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Effect of free-air CO_2 enrichment on nematode communities in a Chinese farmland ecosystem

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Abstract: At a rice-wheat rotational free-air CO_2 enrichment(FACE) platform, the effect of elevated atmospheric CO_2 on soil nematode communities in a farmland ecosystem was studied. Wheat plots were exposed to elevated atmospheric CO_2 (ambient 370 μl/L + 200 μl/L). 32 families and 40 genera of nematode were observed in soil suspensions during the study period. Under FACE treatment, the numbers of total nematodes, bacterivores and fungivores exhibited an increasing trend. Because of the seasonal variation of soil temperature and moisture, the effect of elevated atmospheric CO_2 on soil nematodes was only observed under favorable conditions. The response of nematode communities to elevated atmospheric CO_2 may indicate the change of soil food web.

Keywords: nematode community; trophic group; free-air CO_2 enrichment(FACE); wheat; farmland ecosystem

Introduction

Elevated atmospheric CO_2 usually stimulates plant photosynthesis, and often increases carbon flux from plant root to soil (Hungate, 2000). The populations of soil organisms feeding on living or dead root material or on root exudates may respond to the increased carbon, with the changes in their activity or community composition (Zaller, 1997), and hence, affect the structure of soil food web.

Nematodes are the ubiquitous and important components of soil food webs. They are abundant and trophically diverse in most soils, and can influence ecosystem processes. Therefore, soil nematode is a useful component of soil biota, by which, the effect of increased root growth under elevated CO_2 on soil food webs can be examined(Hoeksema, 2000). Many researchers(Runion, 1994; Yeates, 1997; Hoeksema, 2000; Hungate, 2000) studied the effect of CO_2 enrichment on soil nematodes, but they generally focused on grassland and forest ecosystems. So far, there is little information about the effect of elevated CO_2 on soil nematode trophic groups in Chinese farmland ecosystems (Liang, 2002), while free-air CO_2 enrichment (FACE) system provided a unique opportunity to do this study. With a rice-wheat rotational FACE platform and using soil nematodes as bioindicators, this research studied the effect of elevated CO_2 on soil food webs in a Chinese farmland ecosystem.

1 Materials and methods

The field work was conducted at the Nianyu Farm (31°37′N, 120°28′E), Wuxi Municipality, Jiangsu Province, China. The farm is in the subtropical marine climate zone, with an annual mean temperature 16℃, annual mean precipitation 1000—1200 mm, and a non-frost period around 230 d. The soil at the study site is classified as anthropogenic alluvial soil, and its main physical and chemical properties are shown in Table 1. Rice-wheat rotation system is dominant in this region. During the study period, the field site was planted with winter wheat (*Triticum aestivum* L.) and applied with 180 kgN/hm^2, 75 kgP_2O_5/hm^2 and 75 kgK_2O/hm^2.

Table 1 Main physical and chemical properties of test soil

Bulk density, g/cm^3	Soil porosity, %	Organic matter, g/kg	Total N, g/kg	Total P, g/kg	pH
1.2	54	26	1.6	1.5	6.8

A China FACE system with Japanese design was set up in June 2001 and has operated ever since. Three control plots were under ambient CO_2 (370 μl/L), while three rings were exposed under elevated atmospheric CO_2 (ambient + 200 μl/L)(Liang, 2002). Each ring was 12.5 m in diameter, with pure CO_2 injection for 24 h every day all the year round. In FACE system, the elevated CO_2 concentration was controlled by a computer system platform, according to the ambient CO_2 concentration variation, wind speed, canopy height and day-night change. The set CO_2 was 557 μl/L at daytime and 608 μl/L at night, and its concentration distributed in the FACE rings was uniform(Liu, 2002).

In 2002, soil samples were collected from the depths of 0—5 cm and 5—10 cm at wheat over-wintering stage (12 January), jointing stage(8 March), booting stage(12 April) and ripening stage(3 June). Each sample comprised 5 cores(5 cm diameter), and subsamples were taken from each bulk sample for estimating nematode populations. The samples were protected against overheating, and processed within 7 d.

Nematodes were extracted from 100 g fresh soil by the methods of elutriation and sugar-centrifugation (Ingham,

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1994), and their populations were expressed as individuals per 100 g 105℃ dried soil (Liang, 2003). All extracted nematodes in each soil sample were counted and identified, mainly to genus level if possible, using an inverted compound microscope. The classification of trophic groups was assigned to bacterivores (BF), fungivores (FF), plant-parasites (PP) and omnivore-predators (OP), based on known feeding habitats and esophageal morphology (Liang, 2001;2003).

All the data across 4 sampling dates were subjected to statistical analysis of variance (ANOVA). Difference with $P < 0.05$ was considered significant.

2 Results

2.1 The number of total nematodes

It is shown in Table 3 that at 0—5 cm soil depth of wheat field experimental site, the number of total nematodes ranged between 73 and 517 individuals per 100 g dry soil, with a maximum value (517 ± 6) in FACE treatment at ripening stage. Except at jointing stage, FACE had a higher total number of nematodes than ambient treatment, and significant difference was found between FACE and ambient treatment at booting and ripening stages ($P < 0.05$). At 5—10 cm soil depth, the number of total nematodes ranged between 49 and 594 individuals per 100 g dry soil, also with a maximum value (594 ± 39) in FACE treatment at ripening stage. The number of total nematodes was higher in FACE than in ambient treatment, and significant difference was observed between FACE and ambient treatment at jointing and ripening stages ($P < 0.01$).

2.2 Nematode taxa

Table 2 shows that in the wheat-field experimental site, thirty-two families and 44 genera of nematodes were observed in soil suspensions, and *Brevibucca* and *Tylenchus* were the dominant genera at 0—5 cm and 5—10 cm soil depths in both FACE and ambient treatments.

Table 2 Relative abundance of nematodes in FACE and ambient treatments at both soil depths

Trophic group	Family	Genus	0—5 cm		5—10 cm	
			Ambient	FACE	Ambient	FACE
BF			33.0	31.0	28.1	28.8
	Bastianiidae	*Bastiania*	0.0	0.2	0.0	0.0
	Brevibuccidae	*Brevibucca*	11.1	12.8	10.1	9.8
	Cephalobidae	*Acrobeloides*	0.0	0.0	0.2	0.3
		Cephalobus	2.1	6.2	7.9	5.7
		Eucephalobus	3.3	0.3	0.0	0.3
	Leptolaimidae	*Chronogaster*	0.0	0.0	0.0	0.2
	Monhysteridae	*Monhystrella*	0.0	0.2	0.0	0.0
		Monhystera	1.5	0.8	3.7	1.9
	Panagrolaimidae	*Panagrellus*	0.5	0.0	0.8	0.0
		Panagrolaimus	6.1	4.3	2.1	3.2
	Plectidae	*Plectus*	1.7	1.7	0.7	2.2
	Prismatolaimdae	*Prismatolainus*	0.7	0.0	0.0	0.0
	Diploscapteridae	*Diploscapter*	0.0	0.0	0.0	0.3
	Rhabdolaimidae	*Rhabdolaimus*	3.8	1.2	1.6	1.9
	Rhabditidae	*Rhabditis*	2.3	3.2	1.0	3.0
FF			10.7	12.1	6.9	6.3
	Anguinidae	*Ditylenchus*	6.1	6.1	4.5	5.1
		Nothotylenchus	3.3	1.2	1.0	0.7
	Aphelenchoididae	*Aphelenchoides*	1.1	4.2	1.2	0.5
	Aphelenchidae	*Aphelenchus*	0.3	0.5	0.3	0.0
PP			47.6	46.1	57.9	58.9
	Belondiridae	*Belondira*	0.3	0.4	0.0	0.0
	Dolichodoridae	*Dolichorus*	0.0	0.0	0.0	0.3
		Tylenchorhynchus	0.5	0.0	0.8	1.0
	Hoplolaimidae	*Helicotylenchus*	1.1	1.9	7.0	5.8
		Rotylenchus	0.0	0.0	0.9	1.0
	Longidoridae	*Longidorus*	2.4	2.6	1.9	2.7
	Nordiidae	*Longidorella*	1.6	0.6	0.4	1.0
	Pratylenchidae	*Hirschmanniella*	2.8	5.0	8.2	7.1
		Pratylenchus	1.5	0.0	1.1	0.2
		Radopholus	0.4	0.0	0.2	0.0
	Psilenchidae	*Psilenchus*	4.6	3.6	6.5	6.0
	Tylenchidae	*Boleodorus*	4.4	5.6	6.3	4.4
		Tylenchus	28.0	26.0	24.6	28.6
		Tetylenchus	0.0	0.5	0.0	0.9
OP			8.7	10.8	7.1	6.0
	Aporcelaimidae	*Aporcelaimus*	6.4	5.3	4.7	2.6
	Chromadoridae	*Prochromadora*	0.0	0.3	0.4	0.0
	Chrysonematidae	*Chrysonema*	0.4	0.7	0.8	0.5
	Discolaimidae	*Discolaimus*	0.6	1.3	0.8	1.4
	Dorylaimidae	*Dorylaimus*	0.0	0.3	0.0	0.0
	Ironidae	*Ironus*	0.5	1.1	0.0	0.0
	Mononchidae	*Iotonchus*	0.6	0.2	0.0	0.0
		Judonchulus	0.0	1.1	0.3	0.8
	Thornenematidae	*Mesodorylaimus*	0.0	1.1	0.3	0.8
	Tobrilidae	*Tobrilus*	0.0	0.0	0.0	0.2
	Tripylidae	*Tripla*	0.1	0.3	0.2	0.5

At 0—5 cm soil depth, the relative abundance of bacterivores and plant-parasites was lower, and that of fungivores and omnivores-predators was higher in FACE than in ambient treatment, while an inverse trend was found at 5—10 cm soil depth.

Among the nematodes whose relative abundance was higher than 5%, *Brevibucca*, *Boleodorus*, *Hirschmanniella* and *Psilenchus* were sensitive to the elevated CO_2. Their numbers under FACE treatment exhibited an increasing trend. At ripening stage, the number of *Brevibucca* at 0—5 cm soil depth tended to be higher in FACE than in ambient treatment, and that of *Boleodorus* exhibited an increasing trend. At booting and ripening stages, the number of *Hirschmanniella* was significantly higher in FACE than in ambient treatment($P < 0.05$). At 5—10 cm soil depth, the number of *Psilenchus* at booting stage was significantly higher in FACE than in ambient treatment($P < 0.05$).

2.3 Trophic groups

Table 3 shows that during the study period, the number of bacterivores at 0—5 cm soil depth was higher in FACE than in ambient treatment, and significant difference was found at ripening stage($P < 0.05$). At 5—10 cm soil depth, the number of bacterivores exhibited a similar trend with the 0—5 cm soil depth, and significant difference was also found between FACE and ambient treatments at ripening stage($P < 0.05$).

Table 3 Absolute abundance of total nematodes and their trophic groups

	0—5 cm depth		5—10 cm depth	
	Ambient	FACE	Ambient	FACE
Overwintering stage				
TNEM	73 ± 15	94 ± 6	100 ± 5	106 ± 5
BF	33 ± 12	42 ± 6	34 ± 3	41 ± 4
FF	7 ± 1	11 ± 0*	7 ± 1	12 ± 1
PP	28 ± 9	38 ± 2	53 ± 2	49 ± 1
OP	5 ± 2	3 ± 0	6 ± 1	5 ± 1
Jointing stage				
TNEM	119 ± 12	75 ± 10	49 ± 7	101 ± 1**
BF	25 ± 5	21 ± 6	15 ± 2	20 ± 1
FF	6 ± 1	11 ± 1*	6 ± 2	7 ± 0
PP	60 ± 2	29 ± 6	21 ± 4	63 ± 3*
OP	28 ± 5	13 ± 2	6 ± 1	11 ± 2
Booting stage				
TNEM	139 ± 10	231 ± 15*	218 ± 16	241 ± 7
BF	51 ± 10	58 ± 3	56 ± 6	65 ± 3
FF	16 ± 2	19 ± 1	14 ± 2	15 ± 1
PP	70 ± 4	136 ± 17*	138 ± 9	148 ± 2
OP	2 ± 2	18 ± 1**	2 ± 2	14 ± 3*
Ripening stage				
TNEM	303 ± 49	517 ± 6*	351 ± 1	594 ± 39**
BF	80 ± 8	131 ± 10*	154 ± 18	231 ± 10*
FF	25 ± 2	72 ± 6*	17 ± 2	19 ± 2*
PP	184 ± 38	256 ± 7	148 ± 17	324 ± 43*
OP	14 ± 3	58 ± 5**	34 ± 2	23 ± 3*

Notes: Each entry represents an arithmetic mean ± standard error; each mean value is expressed as individuals per 100 g dry soil; TNEM represents the number of total nematodes; * and ** represent significant level at $P < 0.05$ and 0.01, respectively

The number of fungivores at both soil depths was higher in FACE than in ambient treatment during the growth season. At 0—5 cm soil depth, significant difference was found between FACE and ambient treatment across overwintering, jointing and ripening stages($P < 0.05$), while at 5—10 cm soil depth, such a difference was observed at ripening stage ($P < 0.05$).

The population of plant-parasites was the most abundant trophic groups under the two treatments and at both soil depths. Except at jointing stage, the number of plant-parasites at 0—5 cm soil depth was higher in FACE than in ambient treatment, and significant difference was found at booting stage($P < 0.05$). At 5—10 cm depth, the number of plant-parasites was also higher in FACE than in ambient treatment except at overwintering stage, and significant difference was found at jointing and ripening stages ($P < 0.05$).

The number of omnivores-predators at 0—5 cm soil depth was significantly higher in FACE than in ambient treatment at booting and ripening stages($P < 0.01$). At 5—10 cm soil depth, the number of omnivore-predators was significantly higher in FACE than in ambient treatment at booting stage ($P < 0.05$), while an inverse trend was observed at ripening stage.

3 Discussion

In this study, soil nematodes showed different responses over time to the elevated atmospheric CO_2. The inherent difference in reproductive activity of various soil nematodes during the study period need to be taken into account when interpreting the results(Yeates, 1997). The effect of elevated atmospheric CO_2 on soil nematodes in the wheat field fluctuated with seasons, likely due to the influence of seasonal temperature and moisture regimes on rhizospheric communities. Because of the interactions between atmospheric CO_2 concentration and seasonal variation, the CO_2 concentration effect was only evident under favorable moisture conditions(Runion, 1994).

Whether the decline of some soil nematodes during the course of this study was related to the increase of soil pH throughout the trial is unknown. The soil pH of the wheat field was increased under the elevated atmospheric CO_2 condition. Although soil pH often limits soil nematode populations, a general review of experimental evidence (Yeates, 1987) suggested that soil pH may act indirectly on nematodes by directly affecting their food resources(Yeates, 1999). Root-derived carbon is a key energy source for soil microorganisms and soil fauna. Elevated atmospheric CO_2 has been found to stimulate C_3 plants' photosynthetic rate and their growth(Bowes, 1993), usually resulting in a greater carbon allocation to their underground part(Rogers, 1994), and hence, the rhizospheric microbial populations and the soil food web based on them could be affected(Klironomos,

1996).

Runion *et al*. (Runion, 1994) found greater populations of saprophagous nematodes in a Torrifluvent rhizospheric soil cropped with cotton under elevated CO_2 using free-air CO_2 enrichment in field plots. Our results supported the study in the number of microbivorous nematodes. The numbers of bacterivores and fungivores were significantly higher in FACE than in ambient treatment, which likely to be associated with the increased turnover of soil bacteria and fungi. For microbivorous animals, the size and composition of soil microbial biomass is a determining factor in their food resource. The microbial biomass may not increase and may even decrease due to grazing, but its activity would be enhanced (Couteaux, 2000). Zak *et al*. (Zak, 1993) provided the first evidence that elevated CO_2 may increase the microbial biomass/activity not only in rhizosphere, but also in bulk soil. The increase of bacterivores and fungivores in this study indicated that the activity of soil microorganisms in the wheat field may be increased under elevated CO_2 condition.

Soil biota represents a sensitive link between plant detritus and plant-available nutrients, and thus, factors that influence the detrital quality and quantity are likely to be highly significant (Swift, 1998). In this study, some genera of plant-parasites exhibited an increasing trend. The populations of plant parasites exhibited an increasing trend except at jointing stage at 0—5 cm soil depth and at overwintering stage at 5—10 cm depth, which may be caused by the increase of root production and root exudation. However, the populations of omnivores-predators did not increase throughout the study period, and their numbers fluctuated with seasons. The increase of root production was perhaps only enough to support the lower level of plant-parasites, and not enough to support the higher level of omnivores-predators.

The dynamics of soil nematodes reported here indicated that the changes in soil micro-faunal assemblages played an important role in the overall response of soil to elevated atmospheric CO_2. 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 chain response to elevated CO_2, and long-term studies are necessary to investigate the effect of soil carbon inputs under elevated CO_2 on soil food web.

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