in the wheat phase, while uppercase letters indicate significant ($P < 0.05$) difference among fertilizer treatments in the rice phase. Fertilizer regimes on the x-axis were: CK, no fertilizer. CF, chemical fertilizer. MCF, compound pig manure-chemical fertilizer. SCF, straw + chemical fertilizer. MSCF, pig manure + straw +50% chemical fertilizer.

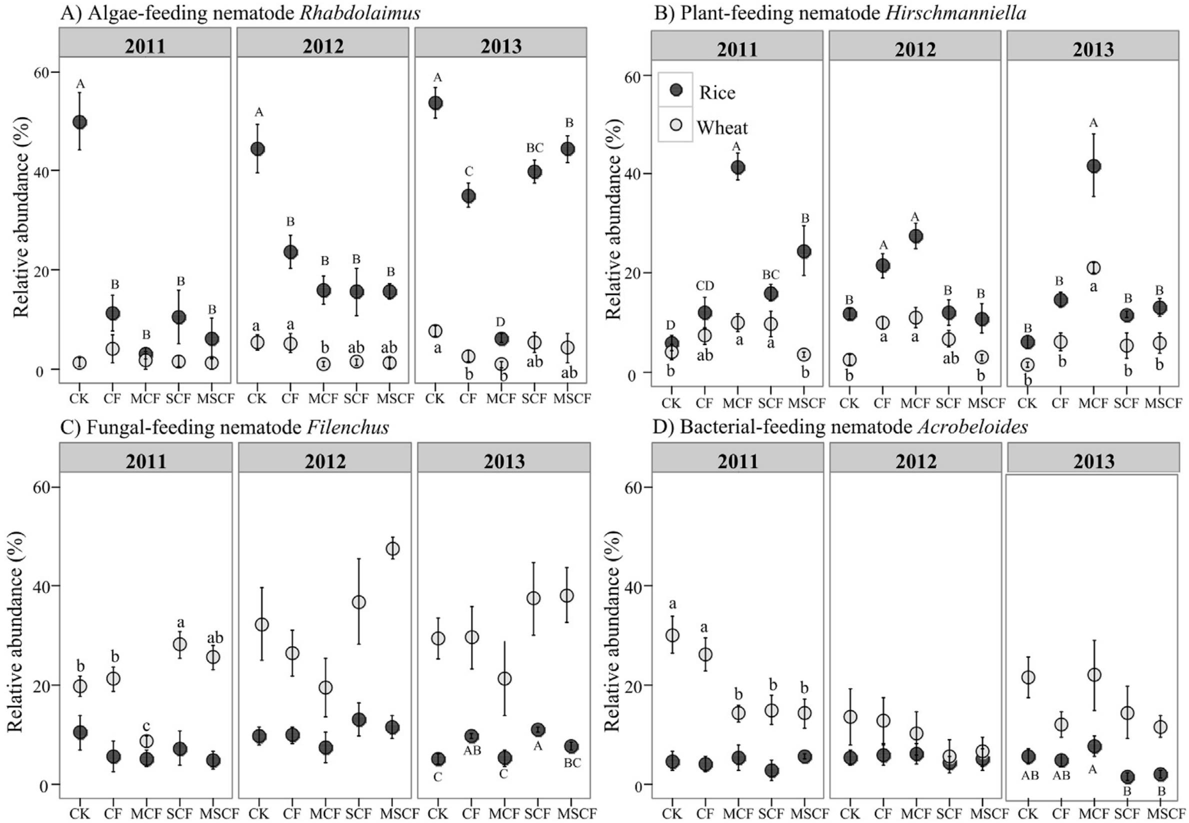

Fig. 2. Relative abundance of four dominant nematode genera in fertilizer treatments applied to a double-cropping system with rice and wheat production from 2011 to 2013. Lowercase letters indicate significant ($P < 0.05$) difference among fertilizer treatments in the wheat phase, while uppercase letters indicate significant ($P < 0.05$) difference among fertilizer treatments in the rice phase. Fertilizer regimes on the x-axis were defined in Fig. 1.

phases (Fig. 2 and Table S1). The algae-feeding nematode *Rhabdolaimus* (25%) and plant-feeding nematode *Hirschmanniella* (18%) were dominant in the rice phase, while fungal-feeding nematode *Filenchus* (28%) and bacterial-feeding nematodes *Acrobeloides* (15%), *Cephalobus* (12%) and *Eucephalobus* (13%) predominated in the wheat phase (Fig. 2 and Table S1). The four dominant genera were greatly influenced by fertilization ($F(4,8)$ values 2.2 to 16.2, P values 0.001 to 0.08). *Rhabdolaimus* populations were lower in fertilized treatments than the CK treatments; for example, there were fewer *Rhabdolaimus* in the MCF treatments than the CK treatments of the rice phase (115–774% reduction, $P = 0.001$, LSD test) and the wheat phase (30–786% reduction, $P = 0.017$, LSD test) (Fig. 2). There were more *Hirschmanniella* in fertilized treatments, which was notable when comparing the MCF and CK treatments in the rice phase (133–616% increment, $P < 0.001$, LSD test) and the wheat phase (136–353% increment, $P = 0.023$, LSD test) (Fig. 2). Compared to the CK treatments, the SCF and MSCF treatments increased the proportion of *Filenchus* by 30–43% in the rice phase and by 18–118% in the wheat phase (Fig. 2). However, the *Acrobeloides* abundance was lower in the SCF and MSCF treatments than the CK treatment, with 8–286% fewer in the rice phase and 49–145% fewer in the wheat phase (P values 0.04 and 0.07 respectively, LSD test) (Fig. 2).

A strong inverse relationship between *Rhabdolaimus* and *Hirschmanniella* associated with the rice phase and *Filenchus* in the wheat phase generated the first axis of the gCCA and accounted for 52% of the variance ($R^2 = 0.28–0.31$, $P < 0.001$) (Fig. 3). The *Rhabodolaimus* and *Hirschmanniella* vectors were parallel to the %WFPS vector, indicating that wetter soil conditions (e.g. anaerobic soils) were favorable to these genera. *Filenchus* was correlated positively with organic C, total N and microbial biomass N ($R^2 = 0.30–0.32$, $P < 0.001$).

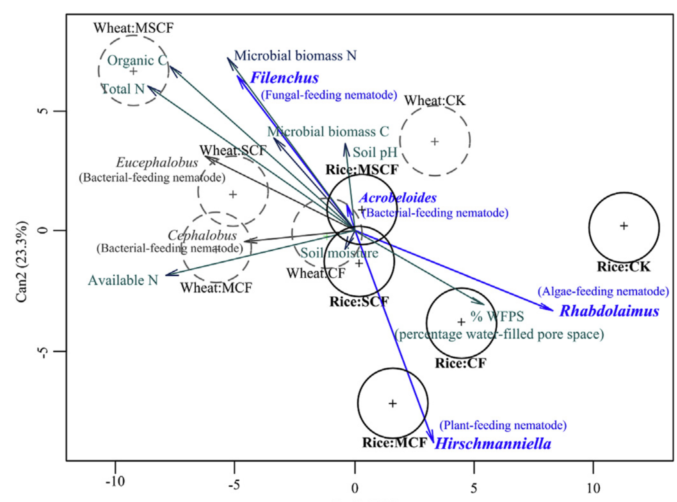

Fig. 3. Generalized canonical discriminant and analysis showing linkages among soil properties and dominant nematode genera in 2012. The broken lines at each site bound the 95% confidence interval around the site-treatment mean. Fertilizer regimes as described in Fig. 1.

4. Discussion

4.1. Dominant genera in the rice phase vs. wheat phase

Our findings show that more bacterial-feeding nematodes (e.g. *Cephalobus*, *Eucephalobus* and *Acrobeloides*) and fungal-feeding nematode *Filenchus* were observed in the upland wheat phase, while high abundance of plant-feeding nematode *Hirschmanniella* and algae-feeding nematode *Rhabdolaimus* predominated in the paddy rice phase. These results were consistent with our hypothesis (1) and suggested that water management regime is important in determining soil nematode community structure, for the aerobic environment of wheat phase is more suitable for the activity and growth of saprophytic bacteria and fungi than the anaerobic rice phase (see the PLFA results in Table S2). In part, this is due to the availability of food for each feeding group, but we cannot overlook the importance of environmental adaptation. Aerobic soil conditions were more suitable for the growth and reproduction of *Acrobeloides* and *Filenchus*, although they can tolerate the anaerobic habitat of paddy rice field for several months at a time [14]. In paddy rice fields, *Hirschmanniella* inhabits roots of rice and other submerged plants such as lotus and derives its nutrition from root biomass [29]. In our study, nearly 8% of *Hirschmanniella* found were observed in the wheat phase, indicating that roots of wheat and its relatives may serve as an alternative niche and food resource for *Hirschmanniella*. Thus, we suppose food specificity is not responsible for the predominance of *Hirschmanniella* in the rice phase, but rather this nematode was better adapted to flooded soils with low oxygen content. The fact that *Hirschmanniella* vector was parallel to the %WFPS vector in the gCCA analysis is an indication that soil moisture content could modulate the *Hirschmanniella* community. This speculation could be supported by Okada et al. [14], who studied soil nematode community under different water management regimes and reported that large numbers of *Hirschmanniella* in paddy rice field were replaced by other plant-feeding nematodes such as *Heterodera* and *Pratylenchus* in an upland rice field with the same rice cultivar.

4.2. Fertilizer effects on nematode abundance in rice and wheat phases

Fertilization had a positive effect on soil nematodes such that the total nematode abundance increased when a greater proportion of organic fertilizers (straw or straw and manure) were added, and this was consistent for the rice and wheat phases of the rotation. Total nematode abundance increased more with the SCF treatment than the CF treatment, and the increment was enhanced by pig manure addition in the MSCF treatment. This result indicated that organic materials such as crop straw and pig manure favored the growth of soil nematodes, especially fungal-feeding nematodes (e.g. *Filenchus*). Villenave et al. [6] also observed that organic fertilizer raised the population of bacterial- and fungal-feeding nematodes, and more fungal-feeding nematodes were detected in plots amended with straw than with manure. As we expected in hypothesis (2), straw inputs of supplied 0.6 to 0.9 t organic matter ha^{-1}, depending on whether wheat or rice straw was added, promoted the abundance of fungal-feeding nematodes in both rice and wheat phases (Table S1) due to the fact that straw increased the fungal biomass by the time that soil samples were collected (about 4–6 months after incorporating straw by ploughing, see our PLFA results from 2012 in Table S2). We believe that our results are dependent on the sampling time, since the initial, rapid decomposition of labile substrates (e.g. soluble compounds and hemicellulose) in straw is mediated by bacterial decomposers whereas fungi are more important in the breakdown of recalcitrant substrates like lignin in the later stages of straw decomposition [30,31].

Total nematode abundance was highest in the MSCF treatment, which had the largest amount of organic matter from straw and manure, whereas crop yield was greatest in SCF treatment, which had the largest amount of nitrogen addition from straw and chemical fertilizer (Table S3). This indicates that the response of total nematode abundance to fertilizers was not consistent with crop yield response to fertilizers. Similarly, the high input of nitrogen from CF treatment did not affect total nematode abundance significantly, although CF promotes a high crop growth and could increase food resources for nematodes (e.g. plant root exudates as substrates for bacteria and fungi; more plant roots for herbivorous nematodes). The low dry matter content of MCF makes it a relatively poor source of complex organic substrates and its application did not promote total nematode abundance significantly in the rice and wheat phases. These findings indicate that total nematode abundance was controlled by the amount of organic matter added rather than nitrogen addition. Further, we conclude that food resources derived from straw have a long-term effect on the soil food web that can sustain the total nematode population up to 4–6 months after the straw was added. Well-fertilized crops produce higher crop yields with larger root system and more plant root exudates than unfertilized crops [32], but while this may not affect the abundance of the total nematode population, it could be important for certain genera.

As we hypothesized, the plant-feeding nematode *Hirschmanniella* had a genera-specific responses to manure addition treatment, for it was always more abundant in MCF treatment than the CK treatment in the rice and wheat phases. We attribute this to the fact that the MCF treatment provided the lowest N input to rice and wheat crops, which leaves the plant vulnerable to herbivory by *Hirschmanniella* since higher N levels cause physiological changes in the plant that may prevent multiplication of *Hirschmanniella*. This supposition is supported by Poussin et al. [33], who observed low N (80 kg ha^{-1}) amendment resulted in significantly greater *Hirschmanniella* populations than the high N (160 kg ha^{-1}) amendment in irrigated rice field. On the other hand, fertilizer treatments depressed the growth of *Rhabdolaimus* relative to the CK treatment in the rice phase. The *Rhabdolaimus* is designated as algae-feeding nematode that feeds on algae and diatoms [14]. Total algae biomass in paddy rice systems can reach 0.6 g m^{-2} [34] and there is a predictable succession where diatoms and unicellular green algae predominate at the tillering stage and are gradually replaced by blue-green algae (cyanobacteria) at the heading to maturity stage [35], which corresponds to our sample collection time. The abundance of the N_2-fixing blue-green algae is related to N limitation and light penetration, which is expected to be lower in fertilized treatments than CK treatment in the rice phase. Consequently, the response to fertilization of plant-feeding nematodes (including those that consume algae) is distinct from that of the bacterial- and fungal-feeding nematodes. We recommend that trophic group responses to fertilization should be evaluated separately from the total nematode population.

5. Conclusion

Our findings support the view that food resources act as a bottom-up modulator of nematode population size in paddy rice–upland wheat systems. Application of organic fertilizers could change the total nematode abundance and dominant nematode genera, and our findings suggest that the quantity and composition of the organic material is important. Food resources derived from straw are substrates for soil microbes, which are of particular importance for the fungal-feeding nematodes several months after straw incorporation to the agroecosystem. Based on the findings of this study, we suppose the big difference of dominant genera between paddy rice and upland wheat was due to the soil moisture regimes rather than crop species. We cannot be certain about this conclusion from our field experiment because several variables (soil moisture, crop type and climate) fluctuated between the paddy rice and upland wheat growth periods. Laboratory experiments that control the climate and crop species but vary the soil moisture conditions will provide insight into how soil moisture controls the nematode community structure and dominant genera. Since crops apparently make little contribution to the bottom-up regulation of nematode communities, relative to organic fertilizers, it will be interesting to confirm this by tracking the energy and material flows from crops and organic fertilizers to the soil nematode community with stable isotopes (e.g. δ^{13} C and δ^{15} N).

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.ejsobi.2015.12.001.

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