Effects of elevated CO_2 concentration and nitrogen supply on biomass and active carbon of freshwater marsh after two growing seasons in Sanjiang Plain, Northeast China

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Abstract

An experiments were carried out with treatments differing in nitrogen supply (0, 5 and 15 g N/m^2) and CO_2 levels (350 and 700 µmol/mol) using OTC (open top chamber) equipment to investigate the biomass of *Calamagrostis angustifolia* and soil active carbon contents after two years. The results showed that elevated CO_2 concentration increased the biomass of *C. angustifolia* and the magnitude of response varied with each growth period. Elevated CO_2 concentration has increased aboveground biomass by 16.7% and 17.6% during the jointing and heading periods and only 3.5% and 9.4% during dough and maturity periods. The increases in belowground biomass due to CO_2 elevation was 26.5%, 34.0% and 28.7% during the heading, dough and maturity periods, respectively. The responses of biomass to enhanced CO_2 concentrations are differed in N levels. Both the increase of aboveground biomass and belowground biomass were greater under high level of N supply (15 g N/m^2). Elevated CO_2 concentration also increased the allocation of biomass and carbon in root. Under elevated CO_2 concentration, the average values of active carbon tended to increase. The increases of soil active soil contents followed the sequence of microbial biomass carbon (10.6%) > dissolved organic carbon (7.5%) > labile oxidable carbon (6.6%) > carbohydrate carbon (4.1%). Stepwise regressions indicated there were significant correlations between the soil active carbon contents and plant biomass. Particularly, microbial biomass carbon, labile oxidable carbon and carbohydrate carbon were found to be correlated with belowground biomass, while dissolved organic carbon has correlation with aboveground biomass. Therefore, increased biomass was regarded as the main driving force for the increase in soil active organic carbon under elevated CO_2 concentration.

Key words: elevated CO_2 concentration; freshwater marsh; biomass; soil active carbon

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Introduction

Anthropogenic activities, such as combustion of fossil fuels, deforestation and intensive agriculture have increased CO_2 concentration from about 280 µmol/mol at the beginning of the industrial revolution to about 375 µmol/mol at the present time, which would be doubled at the middle of this century predicated by IPCC scenario (Meehl *et al.*, 2007). As CO_2 is an important element for plant photosynthesis, elevated CO_2 concentration is expected to have numerous direct and indirect effects on terrestrial ecosystems. The increase of NPP under elevated CO_2 is widely demonstrated in many ecosystems and more carbon allocation from foliage to roots is also reported (Rogers *et al.*, 1994; Zak *et al.*, 2000). The enhanced carbon transfer to the root may result in the enhanced rhi-

zodeposition and subsequent transfer to soil carbon pools (Hoosbeek *et al.*, 2006). The sizes of soil organic carbon pool in many ecosystems are so vast and spatially variable that it masks relatively smaller treatment effects, especially for short-term experiments (Hungate *et al.*, 1996). Temporary fluctuation of soil organic carbon mainly occurs in the portion of active carbon pools (Alessandra *et al.*, 2002). Due to increases in atmospheric CO_2 concentration, the concentrations of soil active carbon would be increased via the inputs of plant-carbon into the soils (Cardon *et al.*, 2001; Pratap *et al.*, 2007). A study of active and labile carbon-pools can serve as a clue for soil organic carbon dynamics on exposure to elevated CO_2.

Furthermore, as atmospheric CO_2 concentration increases, N is likely to be the limiting factor for plant growth (Daepp *et al.*, 2000). Both elevated CO_2 and N have been found to increase plant biomass, and the effect of elevated CO_2 has often been found to be most positive under high N

availability (Daepp *et al*., 2000; Körner, 2000). Moreover, both elevated CO_2 and N addition alter the plant tissue C to N ratio (increased by elevated CO_2 concentration and decreased by high N), which tends to alter the decomposability of plant residues (van Groenigen *et al*., 2005). These effects on plants would be expected to feedback on soil organic matter. Elevated CO_2 often increased soil labile active carbon (Hoosbeek *et al*., 2006; Pratap *et al*., 2007), while fertilization has shown contradictory effects on soil active carbon: suppression (Arnebrant *et al*., 1996), enhancement (Allen and Schlesinger, 2004), or no effect (Flanagan and Van Cleve, 1983). The CO_2 and N levels could interact with each other in influencing the amount of new carbon inputs, potentially altering carbon storage in soils (Xie *et al*., 2005). However, Cotrufo and Gorissen (1997) reported that both elevated CO_2 and N fertilization increased soil microbial carbon but no interaction was observed.

Some researchers have studied the effects of elevated CO_2 concentration on terrestrial ecosystems in China. Bai and Wang (1996) and Wang *et al*. (1997) used open top chamber (OTC) to detect potential impacts of CO_2 concentration enrichment on crop growth. Similar studies were made by Jiang (1997) and Han *et al*. (1999) for grassland and forest ecosystems, respectively. In 2001, the Chinese rice/wheat FACE platform was established at Wuxi City of Jiangsu Province. Compared with other terrestrial ecosystem studies, relatively fewer studies have been made to elucidate possible effects of elevated CO_2 concentration on wetland ecosystems. Wetlands cover only 4%–6% of the land surface, but play an important role in global ecosystems. Wetlands are vast stores of carbon of 455 Pg carbon (Gorham, 1991) as well as substantial sources of greenhouse gases such as CO_2, CH_4 and N_2O (Freeman *et al*., 1993). Even small changes in the net primary of wetlands under elevated atmosphere CO_2 concentration could significantly influence the balance of greenhouse gas fluxes between the atmosphere and biosphere (Kang *et al*., 2001). However, little is known about how dynamics of soil active carbon in wetland ecosystems will respond to elevated CO_2 concentration.

The objectives of this study were to detect: (1) the influence of elevated CO_2 on the biomass of *C. angustifolia* and carbon partition under different nitrogen treatments; (2) the responses of soil active carbon to CO_2 enrichment. The relationship between plant biomass and active carbon under elevated CO_2 was also explained.

1 Materials and methods

1.1 Experiment setup

The experimental site is located at the Sanjiang Mire Wetland Experimental Station (47°35′N, 133°31′E), Chinese Academy of Sciences. The average above sea altitude is 56 m. Mean annual temperature is 1.9°C with an average thaw-freeze period of 125 d (Song *et al*., 2003). Mean annual precipitation is 550–560 mm, with more than 65% of total precipitation in July and August. The open-

top chambers were constructed of a structural octagonal aluminum frame (3 m in diameter and 2.4 m in height) covered with glass. The center of chamber was made with a hollow PVC with perforations for passing CO_2. Pure CO_2 gas was dispersed under controlled pressure. The desired concentration of CO_2 was achieved with a gas flow-meter and gas regulator. Eight fans were fixed at each side of the chamber to mix the air and CO_2. Elevated atmosphere CO_2 concentration was monitored three times daily throughout the growing season using a portable infrared gas analyzer (GXH-3010F, Beijing Huayun Company, China).

The treatments consisted of two CO_2 concentrations: ambient concentration 350 μmol/mol (AC) and elevated concentration 700 μmol/mol (EC). Three nitrogen treatments were imposed on each chamber by application of NH_4NO_3 solution. One treatment (NN) was without any nitrogen input (0 g N/m^2), the medium nitrogen level (MN) was 5 g N/m^2, and the high level (HN) was 15 g N/m^2. Nitrogen fertilization started in June 2007, and was repeated once a month during the growing season of 2007 and 2008.

The soil for the experiment was derived from the *C. angustifolia* wetland which located near Sanjiang Mire Wetland Experimental Station, Chinese Academy of Sciences. Soil properties are given in Table 1. In May 2007, 10 cm tall seedlings of *C. angustifolia* were selected as samples. Twenty-one seedlings were grown in each pot, simulating field plant density.

Table 1   Properties of the experimental soil

Soil property	Value
pH	5.64
Soil type	Meadow soil
Clay < 0.002 mm (g/kg)	393.2
Silt 0.002–0.02 mm (g/kg)	543.2
Sand > 0.02 mm (g/kg)	63.6
Porosity (%)	63.01
Soil organic carbon (g/kg)	39.66
Total nitrogen (g/kg)	2.47

1.2 Soil and plant sampling

Plant and soil sampling were carried out at the jointing, heading, dough and maturity periods in 2007 and at maturity in 2008. The aboveground biomass of plants was cut near the ground. The belowground parts was carefully washed and sealed in plastic bags. All the plant samples were oven-dried at 80°C for 24 h and then weighted. The soils were passed through a 2-mm sieve to preserve at –4°C until analysis for microbial biomass carbon (MBC) and dissolved organic carbon (DOC), while air-dried soils (2-mm sieved) were used for estimating carbohydrate carbon (CHC), labile oxidable carbon (LBC) and total soil organic carbon (SOC).

1.3 Chemical analysis

Soil pH was determined at a 1:2.5 (*m/V*) soil-to-water ratio. To determine soil particles, 0.1 g soil was weighed in 100 mL beaker and 30 mL distilled water was added.

After 20 min ultrasonic wave concussion, the soil solution was measured by a laser particle sizer (LS13320, Beckman Coulter, USA) for 0.1–2000 μm measuring range with error less than 1%. MBC was determined by fumigation-extraction (Vance, 1987). Two portions of fresh soil (equivalent to 20 g dry soil) were weighted. One portion (not fumigated) was immediately extracted with 80 mL of 0.5 mol/L K_2SO_4 for 30 min by oscillating shaking at 200 r/min and filtered. The other portion was fumigated for 24 h at 25°C with ethano-free $CHCl_3$ and then extracted as described above. Organic carbon in the extracts was determined after oxidation with 0.4 mol/L $K_2Cr_2O_7$ at 100°C for 30 min. Both fumigated and non-fumigated samples were replicated three times. Microbial biomass carbon was calculated as a difference between fumigated and non-fumigated samples using extraction factors of $k_{EC} = 0.38$ for carbon. Dissolved organic carbon was determined after fresh soil was extracted (equivalent to 20 g dry soil) with 100 mL distilled water for 0.5 h, then filtered through 0.45 μm cellulose-acetate filters, and the concentration of total organic carbon (TOC) was determined by TOC-V_{CPH} (Chantigny, 2003). Air-dried soil samples were used for estimating CHC (Brink *et al.*, 1960) and 0.333 mol/L $KMnO_4$ LOC (Blair *et al.*, 1995).

1.4 Statistical analysis

Data were analyzed with the statistical package SPSS 10.0. Two-way ANOVA was applied to test the effects of elevated atmosphere CO_2 concentration and N fertilization as well as their interactions on the biomass. Stepwise regression analyses were generated to explore the relationships between the various soil active carbon pools (MBC, DOC, LOC, CHC) and plant biomass.

2 Results

2.1 Plant biomass and carbon allocation

2.1.1 Plant biomass

The effect of CO_2 enrichment on aboveground biomass is revealed in Table 2. Aboveground biomass was enhanced upon exposure to the elevated CO_2 concentration, but magnitude of increases stimulated by elevated CO_2 concentration differed in growth periods. The average increase for the three nitrogen treatments were 16.7%, 17.6% in jointing and heading periods, and only 3.5% and 9.4% in dough and maturity periods, respectively. Increasing N supply also significantly enhanced aboveground biomass under both CO_2 concentrations. Under ambient CO_2 concentration, the aboveground biomass increased by 33.0% ($P < 0.01$) with 5 g N/m² addition, and 111.6% ($P < 0.01$) for 15 g N/m² in maturity period. While under elevated CO_2 concentration, the increases were up to 41.7% ($P < 0.01$) and 117.9% ($P < 0.01$) with 5 and 15 g N/m² addition, respectively. The ANOVA results showed that the interaction of nitrogen and CO_2 concentration on aboveground biomass was not statistically significant ($P > 0.05$).

The response of belowground biomass to elevated CO_2 concentration also differed in each growth period. The effect of CO_2 concentration enrichment on belowground biomass was not significant during the jointing period, and the differences between the two CO_2 concentrations were not significant (Table 3). In the heading period, belowground biomass increased by an average of 26.5% and the enhancement were up to 34.0% and 28.7% in dough and maturity periods, respectively. The N supply also significantly enhanced the belowground biomass under both CO_2 concentrations. Under ambient CO_2 concentration, belowground biomass has increased by 27.8% ($P < 0.01$) and 50.4% ($P < 0.01$) with N addition of 5 and 15 g N/m². While under elevated CO_2 concentration, those increases were up to 57.2% ($P < 0.01$) and 86.9% ($P < 0.01$). The results showed that elevated CO_2 concentration could strengthen the effect of nitrogen fertilization on the belowground biomass of *C. angustifolia*, but the interaction of CO_2 and nitrogen concentration on belowground biomass was found to be significant only in the dough period ($P < 0.01$).

The effect of elevated CO_2 concentration on biomass at the maturity period in 2007 and 2008 are represented in Fig. 1. Compared to the year of 2007, the biomass of *C. angustifolia* in 2008 was smaller, but their difference was not significant ($P < 0.05$).

Table 2 Effects of elevated CO_2 concentration on aboveground biomass with different N levels at each growth period (g/m²)

Sampling period	0 g N/m² supply		5 g N/m² supply		15 g N/m² supply	
	AC	EC	AC	EC	AC	EC
Jointing period	119.28 ± 8.58 a	134.09 ± 16.14 a	141.88 ± 2.55 b	173.95 ± 9.61 a	181.49 ± 9.71 b	208.57 ± 12.26 a
Heading period	231.68 ± 11.72 b	280.17 ± 27.16 a	304.98 ± 28.12 a	355.35 ± 54.77 a	383.84 ± 14.89 b	442.61 ± 23.41 a
Dough period	289.60 ± 18.07 a	302.38 ± 25.95 a	386.96 ± 24.10 a	411.67 ± 32.82 a	617.69 ± 24.54 a	636.89 ± 79.76 a
Maturity period	285.88 ± 16.13 a	303.14 ± 22.25 a	380.30 ± 15.39 b	429.64 ± 39.53 a	604.77 ± 15.39 b	660.47 ± 20.60 a

| Sampling period	ANOVA		
	P_{CO_2}	P_N	$P_{CO_2 \text{ vs. N}}$
Jointing period	**	**	ns
Heading period	**	**	ns
Dough period	ns	**	ns
Maturity period	*	**	ns

AC: ambient CO_2; EC: elevated CO_2.
Data are presented as mean ± SD. ns, * and ** denote significance at $P > 0.05$, $P < 0.05$, and $P < 0.01$, respectively.

Table 3   Effects of elevated CO_2 concentration on belowground biomass with different nitrogen levels at each growth period (g/m^2)

Sampling period	0 g N/m^2 supply		5 g N/m^2 supply		15 g N/m^2 supply	
	AC	EC	AC	EC	AC	EC
Jointing period	162.33 ± 42.45 a	163.33 ± 43.02 a	174.07 ± 43.94 a	174.33 ± 61.21 a	199.13 ± 50.57 a	202.10 ± 35.40 a
Heading period	328.23 ± 44.15 a	386.10 ± 46.43 a	388.17 ± 15.78 b	510.91 ± 50.04 a	407.33 ± 32.72 b	530.67 ± 56.52 a
Dough period	682.60 ± 39.64 b	822.50 ± 60.31 a	999.23 ± 24.10 b	1420.87 ± 51.88 a	1208.07 ± 101.61 b	1682.10 ± 180.10 a
Maturity eriod	867.33 ± 38.73 a	1048.80 ± 123.66 a	1209.03 ± 20.51 b	1574.73 ± 166.40 a	1543.73 ± 70.90 b	2082.47 ± 207.39 a

Sampling period	ANOVA		
	P_{CO_2}	P_N	$P_{CO_2 \text{ vs. N}}$
Jointing period	ns	ns	ns
Heading period	**	**	ns
Dough period	**	**	**
Maturity eriod	**	**	ns
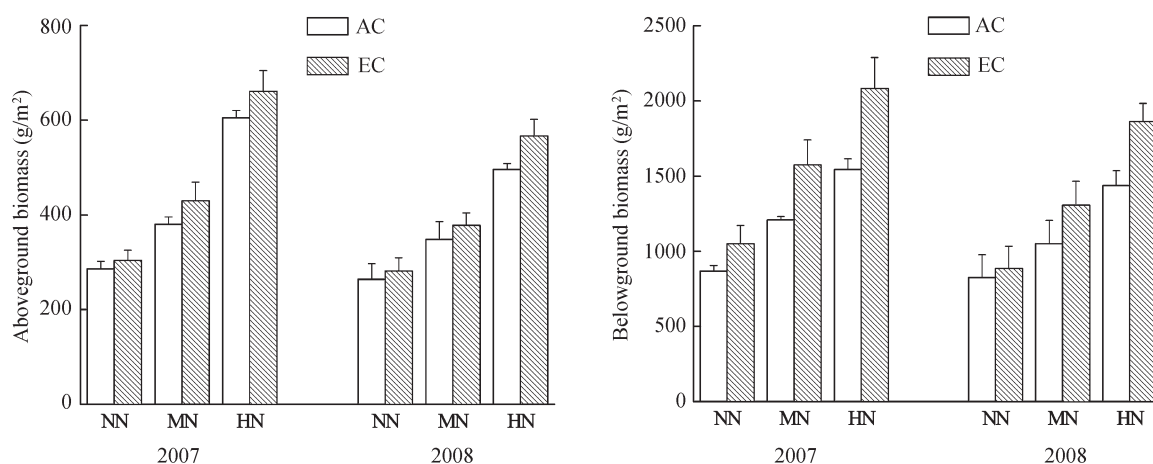
Fig. 1   Response of elevated CO_2 concentration on biomass at maturity period in 2007 and 2008. NN: 0 g N/m^2, MN: 5 g N/m^2; HN: 10 g N/m^2.

2.1.2 Biomass and carbon allocation in plant

The enhancement of CO_2 concentration elevation on belowground biomass was more significant than that of aboveground biomass. This caused a shift in the pattern of biomass partitioning. Irrespective of nitrogen level, the relative apportioning of biomass to belowground part was higher under elevated CO_2 concentration than that under ambient CO_2 concentration (Fig. 2a). The average increase (across the whole growth periods) was 1.3%, 2.1% and 4.9% with 0, 5, and 15 g N/m^2 treatments, respectively.

The effects of elevated CO_2 concentration on carbon allocation of *C. angustifolia* is shown in Fig. 2b. Enrichment of CO_2 concentration has enhanced the carbon allocation proportion in root by 2.8%, 3.0% and 4.9% with 0, 5, and 15 g N/m^2 treatments, respectively. Carbon allocations in stem and leaf decreased by an average of 5.82% and

Table 4   Average increases of active carbon due to elevated CO_2 concentration

Active carbon pools	Increased at elevated CO_2 (%)			Average (%)
	0 g N/m^2 supply	5 g N/m^2 supply	15 g N/m^2 supply	
MBC	6.7	7.9	17.3	10.6
DOC	12.5	3.7	6.4	7.5
LOC	11.2	5.1	3.6	6.6
CHC	7.5	7.1	–2.4	4.1

MBC: microbial biomass carbon; DOC: dissolved organic carbon; LOC: labile oxidable carbon; CHC: carbonhydrate carbon.

5.60%, respectively.

2.2 Soil active carbon pools

Figure 3 shows the dynamics of soil active carbon pools under elevated CO_2 concentration and different nitrogen treatments during the whole growth period. Elevated CO_2 concentration did not change the seasonal dynamics of soil active carbon pools. Under the two CO_2 concentrations, both MBC and DOC contents reached their maximums in the maturity period, while CHC and LOC got to their maximums in the heading and dough periods, respectively.

The average increases of all the soil active carbon in the year of 2007 and 2008 are shown in Table 4. Generally, elevated CO_2 concentration increased all the soil active carbon pools except CHC under high nitrogen treatment, and the average increase degree followed the sequence of MBC (10.6%) > DOC (7.5%) > LOC (6.6%) > CHC (4.1%).

2.3 Relationship between active carbon pools and plant parameters

Stepwise regression analysis was carried out with the respective active carbon pools as dependable variables to explore their dependence on various plant parameters (Table 5). We concluded that there were significant correlations between active carbon pools and plant parameters. Except DOC, all the coefficients of determination were significant at the 0.01 level. Correlative analysis showed
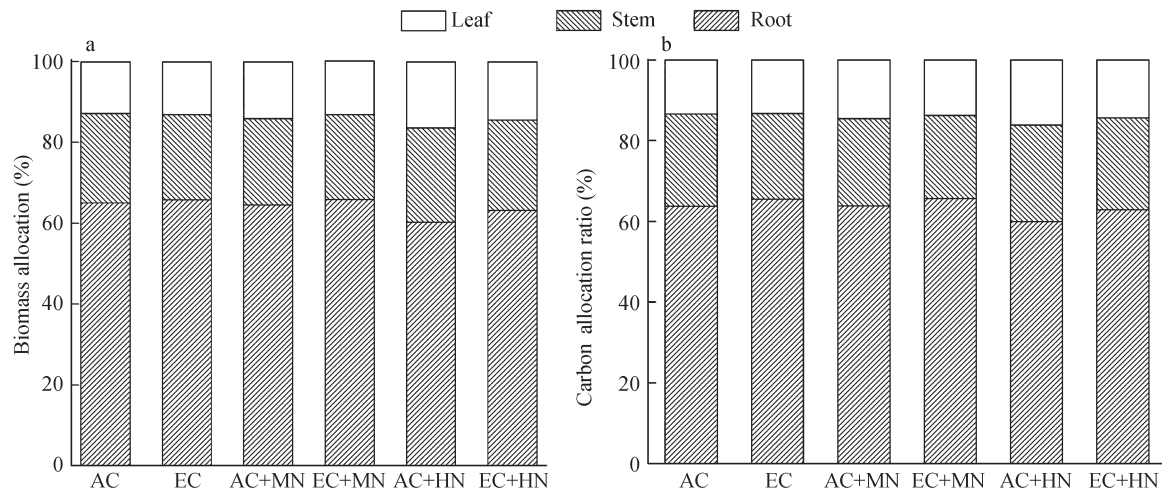
Fig. 2 Effects of elevated CO_2 concentration on biomass allocation (a) and carbon allocation (b) of *Calamagrostis angustifolia*.
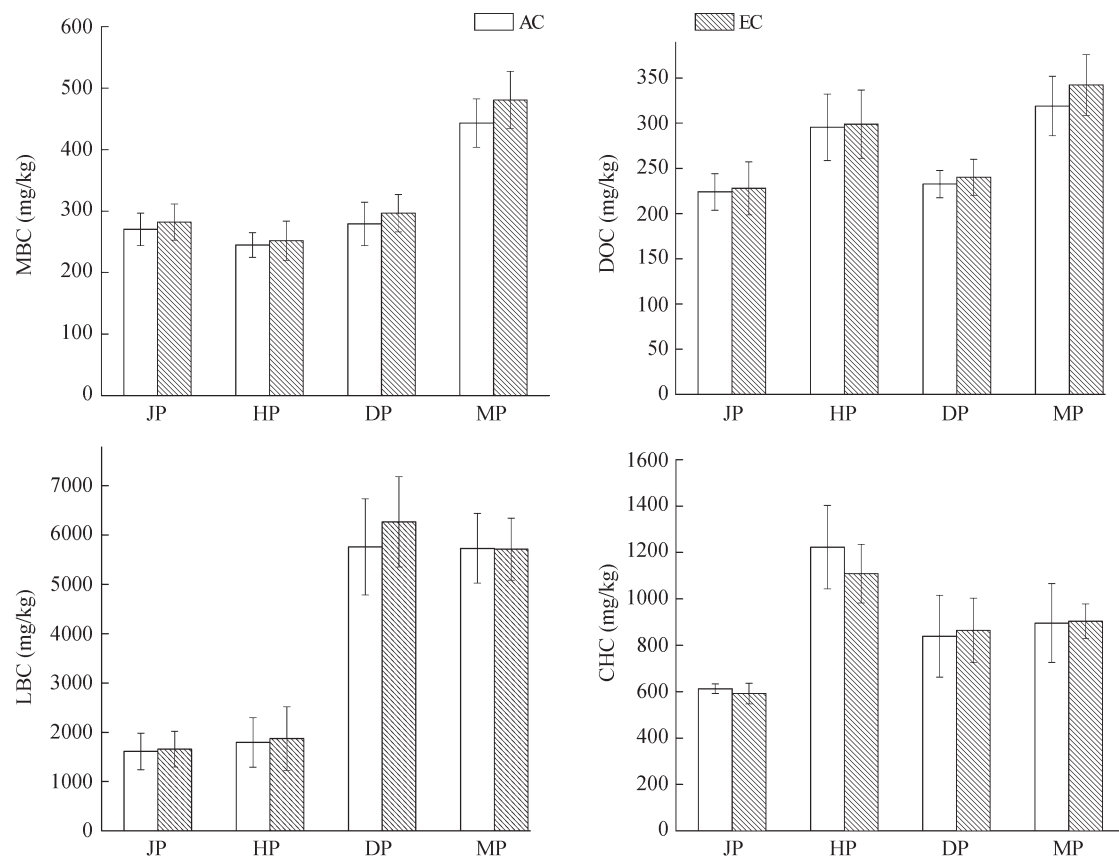

Fig. 3 Effects of elevated CO_2 concentration on soil active carbon at each growth stage in 2007. JS: jointing period; HS: heading period; DS: dough period; MS: maturity period.

that there was a positive correlation between MBC and belowground biomass ($R^2 = 0.59$, $P < 0.01$). The DOC estimate was least reliable ($R^2 = 0.25$, $P < 0.05$), and it was the only parameter to show a regression relationship with aboveground biomass. LOC has remarkable correlation with the plant parameters of belowground biomass and root carbon content ($R^2 = 0.87$, $P < 0.01$); CHC has correlation with the belowground biomass and leaf carbon-uptake ($R^2 = 0.55$, $P < 0.01$).

3 Discussion

3.1 Effects of elevated CO_2 concentration and nitrogen on plants biomass

Numerous studies have elucidated that elevated CO_2 could increase plants biomass (Kang *et al.*, 2001; Kim *et al.*, 2003; Yang *et al.*, 2007). This CO_2-induced biomass increase is attributed to the net increase in C-assimilation rate and reduced loss of photosynthates by

Table 5 Stepwise regression of active carbon pools with plant parameters

Equation	R^2
MBC = 224.32 + 0.12B	0.59**
DOC = 219.98 + 0.152A	0.25*
LOC = 1507.06 + 3.72B − 1.75C	0.87**
CHC = 491.10 + 1.95B − 0.37D	0.55**

A: aboveground biomass; *B*: belowground biomass; *C*: root carbon-uptake; *D*: leaf carbon-uptake.
** and * denote significance at $P < 0.01$ and $P < 0.05$, respectively.

photorespiration. High CO_2 concentration enhanced plant photosynthesis. Cure and Acock (1986) concluded that the net photosynthetic rate increased by 10%–50% under elevated CO_2 concentration. The enhanced photosynthetic rate promoted more biomass production. Moreover, nitrogen was an indispensable substance for the photosynthesis enzyme and has a great impact on plant growth. In our experiment, elevated CO_2 concentration and nitrogen have both been found to increase plant biomass. Furthermore, more significant increases in biomasses were obtained with ample nitrogen than with deficient nitrogen supply. The fact that CO_2 concentration elevation did not significantly increase the biomass accumulation in low nutrient treatment suggested that the growth of *C. angustifolia* was nutrient limited, but not carbon limited. In some terrestrial ecosystems especially that restricted by nitrogen, the extent of elevated CO_2-induced response is strongly dependent on nutrient supply (Daepp *et al.*, 2000). The reason is that plant growth under enriched CO_2 concentration may improve N-used efficiency and thus offset limitations imposed by fertility. Simultaneously, irrespective of CO_2 concentration, high nitrogen availability significantly increased aboveground and belowground biomasses and the enhancement was much greater under elevated CO_2 concentration. Thus, we speculated that CO_2 concentration and nitrogen treatments had interaction on plant biomass, although it was not significant. A possible reason might be the limitation of root caused by the cylinders which could affect the response of root growth to the elevation of CO_2 concentration and nitrogen addition.

3.2 Effects of elevated CO_2 concentration on active carbon

The preferential partitioning of biomass and carbon to roots has also been reported earlier (Arnone *et al.*, 2000). Zak *et al.* (2000) concluded that elevated CO_2 concentration increased plant net primary production and more biomass allocated to belowground. Lambers *et al.* (1996) reported that increased biomass allocated to root was due to the rapid depletion of nutrient in the rhizosphere as a consequence of enhanced growth under the elevated level of CO_2. In our experiment, under elevated CO_2 concentration, the allocation of belowground biomass and carbon have also been found to increase and were much higher with high nitrogen level. Plant responses to elevated CO_2 could affect soil processes through changes in biomass or carbon allocation to root. Living root continually released organic matter into soil and enriched root biomass could produce

more exudation. Cheng and Johnson (1998) confirmed that under elevated CO_2 concentration root exudates and rhizodeposition increased by 60%. Pendall *et al.* (2004) also reported a near doubling of rhizodeposition in a C_3-C_4 grassland ecosystem due to the elevation of atmospheric CO_2 concentration. The root exudates and rhizodeposition could contribute to the active carbon like CHC and DOC by root active metabolize (Pratap *et al.*, 2007). In this study, along with larger belowground biomass and carbon inputs to soil, various active carbon pools (MBC, DOC, LOC and CHC) were also observed to enhance. It was further observed that there were significant correlations between soil active carbon contents and plant biomass. MBC, LOC and CHC were found to be correlated with belowground biomass. MBC was considered as more active fraction of soil organic matter and closely related with living microbe. Increased root exudates and rhizodeposition directly provided ample substrates for soil microbe. Carbohydrates carbon was also a lysis-product of root cell wall (Pratap *et al.*, 2007). Accelerated fine root turnover and circulation due to elevated CO_2 facilitated its presence in higher quantities. Simultaneously, dissolved root cells from the disassembly process made important contributions to the increase of LOC. Thus the MBC, LOC and CHC increased with the enhancement of root biomass, due to their positive correlations with root biomass. Ginkel *et al.* (2000) also confirmed that root biomass was 41% greater at elevated CO_2 than at ambient CO_2 and this root biomass was the driving force for the increase of ^{14}C-labeled carbon in all compartments examined, such as MBC and soil residue. However, dissolved organic carbon showed regression with aboveground biomass. Dissolved organic carbon was primarily associated with low molecular-weight water-soluble carbohydrates and mainly source from litter decomposition process and plant photosynthesis product. The CO_2 concentration enrichment accelerated the increase of *C. angustifolia* aboveground biomass and produced more litter or plant photosynthesis product. The return of the matter produced by new-increasing biomass contributed more DOC. Thus DOC increased with the enhancement of aboveground biomass. Generally, increased soil active organic carbon was due to the plant biomass enhancement under elevated CO_2.

4 Conclusions

In this study, we investigated the effects of elevated CO_2 concentration and nitrogen on the biomass of *C. angustifolia* and wetland soil active carbon. The results showed that both elevated CO_2 concentration and nitrogen have been found to increase plant biomass. There was a definite increase in all the active carbon pools on exposure to elevated CO_2 concentration. Stepwise regression indicated there were significant correlations between various soil active organic carbon and plant biomass. Increased biomass was regarded as the main driving force for the increase in soil active organic carbon under elevated CO_2 concentration.

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