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Effect of elevated CO₂ and N fertilisation on soil nematode abundance and diversity in a wheat field

Qi Li^{a,d}, Wenju Liang^{a,*}, Yong Jiang^a, Yi Shi^a, Jianguo Zhu^b, Deborah A. Neher^c

^a Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, PR China

^b Institute of Soil Science, Chinese Academy of Sciences, Nanjing 210008, PR China

^c Department of Plant and Soil Science, University of Vermont, Burlington, VT 05405, USA

^d Graduate School of the Chinese Academy of Sciences, Beijing 100039, PR China

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ABSTRACT

An experimental platform of free-air CO₂ enrichment (FACE) was established in mid June of 2004 over a rice–wheat rotation ecosystem located at a suburb of Jiangdu, China. We compared the abundance and diversity of soil nematodes from a wheat field with high (225.0 kg N ha⁻¹) and low (112.5 kg N ha⁻¹) levels of N fertilisation exposed to the elevated and ambient CO₂ during the wheat growing season in 2005. The results showed that elevated CO₂ and N fertilisation had significant effects on the abundance and diversity of soil nematodes. Elevated CO₂ increased the abundance of omnivores-predators, the values of maturity index (MI) and structural index (SI) of nematode assemblage at the jointing stage of wheat. Two levels of N fertilisation had significant effects on the abundance of fungivores at the wheat jointing stage, while nematode channel ratio (NCR) showed responses to different N fertilisation and the interaction effects of elevated CO₂ and N fertilisation at the wheat ripening stage.

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1. Introduction

Human induced land use, land use change, and forestry activities worldwide currently account for 20–25% of annual global greenhouse gas emissions, or roughly 1–1.5 billion tonnes of carbon per year (Watson et al., 2000). This trend is driving climate change, and is likely to affect both above- and below-ground processes in many ways (Wardle et al., 2004). The interplay between the carbon cycle and other nutrient cycles will be crucial in understanding the response of plant communities and ecosystems to climatic change. The interactions of C and nitrogen (N) are particularly important being N the nutrient most commonly limiting plant and microbial growth (Cardon et al., 2001).

The soil food chain response to elevated CO₂ can indicate the changes in soil ecological processes and nutrient management in agricultural ecosystems. Soil nematodes play important roles in the detritus food web; laboratory experiments and field studies have suggested that soil nematodes feeding on bacteria and fungi play an important role in affecting the turnover of soil microbial biomass, and thus, the availability of plant nutrients (Bardgett et al., 1999; Yeates et al., 2003; Liang et al., 2005b,c). A variety of statistical techniques or indices have been developed to describe environmental disturbance using nematode species, trophic structure or life strategy (Yeates et al., 1997, 2003; Bongers and Ferris, 1999; Ruess et al., 1999; Ferris et al., 2001).

* Corresponding author. Tel.: +86 24 83970359; fax: +86 24 83970300.

E-mail address: liangwj@iae.ac.cn (W. Liang).

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While there is a variety of reports on the response of soil biological populations to elevation of atmospheric CO₂ concentration under various vegetation types, soil types and experimental regimes (Runion et al., 1994; Yeates et al., 1997, 2003; Hoeksema et al., 2000; Hungate et al., 2000; Neher et al., 2004), these studies generally focus on grassland and forest ecosystems. So far, there is little information about the effect of elevated CO₂ on soil nematodes in Chinese farmland ecosystems (Li et al., 2005). Further how climate change will influence the function of soil biota in farmlands under different levels of N fertilisation is poorly understood.

The objectives of this study were to determine the effect of elevated CO₂ and N fertilisation on soil nematode abundance and diversity in a Chinese farmland ecosystem.

2. Materials and methods

2.1. Experimental site and design

An experimental platform of free-air CO₂ enrichment (FACE) was established in mid June of 2004 over a rice–wheat rotation ecosystem located at a suburb (32°35'N, 119°42'E) of Jiangdu, China. The crop rotation pattern in the region is dominated by a single crop of rice in the summer followed by winter wheat, and accounts for about 60% of the regional paddy area (Zheng et al., 2000). The rice–wheat rotation ecosystem is also very common in other rice production regions with a similar climate, such as the eastern, central and southwestern China (Zheng et al., 2000). This experiment was conducted during the wheat growing season. This region is under the north subtropical monsoon climate. The mean annual precipitation is 918–978 mm, of which 60% occurs from June to September. The annual mean temperature is 14–16 °C, and the annual frost-free period is about 220 days. The soil at the study site is Shajiang-Aquic Cambosols (CRGCST, 2001), with 18.4 g kg⁻¹ total C, 1.5 g kg⁻¹ total N, 57.8% sand, 28.5% silt and 13.7% clay at 0–15 cm depth.

A randomized complete block design was established with two levels of target atmospheric CO₂ concentration. It consisted of three replicate rings for the elevated CO₂ (hereinafter referred to as FACE) and three for the ambient (hereinafter referred to as ambient). The atmospheric CO₂ of each FACE ring was enriched by 200 μmol CO₂ mol⁻¹ over the ambient (370 μmol CO₂ mol⁻¹). To minimize CO₂ contamination, the ambient plots were situated at least 90 m from the nearest FACE ring. A FACE ring consisted of eight CO₂-emitting tubes in an octagonal arrangement, from which pure CO₂ was sprayed towards the center. All FACE rings were 12.5 m in diameter, with a useful area of 80 m². A full description of the FACE apparatus and its operation is reported elsewhere (Liu et al., 2002). In each FACE and ambient plot, two levels of N fertilisation were applied. Ammonium-based nitrogen fertiliser was applied in the wheat season at the rates of 225.0 kg N ha⁻¹ (HN) and 112.5 kg N ha⁻¹ (LN), respectively, with 50% basally applied on November 2nd in 2004 (sowing stage), 10% on March 3rd and 40% on April 5th in 2005. The application rate of phosphorus fertiliser was 75 kg P₂O₅ ha⁻¹ and potassium fertiliser was 75 kg K₂O ha⁻¹. Crop residues from the last

growing season were all incorporated to the soil. No organic manure was incorporated into the wheat field.

During the wheat growing season, soil samples were collected from 0 to 15 cm depth in each plot on 1st April (jointing stage), 19th April (booting stage), and 2nd June (ripening stage). Each soil sample pooled from five soil cores (2.5 cm diameter) was stored in individual plastic bags, and transferred to a 4 °C cold room.

A sub-sample (100 g) of each composite sample was taken for nematode extraction by elutriation and sugar-centrifugation (Li et al., 2005), and nematode populations expressed as number of nematodes per 100 g dry soil. At least 100 nematodes from each sample were identified to genus level using an inverted compound microscope. The classification of trophic groups was assigned to: (1) bacterivores (BF); (2) fungivores (FF); (3) plant-parasites (PP); (4) omnivores-predators (OP), based on known feeding habits or stoma and esophageal morphology (Yeates et al., 1993; Liang et al., 2005a).

Several ecological indices of nematode communities were calculated: (1) Shannon–Weaver diversity $H' = -\sum p_i(\ln p_i)$; (2) dominance $\lambda = \sum p_i^2$; where p_i is the proportion of individuals in the i th taxon and S is the number of taxa; (3) nematode channel ratio $NCR = BF/(BF + FF)$ (Neher et al., 1995; Yeates, 1999); (4) maturity index $(MI) = \sum v_i f_i$, where v_i is the c - P value of taxon i , f_i is the frequency of taxon i in a sample; (5) plant parasite index (PPI), which was determined in a similar manner for plant parasitic genera (Bongers, 1990); (6) enrichment index $(EI) = 100 \times (e/(e + b))$, and (7) structural index $(SI) = 100 \times (s/(b + s))$, where e is the abundance of individuals in guilds in the enrichment component weighted by their respective k_e values, b is the abundance of individuals in the basal component weighted by their k_b values, and s is the abundance of individuals in the structural component weighted by their k_s values (Ferris et al., 2001).

2.2. Statistical analysis

Nematode abundances were $\ln(x + 1)$ transformed prior to statistical analysis. Statistical analysis was performed for the nematode data and genera representing a relative abundance >5% of total nematodes under all treatments. Two-way ANOVA was applied to test the effects of elevated atmospheric

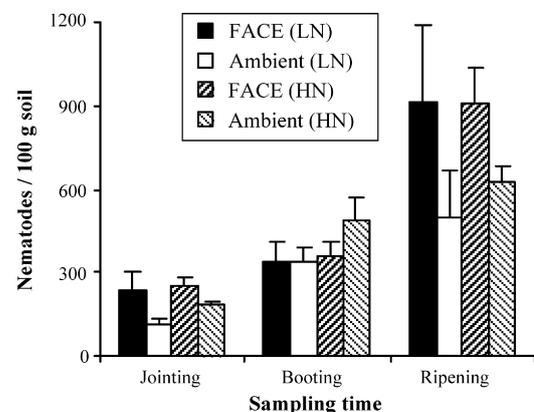


Fig. 1 – The effect of elevated CO₂ and N fertilisation on the numbers of total nematodes across the wheat growth stages.

CO₂ and N fertilisation as main effects and their two-way interaction on nematode across the wheat growth period. Linear correlations between nematodes and selected soil chemical properties were quantified using Pearson's correlation coefficients. Statistical analyses were performed using SPSS statistical software (SPSS Inc., Chicago, IL). Differences with $P < 0.05$ were considered significant.

3. Results

3.1. Total number of nematodes

Following the CO₂ enrichment, the total numbers of nematodes showed an increasing trend compared with the ambient

at two levels of N application at the wheat jointing and ripening stages, with the highest number (912 individuals 100 g⁻¹ soil) observed under FACE (LN) at the ripening stage and the lowest number (117 individuals 100 g⁻¹ soil) under ambient (LN) at the jointing stage (Fig. 1). However, effects of elevated CO₂ and N fertilisation effects were not significant during the study period.

The mean populations of 35 nematode taxa were identified under ambient and FACE conditions (Table 1). Among the nematode taxa, *Acrobeloides*, *Chronogaster*, *Filenchus*, *Hirschmanniella*, *Psilenchus* and *Tylenchus* were dominant genera (relative abundance > 5%) across all treatment combinations. Other genera, including *Thonus* and *Mesodorylaimus* exceeded 5% of total abundance in some but not all treatment combinations. Significant elevated CO₂ effects were only

Table 1 – Proportional contribution (%) of various nematodes to the nematode assemblage under ambient or FACE condition at two levels of N application across the three sampling dates

Trophic group	Family	Genus	LN		HN	
			Ambient	FACE	Ambient	FACE
	Alaimidae	<i>Alaimus</i>	0.4	0.0	0.0	0.0
	Cephalobidae	<i>Acrobeloides</i>	15.8	14.0	11.5	12.3
		<i>Cephalobus</i>	1.7	0.3	0.4	0.2
		<i>Chiloplacus</i>	2.1	1.6	2.9	1.6
		<i>Eucephalobus</i>	0.5	0.1	1.7	0.3
		<i>Heterocephalobus</i>	6.6	3.8	2.0	1.7
	Leptolaimidae	<i>Chronogaster</i>	13.8	7.2	9.0	9.0
		<i>Leptolaimus</i>	0.2	0.0	0.4	0.0
	Monhysteridae	<i>Eumonhystera</i>	0.7	2.2	0.5	1.4
		<i>Monhystera</i>	0	0.3	0.6	0.5
	Panagrolaimidae	<i>Panagrolaimus</i>	2.0	3.4	3.9	5.1
	Plectidae	<i>Plectus</i>	1.6	0.6	1.0	1.8
	Rhabditidae	<i>Mesorhabditis</i>	0.3	0.0	0.3	0.7
		<i>Protorhabditis</i>	0	0.3	8.6	0.3
	Rhabdolaimidae	<i>Rhabdolaimus</i>	0.3	0.3	0.0	0.0
Bacterivores			46.0	34.1	42.8	34.9
	Anguinidae	<i>Ditylenchus</i>	0.5	2.4	0.4	0.0
	Aphelenchoididae	<i>Aphelenchoides</i>	3.2	3.3	4.2	4.5
	Belondiridae	<i>Dorylaimellus</i>	0.0	0.0	0.5	0.0
Fungivores			3.7	5.7	5.1	4.5
	Belondiridae	<i>Oxydirus</i>	0.0	1.1	1.6	1.4
	Hemicyclophoridae	<i>Hemicyclophora</i>	0.0	0.0	0.4	0.0
	Nordiidae	<i>Pungenturs</i>	1.6	1.2	1.3	2.0
	Pratylenchidae	<i>Hirschmanniella</i>	5.8	7.6	5.7	8.9
	Psilenchidae	<i>Psilenchus</i>	9.8	10.3	2.2	8.2
	Tylenchidae	<i>Filenchus</i>	12.5	14.3	14.0	17.9
		<i>Tylenchus</i>	4.9	9.5	8.5	6.4
Plant-parasites			34.6	44.0	33.7	44.8
	Aporcelaimidae	<i>Aporcelaimellus</i>	1.7	1.4	1.4	1.2
	Leptonchidae	<i>Dorylaimoides</i>	0.5	1.1	0.0	0.0
	Nygolaimidae	<i>Nygolaimus</i>	0.6	1.3	1.6	0.8
	Qudsianematidae	<i>Epidorylaimus</i>	2.6	1.1	2.2	0.2
		<i>Eudorylaimus</i>	0.0	1.0	0.0	0.0
		<i>Microdorylaimus</i>	0.0	0.8	1.1	1.8
		<i>Thonus</i>	5.2	2.2	1.6	2.9
	Thornenematidae	<i>Laimydorus</i>	0.0	0.4	0.0	0.5
		<i>Mesodorylaimus</i>	3.3	3.0	6.1	3.9
		<i>Prodorylaimus</i>	1.8	3.9	4.4	4.5
Omnivore-predators			15.7	16.2	18.4	15.8

Bold numbers are the total percentage of each trophic group.

found in the numbers of *Psilenchus* at the booting stage, with higher values observed in the FACE (HN) in comparison with the ambient (HN) ($P < 0.05$), and no significant N fertilisation effects were observed during the wheat growth stages. Significant correlations were found between the numbers of *Acrobeloides* and the contents of $\text{NH}_4^+\text{-N}$ ($r = -0.391$, $P < 0.05$) and $\text{NO}_3^-\text{-N}$ ($r = -0.553$, $P < 0.01$).

3.2. Nematode trophic structure

During the study period, abundance of total nematodes increased with crop maturity. This was true among all four trophic groups (Fig. 2). Bacterivores and plant-parasites were the most abundant trophic groups within the community, followed by omnivore-predators and fungivores (Table 1). The mean relative proportion of bacterivores was greater in ambient than elevated CO_2 whereas the opposite pattern was observed for plant-parasitic nematodes (Table 1). This trend was observed regardless of N treatment. While neither elevated CO_2 nor N fertilisation affected the abundance of bacterivores and plant-parasites significantly at any wheat growth stage (Fig. 2A and C). The abundance of omnivore-predators increased

with elevated CO_2 at the jointing stage of wheat ($P < 0.05$) but was not affected by N fertilisation (Fig. 2D). Fungivores were the trophic group of least abundance (Fig. 2B). Abundance of fungivores increased with increased levels of N fertilisation ($P < 0.05$) at the jointing stage of wheat but was not affected by concentration of CO_2 .

3.3. Nematode ecological indices

Among the ecological indices of the nematode fauna assessed in the study, neither significant elevated CO_2 nor N fertilisation effects were found in the values of λ and EI. Significant elevated CO_2 effects were found in the values of SI at the jointing stage ($P < 0.05$), and the values of SI were higher under FACE than under ambient regardless of N fertilisation. Significant correlations were observed in the values of SI and the contents of $\text{NO}_3^-\text{-N}$ ($r = 0.442$, $P < 0.01$). Similar trend was also found in the values of MI at the jointing stage, with higher values found under FACE at two levels of N application ($P < 0.05$). Significant N fertilisation effects were observed in the values of NCR at the jointing and ripening stages ($P < 0.05$), higher values of NCR were found in the HN treatment than in

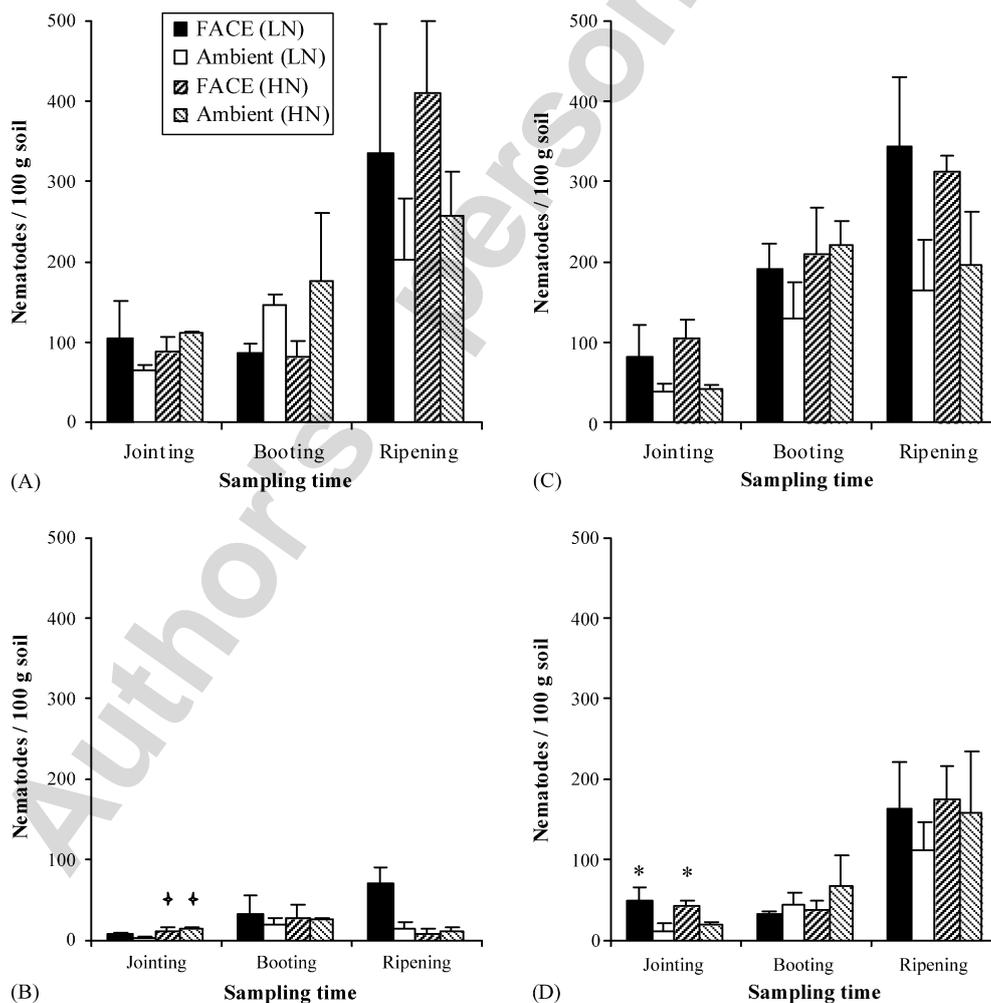


Fig. 2 – The effect of elevated CO_2 and N fertilisation on the numbers of nematode trophic groups across the wheat growth stages: (A) bacterivores, (B) fungivores, (C) plant-parasites, and (D) omnivore-predators. (* Indicate significant CO_2 effects at $P < 0.05$ and + indicate significant N fertilisation effects at $P < 0.05$, at a sampling date).

Table 2 – Ecological indices of the nematode assemblage under ambient or elevated CO₂ of two nitrogen levels at each sampling date (mean ± S.E.); significance of elevated CO₂ and N fertilisation effects, and their interaction are given

Sampling date	Indices	LN		HN		CO ₂ effects	N effects	Interaction
		Ambient	FACE	Ambient	FACE			
April 1 (jointing)	NCR	0.96 ± 0.02	0.95 ± 0.03	0.60 ± 0.28	0.88 ± 0.02	ns	0.013	ns
	λ	0.12 ± 0.02	0.16 ± 0.01	0.08 ± 0.04	0.14 ± 0.03	ns	ns	ns
	H'	2.25 ± 0.16	2.14 ± 0.06	1.54 ± 0.74	2.30 ± 0.11	ns	ns	ns
	MI	2.28 ± 1.15	2.68 ± 0.11	1.43 ± 0.67	2.69 ± 0.17	0.018	ns	ns
	PPI	2.17 ± 0.10	2.20 ± 0.03	1.61 ± 0.80	2.34 ± 0.10	ns	ns	ns
	SI	42.37 ± 14.82	73.51 ± 2.18	41.20 ± 13.21	74.85 ± 7.88	0.031	ns	ns
	EI	23.68 ± 14.49	39.72 ± 13.14	41.02 ± 19.91	52.23 ± 14.77	ns	ns	ns
April 19 (booting)	NCR	0.85 ± 0.09	0.78 ± 0.12	0.83 ± 0.07	0.75 ± 0.14	ns	ns	ns
	λ	0.12 ± 0.01	0.12 ± 0.02	0.17 ± 0.04	0.15 ± 0.01	ns	ns	ns
	H'	2.33 ± 0.07	2.31 ± 0.11	2.10 ± 0.22	2.03 ± 0.07	ns	ns	ns
	MI	2.54 ± 0.18	2.40 ± 0.09	2.54 ± 0.62	2.44 ± 0.15	ns	ns	ns
	PPI	2.17 ± 0.08	2.41 ± 0.16	2.34 ± 0.05	2.53 ± 0.09	ns	ns	ns
	SI	61.79 ± 6.42	71.66 ± 6.60	56.42 ± 28.32	69.75 ± 17.45	ns	ns	ns
	EI	23.57 ± 8.37	61.33 ± 13.22	61.71 ± 14.04	62.48 ± 19.58	ns	ns	ns
June 2 (ripening)	NCR	0.95 ± 0.03	0.80 ± 0.06	0.97 ± 0.02	0.99 ± 0.01	ns	0.025	0.042
	λ	0.13 ± 0.02	0.13 ± 0.02	0.12 ± 0.01	0.13 ± 0.01	ns	ns	ns
	H'	2.28 ± 0.21	2.35 ± 0.14	2.35 ± 0.04	2.33 ± 0.02	ns	ns	ns
	MI	2.85 ± 0.10	2.77 ± 0.14	2.52 ± 0.43	2.72 ± 0.17	ns	ns	ns
	PPI	2.42 ± 0.06	2.26 ± 0.07	2.85 ± 0.41	2.19 ± 0.03	ns	ns	ns
	SI	73.12 ± 4.27	70.93 ± 4.08	72.65 ± 10.86	70.43 ± 6.13	ns	ns	ns
	EI	6.67 ± 6.67	18.96 ± 11.18	41.76 ± 9.27	24.62 ± 12.32	ns	ns	ns

ns: non-significant.

the LN treatment under FACE at the ripening stage (Table 2). Significant interaction effects of elevated CO₂ and N fertilisation were only found in the values of NCR at the ripening stage ($P < 0.05$).

4. Discussion

Total abundance of nematodes was not affected by changes in atmospheric CO₂ concentration and N fertilisation. However, shifts in relative availability of N and C impacted community structure, apparent at the resolution of trophic groups as discussed below.

4.1. Effects of elevated CO₂ on nematode abundance and diversity

Enhanced CO₂ can indirectly affect soil organisms through shifts in the quantity and quality of plant litter returned to soil, the rate of root turnover, and the exudation of carbon and other nutrients into the rhizosphere (Coûteaux and Thomas, 2000; Wardle et al., 2004). The data obtained in the present study indicated that elevated CO₂ had significant effects on the abundance of omnivores-predators at the wheat jointing stage; the numbers of omnivores-predators were higher under FACE than under ambient at two levels of N application. These results were consistent with the findings of Yeates et al. (2003) who observed the doubling of populations of omnivores-predators in grazed pasture in response to elevated CO₂. Since the interactions among the various functional groups of below-ground microfauna are complex, the effects of C distribution on below-ground food webs may be soil, climate

and season specific (Wardle et al., 2001; Yeates et al., 2003). In our study, plant-parasites were insensitive to the elevated CO₂, while *Psilenchus* belonging to the plant-parasites showed response to the elevated CO₂. At the booting stage, the numbers of *Psilenchus* were higher under FACE (HN) than under ambient (HN). Similar results were also found in our previous study in the anthropogenic alluvial soil, the abundance of *Psilenchus* increased significantly at the wheat booting stage under the elevated CO₂ (Li et al., 2005). Since both studies were carried on rice-wheat rotation system, *Psilenchus* could be regarded as a potential 'key' genus in showing the effect of elevated CO₂ on the nematode fauna. In addition, the relative short period exposure to elevated CO₂ might help to explain the unobvious responses of other nematode trophic groups and nematode taxa in the present study.

During the study period, significant elevated CO₂ effects were only observed in the values of MI and SI at the jointing stage, with higher values found under FACE than under ambient at two levels of N application. Greater MI and SI values indicated a complex community structure with relatively more linkages in the food web under elevated CO₂ (Ferris et al., 2001), and a multitrophic response among the soil biota to the elevated CO₂ in comparison with the ambient. In the present study, significant elevated CO₂ effects were only observed in the jointing stage of wheat, which consistent with the results of Hungate et al. (2000) who observed the responses of soil microbiota after 4 years of exposure to elevated atmospheric CO₂ in two annual grasslands, that the elevated CO₂ effects were more pronounced during the early part of the growing season and disappeared later in the season as plants approached their maximum biomass.

4.2. Effects of N fertilisation on nematode abundance and diversity

The ecological roles of soil invertebrates include plant herbivory and the mineralisation of nutrients in the detrital food web, both of which may be affected by change in carbon-flow patterns and, in turn, have important impacts on ecosystem behaviour (Neher et al., 2004). In the present study, significant N fertilisation effects were found, higher numbers of fungivores being observed under FACE (HN) and ambient (HN) at the jointing stage. In two soils of subarctic Sweden, similar results were found by Ruess et al. (1999) that increasing NPK fertilisation has been found to change the composition of the nematode fauna, generally in favor of fungal- and plant-feeding species. Ma et al. (2005) reported that the elevated CO₂ could significantly increase the C/N ratio of root in the LN treatment across the wheat growth stages, and at the ripening stage, the C/N ratio of root was significantly higher under FACE (LN), which may contribute to the increasing numbers of fungivores under FACE (LN) at the booting and ripening stages of wheat, since fungivores tend to predominate when the organic material is of high C/N ratio (Ferris and Matute, 2003).

The nematode channel ratio (NCR) is known to be an important indicator of the decomposition pathway in the detritus food webs (Yeates et al., 2003). The values of NCR were sensitive to the interaction effects of elevated CO₂ and N fertilisation at the ripening stage. And no significant CO₂ effects were observed in the values of NCR. The results obtained in this study were partially consistent with Yeates et al. (2003) that the relative contributions of basic functional pathways were essentially unchanged under elevated CO₂ condition, while the obtained results in the present study also suggest that the decomposition pathway might be affected by the interaction effects of elevated CO₂ and N fertilisation. The values of NCR at the ripening stage under FACE indicated that the bacterial decomposition pathway was relatively more dominant under FACE (HN) and played a more important role in nutrient cycling and nutrient supply to plants, while the fungal decomposition pathway was relatively important under FACE (LN). The relative importance of the bacterial and fungal pathways of decomposition varies in space and time within ecosystems, with dominance of the fungal pathway often reflecting lower rates of decomposition (Cadisch and Giller, 1997).

5. Conclusion

After the whole wheat growing season of observation, the obtained data indicated that effects of elevated CO₂ and N fertilisation on the nematode abundance and diversity might be pronounced at the early part of the growing season, and the interaction of elevated CO₂ and N fertilisation might influence the decomposition pathway of detritus food web later in the wheat growth season. In order to indicate the changes in soil ecosystem processes and to implement nutrient management in farmland ecosystems, it is important to know the soil food web chain response to elevated CO₂ and N fertilisation, and long-term studies are necessary to assess the impacts of climate change on soil processes and biodiversity.

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