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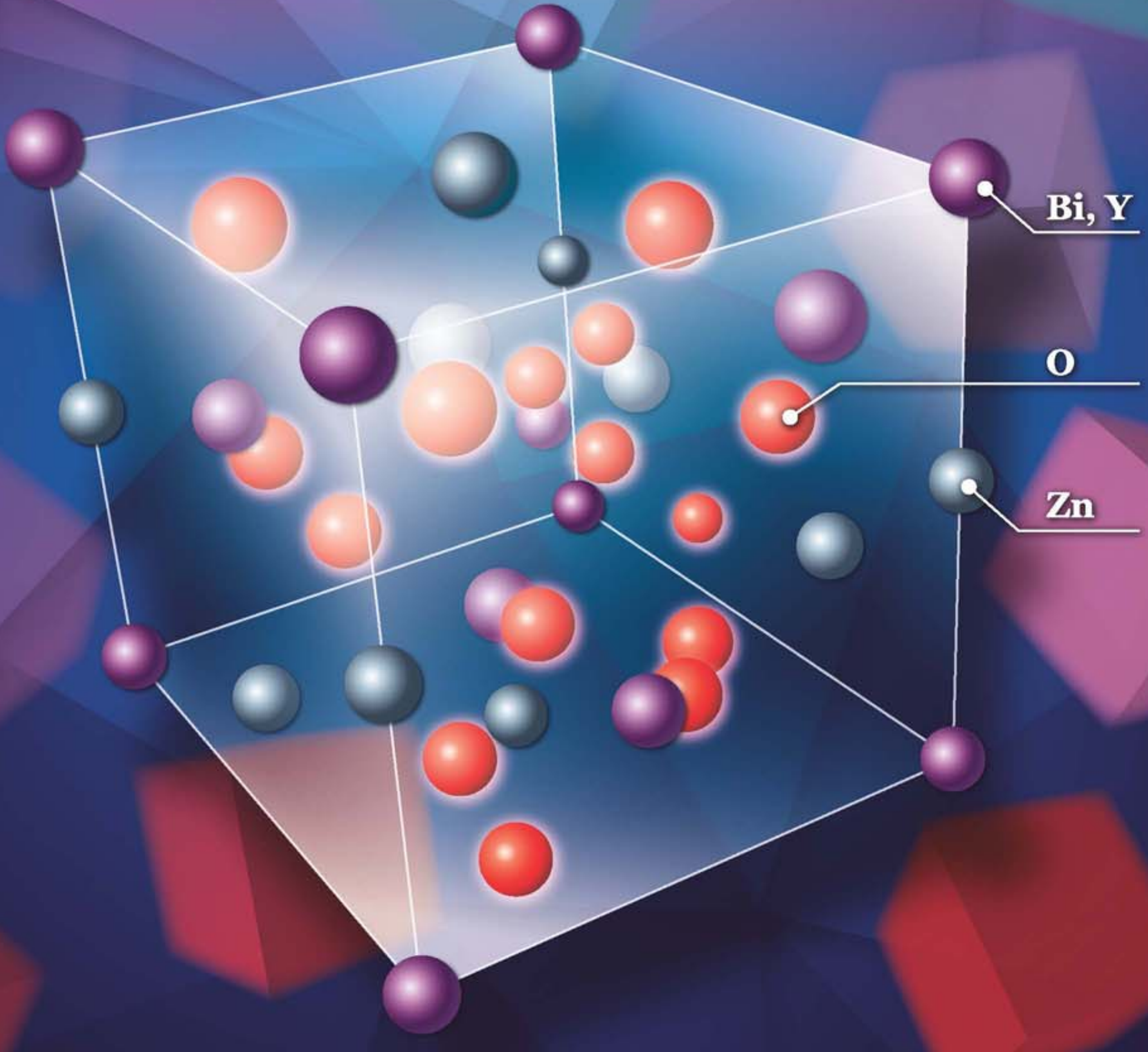

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Elevated CO_2 facilitates C and N accumulation in a rice paddy ecosystem

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ABSTRACT

Elevated CO_2 can stimulate wetland carbon (C) and nitrogen (N) exports through gaseous and dissolved pathways, however, the consequent influences on the C and N pools are still not fully known. Therefore, we set up a free-air CO_2 enrichment experiment in a paddy field in Eastern China. After five year fumigation, we studied C and N in the plant–water–soil system. The results showed: (1) elevated CO_2 stimulated rice aboveground biomass and N accumulations by 19.1% and 12.5%, respectively. (2) Elevated CO_2 significantly increased paddy soil TOC and TN contents by 12.5% and 15.5%, respectively in the 0–15 cm layer, and 22.7% and 26.0% in the 15–30 cm soil layer. (3) Averaged across the rice growing period, elevated CO_2 greatly increased TOC and TN contents in the surface water by 7.6% and 11.4%, respectively. (4) The TOC/TN ratio and natural $\delta^{15}N$ value in the surface soil showed a decreasing trend under elevated CO_2. The above results indicate that elevated CO_2 can benefit C and N accumulation in paddy fields. Given the similarity between the paddies and natural wetlands, our results also suggest a great potential for long-term C and N accumulation in natural wetlands under future climate patterns.

Introduction

During the last three decades, great efforts have been made to elucidate the effects of CO_2 enrichment on ecosystem carbon (C) and nitrogen (N) dynamics. However, most studies have been focused on terrestrial ecosystems with few paying attention to wetlands (Keller et al., 2009). Wetlands play a great role in global C and N cycling. About 513 Pg C (1 Pg = 10^{15} g) is stored in the wetland soils, roughly one-third of the total global soil C pool (Bridgham et al., 2006). In addition, about 40% of the global CH_4 emission (Dacey et al., 1994) and 20% of the terrestrial dissolved organic carbon (DOC) export (Fenner et al., 2007) originate from wetlands. Meanwhile, both the gaseous and dissolved C exports can be stimulated by environmental changes, such as air CO_2 enrichment (Dacey et al., 1994; Freeman et al., 2004; Guo et al., 2011; Inubushi et al., 2003). Thus, learning the CO_2-led impacts on wetland C and N dynamics will greatly enhance our understanding of global C and N cycling in future climates.

Increasing evidence has shown that elevated CO_2 may significantly affect C and N budgets in wetlands. On one hand, elevated CO_2 can increase C inputs into wetland ecosystems

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through enhancing plant biomass accumulation and root exudation (Erickson et al., 2007; Ma et al., 2004). The CO_2-enhanced C accumulation may simultaneously stimulate N accumulation in wetlands because C and N cycles are strongly coupled in most ecosystems (Luo et al., 2004). Meanwhile, the CO_2-enhanced available C source as rhizodeposition can stimulate biological N fixation (BNF) in wetland ecosystems (Dakora and Drake, 2000; Hoque et al., 2001; Inubushi et al., 2003), which may further benefit C and N accumulation in wetlands. On the other hand, elevated CO_2 can promote C outputs from wetlands through gaseous (Dacey et al., 1994; Inubushi et al., 2003) and dissolved (Freeman et al., 2004; Guo et al., 2011) pathways. The enhanced C exports may also increase N loss (Guo et al., 2011) from wetlands due to the coupled cycling of C and N. Therefore, these CO_2-led changes in the inputs and outputs of wetland C and N may consequently affect the C and N pools. Both in a scrub-oak ecosystem and a C_3/C_4 grassland ecosystem, long-term CO_2 enrichment did not promote ecosystem C and N sequestration (Hungate et al., 2006; Gill et al., 2006), while in the Duke Forest FACE and Sweetgum Forest FACE, long-term CO_2 enrichment was found to promote C and N sequestration (Finzi et al., 2006; Norby and Iversen, 2006). However, there is still a lack of evidence concerning the CO_2-induced impacts on wetland C and N pools.

Long-term CO_2 experiments can contribute a great deal to research on the changes of wetland C and N pools. To our knowledge, there are two ongoing long-term CO_2 experiments being performed in wetlands *in situ*. One was initiated in 1987 with an open-top chamber (1 m in height and 0.47 m^2 in area) in a tidal wetland, Chesapeake Bay, USA (Erickson et al., 2007). This experiment has provided us many novel findings about wetland responses to CO_2 enrichment (Dakora and Drake, 2000; Langley et al., 2009; Langley and Megonigal, 2010). Nevertheless, the CO_2-led impacts on C and N pools are still not clear likely due to the limited experimental size and unstable aquatic conditions for water and soil sampling. The other is our paddy free-air CO_2 enrichment (FACE) experiment conducted since 2004 in China (Cheng et al., 2010). Observations from our experiment showed that elevated CO_2 can significantly stimulate C and N inputs in the form of crop biomass, N accumulation and root exudation (Cheng et al., 2010; Ma et al., 2004), and C and N outputs as CH_4 emission (Zheng et al., 2006) and DOC and dissolved N (DN) export (Guo et al., 2011). However, the consequent impacts on the C and N pools still remain to be investigated.

The rice paddy ecosystem is the largest artificial wetland. It not only supplies the staple food for nearly 50% of the world's population (Sass and Cicerone, 2002), but also plays an important role in global C and N cycling (Pan et al., 2003). In addition to the great similarity with natural wetlands, paddy fields also maintain relatively stable conditions for water and soil sampling during the whole rice growing season. The FACE experiment in a rice paddy field can provide great opportunities to learn the responses of wetland C and N dynamics to elevated CO_2. Therefore, after five-year CO_2 fumigation, we investigated the C and N dynamics in the plant–water–soil system in a rice paddy ecosystem to learn the responses of coupled C and N cycles to atmospheric CO_2 enrichment.

1. Materials and methods

1.1. Experiment site description

The rice–wheat cropping FACE system was set up in June 2004 near Jiangdu city, Jiangsu province, China (32°35′5″N, 119°42′0″E, 5 m a.s.l.) on a calcareous soil (a Mollisol in USA-ST, pH = 7.2). The cropping system has prevailed in this region for more than 1000 yr and is a typical cropping system in South and East Asia. The climate conditions are subtropical with mean annual precipitation of 980 mm, mean annual temperature 14.9°C, annual sunshine time more than 2100 hr, and frostless period more than 220 days. Relevant soil properties are as follows: clay (<0.002 mm) 13.6%; silt (0.002–0.02 mm) 28.5%; sand (0.02–2 mm) 57.8%; bulk density 1.16 g/cm^3; TOC 18.4 g/kg; TN 1.45 g/kg; TP 0.63 g/kg.

1.2. FACE system design

The FACE system had two target CO_2 concentrations randomly located in six replicate octagonal plots with each having a useful area of 80 m^2 (three for elevated CO_2 and the others for ambient CO_2). The CO_2 concentration in the elevated plots (hereinafter referred to as FACE) was controlled constantly about 200 μmol/mol higher than that in the ambient. Each plot was split into two subplots with different N levels (25 and 12.5 g/m^2, respectively, where 25 g/m^2 was the local normal N application level) and separated from the surrounding area by a polyvinyl chloride (PVC) board. In each plot, a 30 cm tall PVC board was inserted into soil between the two N level subplots (10 cm into the soil and 20 cm above the soil surface) to prevent the cross-over of water and nutrients. More details of the FACE system such as design, rationale, operation and performance are provided by Liu et al. (2002) and Okada et al. (2001).

1.3. Crop management

Rice seeds were respectively sown under elevated and ambient CO_2 in mid-May. In mid-June, rice seedlings were transplanted manually into their corresponding field plots at a density of three seedlings per hill and 24 hills/m^2. About 36% of the total N was applied as a basal dressing one day prior to transplanting and 24% as a side dressing at early tillering six days after transplanting (DAT), and the other 40% at panicle initiation on 43 DAT. Typical irrigation regimes of the surrounding areas were conducted. Each plot was randomly irrigated with nearby river water through agricultural irrigation ditches, submerged with water (about 5 cm in depth) from mid-June to mid-July, then drained several times up to the beginning of August, and afterwards flooded with intermittent irrigation until 10 days before harvest. Other field management of the plots also followed the local agronomic practices.

1.4. Sampling method and measurement

Rice plant samples were taken at harvest and then separated into leaf, stem (including leaf sheath) and panicles. All parts were oven-dried at 80°C to a constant weight and weighed. Afterwards, they were ground and passed through a 0.5 mm mesh sieve for the determination of N concentrations by Kjeldahl digestion. N accumulation in every part was calculated as N concentration × biomass. The aboveground biomass and N accumulation were calculated by directly adding up their accumulations in all plant parts.

The water samples and the 0–15 cm soil cores for DOC and DN determinations were collected on 22, 40, 59 and 76 DAT, and the sampling methods were the same as the methods used in Guo et al. (2011). After rice was harvested, soil cores (2 cm in diameter and 50 cm depth) were collected to obtain 0–15, 15–30 and 30–50 cm deep samples for the determinations of TOC, TN and natural $\delta^{15}N$ value. Samples from each subplot were chosen randomly from six spots and repetition of sampling spots was avoided. The storage and pre-treatment of the samples were also the same as the methods used in Guo et al. (2011). The TOC and TN in the surface water as well as DOC and DN in the soil were determined as soon as possible within one week. The TOC, TN and natural $\delta^{15}N$ value in soil were measured after the samples were air-dried, ground and sieved.

The TOC and TN in the surface water were measured by a TOC-Analyzer (Multi N/C 3000, Analytik Jena AG, Jena, Freistaat Thüringen, Germany) and flowing analyzer (San++ system, Skalar, Breda, Noord-Brabant, The Netherlands) following a UV-digestion technique, respectively. The solution for measurement of soil DOC and DN was extracted by shaking (200 r/min) 10 g unsieved, field-moist soil with distilled water (1:5 w/v soil-to-solution ratio) for 1 hr at 20°C (Jones and Willett, 2006) and then filtered through a 0.45 μm filter membrane. The DOC and DN in the extracting solution were determined by the same methods as TOC and TN in the surface water. The TOC and TN in soil were determined by an Element Analyzer (Vario Max, Elementar, Hanau, Schwarzwald, Germany). The natural $\delta^{15}N$ value in soil was determined by an isotope mass spectrometer (MAT251, Thermo Finnigan, Silicon Valley, California, America) as described by Shearer et al. (1974).

1.5. *Statistical analysis*

Data were analyzed with Excel 2003 for Windows (Microsoft, Redmond, Washington State, America) and the statistical package SPSS11.5. ANOVA with general linear models was used. Differences were considered significant at $p < 0.05$. Like the report by Cheng et al. (2010) and due to the reasons elucidated by Guo et al. (2011), there were no significant effects of N and N × CO_2 on any of the indexes. Therefore the mean of two measurements under two N treatments in each CO_2 ring was taken as the plot value.

2. Results

2.1. *Crop aboveground biomass and N accumulation*

Rice aboveground biomass, except for leaf, was stimulated by elevated CO_2 (Fig. 1a). The stem, panicle and total aboveground biomass significantly increased by 21.9%, 24.0% and 19.1%, respectively, in the FACE plots. Along with the biomass increment, N accumulations in stem, panicle and total aboveground biomass also correspondingly increased by 1.5%, 16.4% and 12.5%, respectively, in the FACE plots (Fig. 1b).

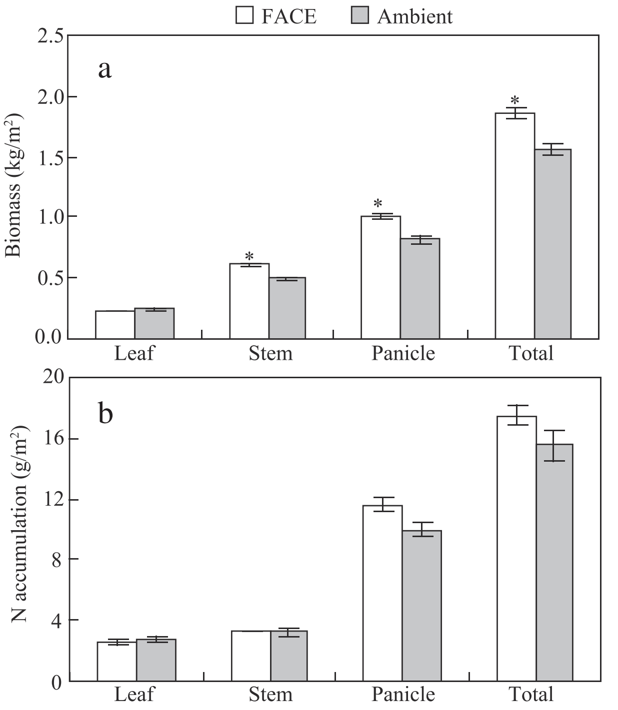

Fig. 1 – Rice (a) aboveground biomass and (b) N accumulation under elevated CO_2 (FACE) and ambient CO_2 (ambient). Values are means ± 1SE, * stands for $p < 0.05$.

2.2. *TOC and TN concentrations in the surface water*

The TOC and TN were both enhanced by elevated CO_2 during the rice growing season (Fig. 2). Averaged across all sampling dates, elevated CO_2 increased TOC concentration in the surface water by 7.6%, with a significant effect on 22 DAT. At the same time, elevated CO_2 also increased TN concentration in the surface water by 11.4% with significant effects on 22 and 59 DAT.

2.3. *TOC and TN concentrations and natural $\delta^{15}N$ value in different soil layers*

Compared to the ambient, elevated CO_2 significantly increased the concentrations of TOC and TN by 12.5% and 15.5% in the 0–15 cm soil layer, and 22.7% and 26.0% in the 15–30 cm layer (Fig. 3). Similar effects occurred in the 30–50 cm soil layer, though they were not significant.

Elevated CO_2 significantly decreased the natural $\delta^{15}N$ value by 19.3% in the 0–15 cm soil layer (Fig. 3). Similarly, the natural $\delta^{15}N$ values in the 15–30 and 30–50 cm layers were respectively 11.7% and 7.0% lower in the FACE plots than in the ambient. No significant difference of natural $\delta^{15}N$ values existed between soil layers (Fig. 3).

2.4. *DOC and DN concentrations in 0–15 cm soil layer*

Different from the responses of soil TOC and TN to elevated CO_2, DOC and DN contents in the 0–15 cm soil layer showed opposite responses to elevated CO_2 during the whole rice season (Fig. 4). Averaged across all sampling dates, the DOC contents in the 0–15 cm soil layer increased by 26.3% in the FACE plots, with significant increments on all sampling dates. However, elevated CO_2 decreased DN contents in the 0–15 cm soil layer by 17.8% on average during rice growing duration, with significant effects on 22 and 40 DAT (Fig. 4).

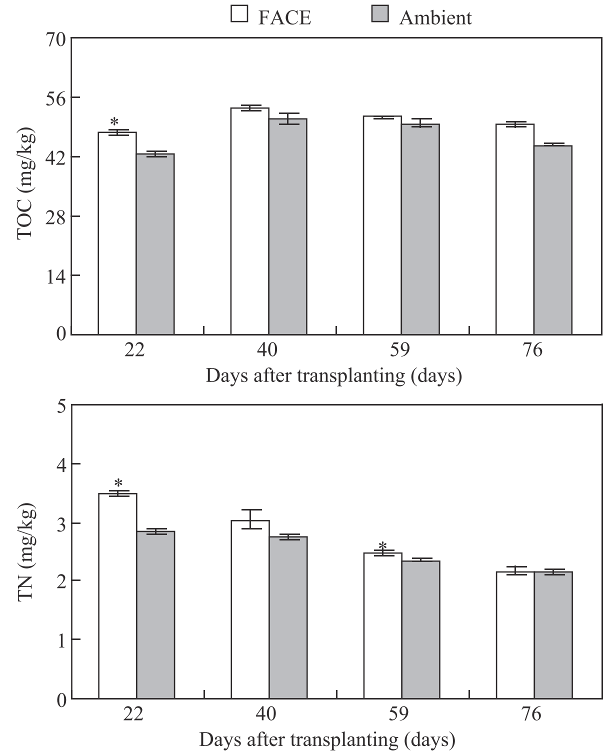

Fig. 2 – Concentrations of TOC and TN in the surface water under elevated CO_2 (FACE) and ambient CO_2 (ambient). Values are means ± 1SE, * stands for $p < 0.05$.

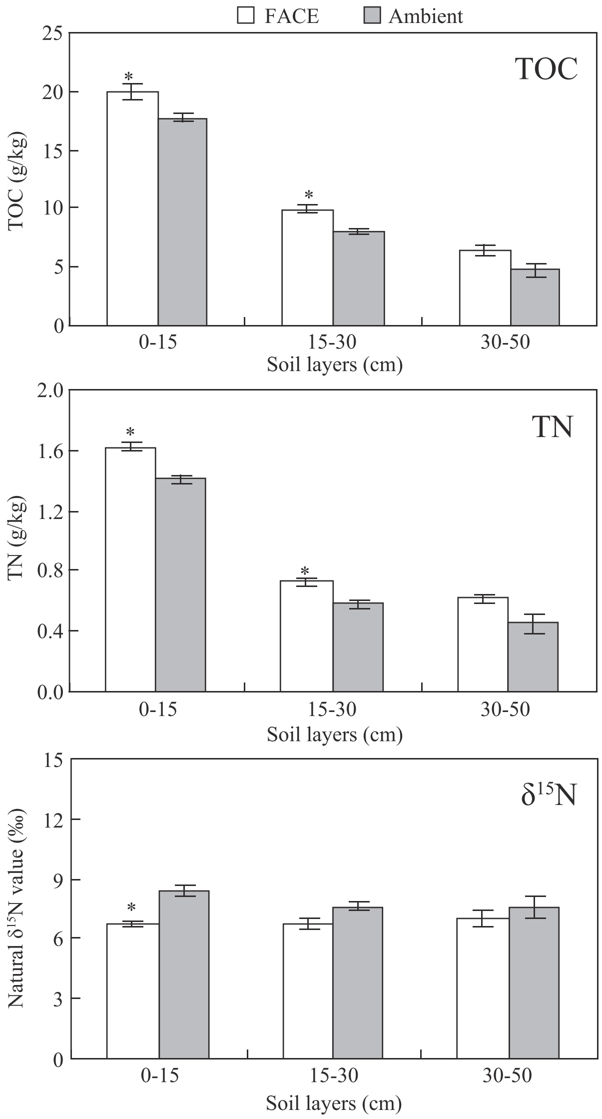

Fig. 3 – Concentrations of TOC and TN, and natural ^{15}N value in different soil layers under elevated CO_2 (FACE) and ambient CO_2 (Ambient). Values are means ± 1SE, * stands for $p < 0.05$.

2.5. C/N ratios in the surface water and soil

Elevated CO_2 decreased the TOC/TN ratio in the surface water on 22, 40 and 59 DAT, with significant effects on 22 and 40 DAT (Fig. 5a). Averaged across 22, 40 and 59 DAT, the TOC/TN ratio in the surface water was 8.7% lower in the FACE plots than in the ambient. Meanwhile, elevated CO_2 also tended to decrease the TOC/TN ratios in the soil layers of 0–15 and 15–30 cm by 2.6% and 2.9%, respectively (Fig. 5b). The DOC/DN ratio in the 0–15 cm soil layer was increased by elevated CO_2, with significant increment on 22 and 40 DAT (Fig. 5c). Averaged across all sampling dates, the DOC/DN ratio in the 0–15 cm soil layer was 38.1% higher in the FACE plots than in the ambient. Compared with the TOC/TN ratios in the surface water and soil, the DOC/DN ratio was significantly lower. There was no obvious difference in the TOC/TN ratio between the surface water and soil.

3. Discussion

Former research from our site and other natural wetlands showed evidence that CO_2 enrichment can increase C outputs through gaseous (Dacey et al., 1994; Zheng et al., 2006) and dissolved (Freeman et al., 2004; Guo et al., 2011) pathways. This suggests that CO_2 enrichment may impede C accumulation in the wetlands. However, the increments of crop biomass (Fig. 1), TOC contents in the surface water (Fig. 2) and soil (Fig. 3) together demonstrate that elevated CO_2 can facilitate C accumulation in the paddy ecosystem. Our results indicate that CO_2-led stimulation of C output is less than the stimulation of C input in the paddy field. Through stimulating rice aboveground biomass growth (Fig. 1) (Kim et al., 2003; Cheng et al., 2010), elevated CO_2 can promote more C allocated belowground as root biomass (Yang et al., 2008) and exudation (Ma et al., 2004). Additionally, the CO_2-stimulated aboveground biomass growth can also increase litterfall to enhance C pools in the soil (Paterson et al., 1997). Although the CO_2-enhanced root-related available C source can increase C export as CH_4 (Zheng et al., 2006) and DOC (Guo et al., 2011), most newly-added C will still accumulate in soil as long-lasting patterns due to the anaerobic conditions in paddy fields (Witt et al., 2000). Under anaerobic conditions, the decomposition and/or mineralization rates of organic matter are much lower than under aerobic conditions (Witt et al., 2000). Furthermore, intensive rice cropping can

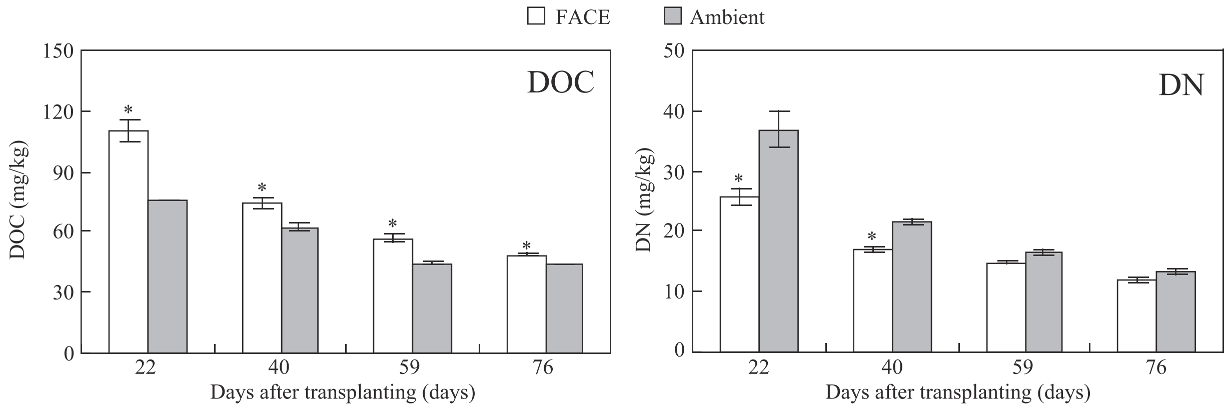

Fig. 4 – Concentrations of DOC and DN in 0–15 cm soil layer under elevated CO_2 (FACE) and ambient CO_2 (ambient). Values are means ± 1SE, * stands for $p < 0.05$.

accumulate many phenolic lignin compounds to resist organic matter decomposition under submergence (Olk et al., 2000). As a result, more C can be accumulated in the paddy field under CO_2 enrichment.

Considering the crop biomass harvesting and paddy drainage, CO_2-enhanced biomass N (Fig. 1) and aquatic N (Fig. 2) indicate that more N might have been exported from the FACE plots. However, the higher soil TN content in the FACE plots than in the ambient (Fig. 3) suggests that CO_2 enrichment also benefits N accumulation in paddy fields. Three reasons may contribute to the CO_2-led increment of N content in the soil. Firstly, the CO_2-led C accumulation in soil can simultaneously combine more soil-available N to form long-living soil organic matter (SOM) due to the coupled cycling of C and N (Luo et al., 2004). Similar CO_2-led stimulation of C and N accumulation was also found in the Duke Forest FACE after six-year CO_2 fumigation (Finzi et al., 2006). Secondly, CO_2 enrichment can enhance microbial growth and activity in paddy soil (Li et al., 2004), consequently resulting in more N immobilized in microbial biomass. For example, in a Japanese paddy FACE, elevated CO_2 significantly increased microbial biomass N by 25%–42% in

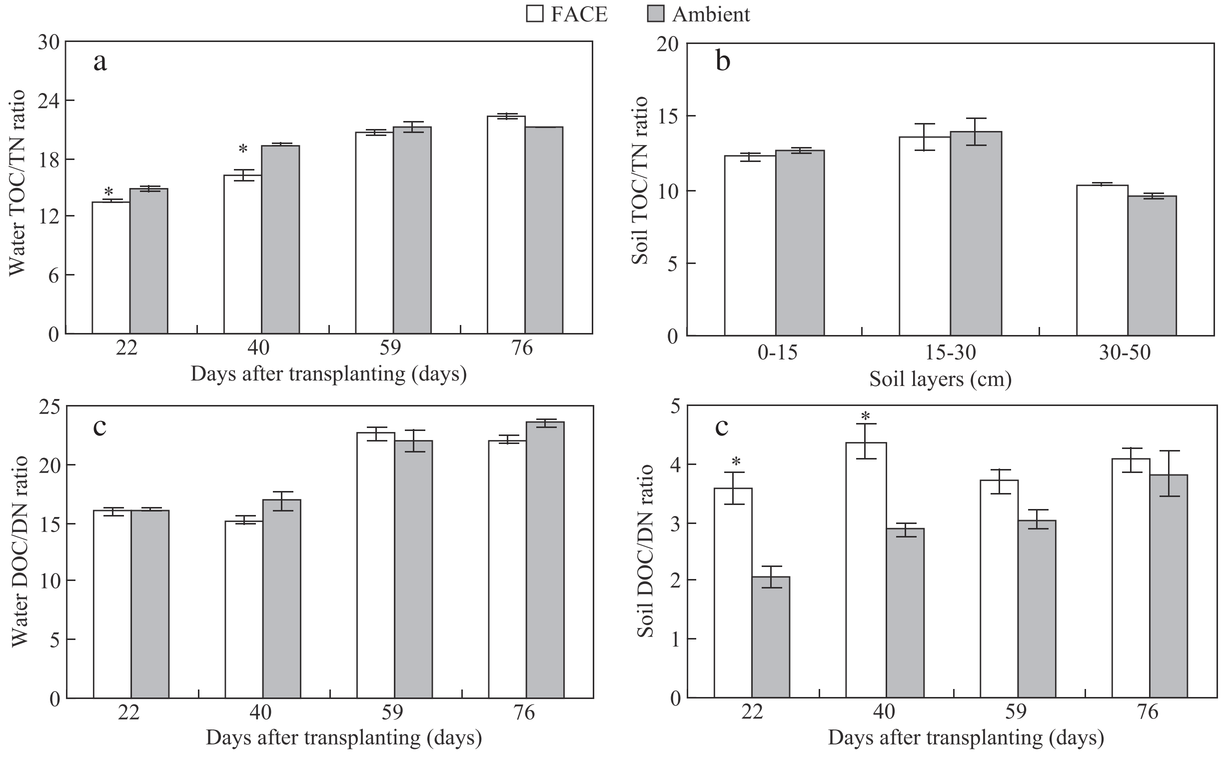

Fig. 5 – TOC/TN ratios in (a) the surface water and (b) soil and the DOC/DN ratio in (c) 0–15 cm soil layer under elevated CO_2 (FACE) and ambient CO_2 (Ambient). Values are means ± 1SE, * stands for $p < 0.05$.

0–1 cm soil layer at rice harvest (Hoque et al., 2002). Thirdly, the CO_2-enhanced C source can stimulate BNF in paddy fields, further facilitating N accumulation. It was estimated that 50–75 kg N/(ha · yr) added into the paddy field mainly came from BNF (Ladha et al., 1983), so the BNF contributes significantly to the N inputs into the paddy ecosystem (Roger and Ladha, 1992). Previous studies showed that BNF activity in 0–10 cm paddy soil could be significantly enhanced by elevated CO_2 both in FACE (Hoque et al., 2001) and chamber (Cheng et al., 2001) experiments. In addition, the algal growth in 0–1 cm paddy soil was also significantly increased by elevated CO_2 (Hoque et al., 2001). The CO_2-led decrement of soil natural $\delta^{15}N$ abundance (Fig. 3) also indicates the presence of CO_2-stimulated BNF because BNF can decrease soil natural $\delta^{15}N$ abundance (Shearer et al., 1978). Similarly, Dakora and Drake (2000) found that the nitrogenase activities in C_3 and C_4 plant-free sediments were also significantly enhanced by elevated CO_2 in the Chesapeake Bay wetland. Our recent observation found that elevated CO_2 improved the mineral nutrients (*e.g.*, Ca^{2+}, Mg^{2+}) in paddy soil (Cheng et al., 2010), which can further enhance CO_2-led N_2 fixation (van Groenigen et al., 2006).

In our experiment, elevated CO_2 increased the biomass/N ratios by 10.4%, 18.3%, 7.3% and 12.3% in the leaf, stem, panicle and the total aboveground, respectively. This means that more CO_2 can be assimilated in rice plants with the same available N. Meanwhile, the CO_2-led decreasing trends of TOC/TN ratio (Fig. 5) in the surface water and soil indicate that more N can be accumulated in the paddy field with the same organic C. The C/N ratio changes further suggest that CO_2 enrichment may benefit C and N accumulation in the paddy field. Although CO_2 enrichment increased TOC and TN contents in the surface water, the significant difference between the TOC/TN ratio (Fig. 5a) and the DOC/DN ratio (Fig. 5c) indicated that the TOC and TN in the surface water might not mainly come from the soil. Since the C/N ratio of organisms is greatly lower than that of crops (Kaye and Hart, 1997), the CO_2-stimulated growth of aquatic organisms may contribute a lot to the increments of water TOC and TN contents (Hoque et al., 2001; Inubushi et al., 2003). This implies that CO_2-led increments in water TOC and TN may not weaken C and N accumulation in paddy fields, especially in the soil. Considering the great similarity between the paddy field and the natural wetland, our results suggest that elevated CO_2 may also facilitate C and N accumulation in natural wetlands.

4. Conclusions

The field-based data in our research showed that, after five year fumigation, elevated CO_2 can stimulate the C and N accumulations in a rice paddy ecosystem. Firstly, elevated CO_2 increased the aboveground biomass and N accumulations of plants. Secondly, elevated CO_2 significantly increased TOC and TN concentrations in the surface water averaged across the whole growing period. Finally, elevated CO_2 also greatly increased the paddy soil TOC and TN contents at 0–30 cm depth. Together with the result of the decreasing trend of TOC/TN ratio and natural $\delta^{15}N$ value in the surface soil under elevated CO_2, we concluded that elevated CO_2 can benefit C and N accumulation in a rice paddy ecosystem, in which the biological N fixation may play an important role. Due to the similarity between paddies and natural wetlands, the results illustrate the positive impacts of elevated atmospheric CO_2 on long-term C and N accumulation in natural wetlands in the future.

Acknowledgments

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