Biogeosciences

Responses of soil respiration to elevated carbon dioxide and nitrogen addition in young subtropical forest ecosystems in China

Q. Deng[1,2], G. Zhou[1], J. Liu[1], S. Liu[1], H. Duan[1,2], and D. Zhang[1]

[1]South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China
[2]Graduate University of Chinese Academy of Sciences, Beijing 100039, China

Abstract. Global climate change in the real world always exhibits simultaneous changes in multiple factors. Prediction of ecosystem responses to multi-factor global changes in a future world strongly relies on our understanding of their interactions. However, it is still unclear how nitrogen (N) deposition and elevated atmospheric carbon dioxide concentration [CO_2] would interactively influence forest floor soil respiration in subtropical China. We assessed the main and interactive effects of elevated [CO_2] and N addition on soil respiration by growing tree seedlings in ten large open-top chambers under CO_2 (ambient CO_2 and $700\,\mu mol\,mol^{-1}$) and nitrogen (ambient and $100\,kg\,N\,ha^{-1}\,yr^{-1}$) treatments. Soil respiration, soil temperature and soil moisture were measured for 30 months, as well as above-ground biomass, root biomass and soil organic matter (SOM). Results showed that soil respiration displayed strong seasonal patterns with higher values observed in the wet season (April–September) and lower values in the dry season (October–March) in all treatments. Significant exponential relationships between soil respiration rates and soil temperatures, as well as significant linear relationships between soil respiration rates and soil moistures (below 15%) were found. Both CO_2 and N treatments significantly affected soil respiration, and there was significant interaction between elevated [CO_2] and N addition ($p < 0.001$, $p = 0.003$, and $p = 0.006$, respectively). We also observed that the stimulatory effect of individual elevated [CO_2] (about 29% increased) was maintained throughout the experimental period. The positive effect of N addition was found only in 2006 (8.17% increased), and then had been weakened over time. Their combined effect on soil respiration (about 50% increased) was greater than the impact of either one alone. Mean value of annual soil respiration was 5.32 ± 0.08, 4.54 ± 0.10, 3.56 ± 0.03 and $3.53 \pm 0.03\,kg\,CO_2\,m^{-2}\,yr^{-1}$ in the chambers exposed to elevated [CO_2] and high N deposition (CN), elevated [CO_2] and ambient N deposition (CC), ambient [CO_2] and high N deposition (NN), and ambient [CO_2] and ambient N deposition (CK as a control), respectively. Greater above-ground biomass and root biomass was obtained in the CN, CC and NN treatments, and higher soil organic matter was observed only in the CN treatment. In conclusion, the combined effect of elevated [CO_2] and N addition on soil respiration was apparent interaction. They should be evaluated in combination in subtropical forest ecosystems in China where the atmospheric CO_2 and N deposition have been increasing simultaneously and remarkably.

1 Introduction

Soil respiration consists of autotrophic root respiration and heterotrophic respiration which is associated with decomposition of litter, roots and soil organic matter (SOM) (Bernhardt et al., 2006). It is one of the largest fluxes in the global carbon cycle ($68–75 \times 10^{15}\,g\,C\,yr^{-1}$) (Raich and Schlesinger, 1992). Global modeling studies have demonstrated that even a small change in soil CO_2 emissions due to global change has the potential to impact atmosphere CO_2 accumulation and global carbon budget (Woodwell et al., 1998 Cox et al., 2000; Cramer et al., 2001). Since global climate change in the real world always exhibits concurrent changes in multiple factors (Shaw et al., 2002; Norby and Luo 2004), understanding regulations of soil respiration by multiple global change factors is necessary to project global carbon cycling in the future.

Correspondence to: D. Zhang
(zhangdeq@scbg.ac.cn)

The atmospheric carbon dioxide concentration [CO_2] has increased by approximately 35% during the past decades and is predicted to reach 700 µmol mol^{-1} by the end of this century (IPCC, 2001). Numerous experiments have been carried out to investigate the responses of soil respiration to elevated [CO_2] (Lin et al., 2001; King et al., 2004; Astrid et al., 2004; Bernhardt et al., 2006; Pregitzer et al., 2008). Elevated [CO_2] can reduce diffusive conductance (Pearson et al., 1995; Niklaus et al., 1998) and stomatal conductance of the leaves (Saxe et al., 1998), which leads to decreased rates of canopy transpiration and increased soil moisture in CO_2 enrichment plots (Bunce, 2004). As a result, soil microbial processes such as litter decomposition and nutrient mineralization were stimulated (Niklaus et al., 1998). Soil respiration was closely related to photosynthetic activity (Moyano et al., 2008). Elevated [CO_2] could enhance photosynthetic assimilation rates, and hence increased the above- and below-ground biomass production. The increase in below-ground biomass would increase CO_2 loss from the soil (Luo et al., 1996; Edwards and Norby, 1999) and enhance carbon release into the rhizosphere by root exudation (van Ginkel et al., 2000; Allard et al., 2006). The increase in aboveground biomass would produce more litter-fall. All these will contribute to higher soil respiration under elevated [CO_2] (Zak et al., 2000).

However, in Asia, due to the rapid expansion of industrial and agricultural activities, the use and emission of reactive N increased from 14 Tg N yr^{-1} in 1961 to 68 Tg N yr^{-1} in 2000 and is expected to reach 105 Tg N yr^{-1} in 2030 (Zheng et al., 2002). Atmospheric N deposition (NH_4^+-N and NO_3^--N) in southern China has also been increasing remarkably (Galloway et al., 2004; Mo et al., 2006, 2007; Chen and Mulder, 2007) and reached 30–73 kg N ha^{-1} yr^{-1} in precipitation in some subtropical forests (Ma, 1989; Ren et al., 2000; Xu et al., 2001). How the increase of [CO_2] would influence soil respiration under high ambient N deposition in subtropical forests in China remains unclear.

Plants require more nutrients for plant growth under the elevated CO_2 treatments. If increases in photosynthetic carbon gain under elevated [CO_2] are not matched by the increases in nutrient supply and/or increases in plant nutrient-use efficiency, the effect of CO_2 enrichment to plant growth may decline or weaken over time (Norby et al., 1986; Murray et al., 2000; Luo et al., 2004; Bernhardt et al., 2006), which also would affect soil respiration. However, soil moisture might become lower with increased diffusive conductance and stomatal conductance of the leaves under N addition (Li et al., 2004), which will reduce soil microbial activity (Kucera et al., 1971). N addition also leads to soil acidification (Huber et al., 2004) especially in tropical forests where the soils are often highly acidic, which will further affect soil microbial activity and SOM decomposition rate (Anderson and Joergensen, 1997; Kemmitt et al., 2006). In addition, it had been reported that N addition decreased root biomass and soil microbial biomass over time (Mo et al., 2007, 2008).

High N deposition might reduce litter decomposition rate (Mo et al., 2006). As a result, the effects of N addition to soil respiration are still not conclusive. Both increases, decreases, and unchanged in soil respiration with N additions to forest soils have been reported (Bowden et al., 2000 and 2004; Burton et al., 2004; Micks et al., 2004; Cleveland and Townsend, 2006; Mo et al., 2007 and 2008). Mo et al. (2007) recently showed that the response of soil respiration to atmospheric N deposition may vary depending on the rate of N deposition and the degree of initial soil nutrient status. How N deposition and elevated [CO_2] would interactively influence soil respiration in subtropical forests has not been well investigated.

We conducted a two-factor experiment investigating the interactive effects of elevated [CO_2] and N deposition on soil respiration in young subtropical forest ecosystems. We hypothesized that

1. elevated [CO_2] would stimulate soil respiration due to greater soil C input;

2. the stimulatory effect would be sustained over time due to the high ambient N deposition in subtropical China; and

3. the combined effect of elevated [CO_2] and N addition would be greater than the impact of either one alone due to positive interaction. To test the hypotheses, we measured soil respiration, soil temperature and soil moisture for 30 months, as well as above-ground biomass, root biomass and SOM in an open-top chamber experiment.

2 Materials and methods

2.1 Site description

The experiment was conducted at South China Botanical Garden, Chinese Academy of Sciences, Guangzhou, China (23°20′ N and 113°30′ E). The area is characterized by a typical south subtropical monsoon climate, with annual precipitation ranging from 1600 mm to 1900 mm, of which nearly 80% falls in the hot-humid wet/rainy season (April–September) and 20% in the dry season (October–March). Total annual solar radiation reaches 4.37–4.60 GJ m^{-2} yr^{-1} in the photosynthetic active radiation (PAR) range. The mean annual temperature is 21.5 °C, and the mean relative humidity is 77% (Liu et al., 2008).

2.2 Open-top chamber design

Ten open-top chambers were built for this experiment. Each 3-m diameter chamber is 3-m tall and 0.7-m deep. The above-ground part was wrapped with impermeable and transparent plastic sheets, leaving the top of the chamber totally

Table 1. Height and basal diameter of the plant seedlings among all treatments at the beginning of the experiment (mean ± standard deviations). The treatments are: CK = control, NN = high N, CC = elevated CO_2, CN = elevated CO_2 + high N.

Parameters	Species	CN	CC	NN	CK
	Acmena acuminatissima	25.54 ± 0.47	24.40 ± 0.57	25.03 ± 0.84	24.83 ± 1.09
	Castanopsis hystrix	67.91 ± 1.39	68.83 ± 1.25	64.13 ± 2.28	68.50 ± 2.45
	Ormosia pinnata	19.47 ± 0.55	18.96 ± 0.71	18.53 ± 0.85	18.47 ± 0.77
Height (cm)	*Pinus massoniana*	49.33 ± 2.33	48.31 ± 2.18	47.41 ± 2.16	49.59 ± 2.42
	Schima superba	38.04 ± 1.10	37.23 ± 1.86	36.34 ± 1.29	35.94 ± 1.00
	Syzygium hancei	58.62 ± 2.19	58.60 ± 1.75	59.00 ± 2.43	60.47 ± 2.41
	Acmena acuminatissima	0.28 ± 0.01	0.26 ± 0.01	0.27 ± 0.01	0.28 ± 0.01
	Castanopsis hystrix	0.65 ± 0.03	0.62 ± 0.02	0.55 ± 0.02	0.61 ± 0.02
	Ormosia pinnata	0.53 ± 0.01	0.54 ± 0.01	0.53 ± 0.02	0.52 ± 0.02
Basal diametre (cm)	*Pinus massoniana*	0.59 ± 0.04	0.58 ± 0.04	0.59 ± 0.03	0.57 ± 0.05
	Schima superba	0.45 ± 0.01	0.46 ± 0.02	0.49 ± 0.04	0.46 ± 0.02
	Syzygium hancei	0.56 ± 0.02	0.52 ± 0.02	0.57 ± 0.02	0.59 ± 0.03

open. Light intensity in the chamber was 97% of that in open space and no spectral change was detected. Measured rainfall intensity was identical inside and outside of the chambers and the temperature was not significantly different. The below-ground part was delimited by concrete brick wall that prevented any lateral or vertical water and/or element fluxes with the outside surrounding soil. Three holes at the bottom of the wall were connected to a stainless steel water collection box. Holes were capped by a 2-mm net to prevent losses other than those of leachates. In the treatment chambers with elevated [CO_2], the additional CO_2 was distributed from a CO_2 tank by a transparent pipe with pinholes. A big fan was connected to the pipe to ensure equal distribution of CO_2 in the entire chamber. Air was introduced into the chambers via the fan at an exchange rate of about 1.5 chamber volumes per minute. The CO_2 flux from the tank was controlled by a flow meter and the CO_2 concentrations in the chambers were periodically checked by using a Li-Cor 6400 (Li-COR, Inc., Lincoln, Nebraska, USA).

The soils used in the experiment were collected from a nearby ever-green broad-leaved forest after harvesting from 26 February 2005 to 3 March 2005. Simultaneously, the soil was collected as three different layers (0–20, 20–40 and 40–70 cm depth) that were homogenised separately and used to fill the below-ground part of the chambers. The lateritic soil with its chemical properties (before the soil was collected) was shown in Liu et al. (2008). On 10 March 2005, one to two year old seedlings grown in a nursery were transplanted in the chambers without damaging the roots. All the chambers were planted with 48 randomly selected seedlings with 8 seedlings each of the following 6 species: *Castanopsis hystrix* Hook.f. & Thomson ex A.DC, *Syzygium hancei* Merr. et Perry, *Pinus massoniana* Lambert, *Schima superba* Gardn. and Champ., *Acmena acuminatissima* (Blume) Merr. et Perry, and *Ormosia pinnata* (Lour.) Merr. These 6 species were selected because they are all native and all

widely distributed in southern China. No significant difference in height and basal diameter of the plant seedlings was found among all treatments at the beginning of the experiment (Table. 1).

2.3 Experiment design

We used a completely randomized design with four treatments considering two levels of CO_2 and two levels of N. Since we have ten open-top chambers, the replication number for the treatments was not equal. For elevated [CO_2] and high N deposition (CN), and elevated [CO_2] and ambient N deposition (CC), 3 chambers were used, respectively. For ambient CO_2 and high N deposition (NN), and no treatment as a control (CK), 2 chambers were used, respectively. The elevated CO_2 treatments were achieved by supplying additional CO_2 from a tank until reaching a CO_2 concentration of ca. 700 µmol mol^{-1} in the chambers. The N addition treatments were achieved by spraying seedlings once a week for a total amount of NH_4NO_3 at 100 kg N ha^{-1} yr^{-1}. No other fertilizer was used. Since the walls of the chambers belowground parts blocked lateral and vertical water fluxes, the seedlings were watered with tap water. All the chambers received the same amount of water as the CK chambers. These treatments started in April 2005.

2.4 Soil respiration measurement

Four PVC soil collars (80 cm^2 in area and 5 cm in height) were permanently installed 3 cm into the soil in each chamber in April 2006. The distance between adjacent collars was more than 50 cm. To eliminate the influence of plants on soil respiration, all living plants in the collars were removed one day before soil respiration measurement. From 26 June 2006 to 22 December 2008, soil respiration was measured once a week using a Li-Cor 6400 infrared gas analyzer

(Li-COR, Inc., Lincoln, Nebraska, USA) connected with a Li-Cor 6400-09 soil respiration chamber (9.55 cm diameter) (Li-COR, Inc., Lincoln, Nebraska, USA). The measurements were made between 9:00 am and 12:00 pm local time. The soil respiration chamber (with a foam gasket) was put on the PVC soil collars making an air-tight seal. Soil respiration was measured three times for each soil collar. Soil respiration in a treatment chamber was calculated as the mean of four collar measurements (the measurement at four collars in a chamber differed by less than 5% at any measurement period). Soil temperature at 5 cm below the soil surface was also monitored with a thermocouple sensor attached to the respiration chamber during the soil respiration measurement. Volumetric soil moisture of the top 5 cm soil layer was measured on five random locations within a treatment chamber using a PMKit (Tang et al., 2006) at the same time when the soil respiration measurements were being taken.

2.5 Annual soil respiration calculation

Annual or semiannual soil respiration for each treatment was estimated by summing the products of weekly mean soil respiration and the number of days between samples. The soil respiration measurements made between 9:00 am and 12:00 pm represent the daytime averages, based on a study at a similar site where diurnal pattern of soil respiration was measured (Tang et al., 2006). Because the measurement of soil respiration began in 26 June 2006, we only estimated semiannual soil respiration from July to December in 2006.

2.6 Above-ground biomass, root biomass and soil organic matter

Plant height and basal diameter were measured at the time of planting in early March 2005 and then were assessed five times in August 2005, November 2005, May 2006, September 2007 and January 2008. Plant height was measured from the soil surface to the tip of the apical bud and the basal diameter was assessed at the soil surface. To measure plant biomass, one tree of each species in every chamber was harvested in January 2008. This tree was separated into roots, stems and leaves. Tree samples were oven-dried at 60 °C before being weighed. The biomass of each harvested tree was calculated with sample biomass using dry/fresh ratio. Strong correlations among dry biomass for each component part, basal area and height existed irrespective of size in trees harvested, which were stated in the equation (Whittake and Woodwell, 1986; Wen et al., 1997):

$$W = a(D^2 H)^b \tag{1}$$

Where W is dry biomass of each tree components including root, stem and leaf (kg m^{-2}), D is plant basal diameter (cm), H is height (cm), and a, b are regression coefficients.

The biomass of other un-harvested trees was calculated separately by using their height and basal diameter into the equation above. Here plant biomass is the total biomass of all trees in a chamber irrespective of species. The above-ground biomass was the sum of stem and leaf biomass.

Soil samples were collected on November, 2008 to determine soil organic matter (SOM). Three samples (0–20 cm depth) were collected randomly in each chamber. Each sample was composted from three cores using a standard soil probe (2.5 cm inside diameter). The composite samples were gently mixed. SOM was determined following Walkley Black's wet digestion method (Nelson and Sommers, 1982).

2.7 Data analysis

Repeated measures ANOVA with Tukey's HSD test was used to examine treatment effects (including the main effects of CO_2, N, time-of-season and their interactions) on soil respiration rate, soil temperature and soil moisture. Repeated measures ANOVA with Tukey's HSD test was used to examine treatment difference in soil respiration rate, soil temperature and soil moisture. Standard t-test was used to test the seasonal difference in means of soil respiration rate, soil temperature and soil moisture. To compare the effects among our three measured years, One-way ANOVA with Tukey's HSD test was used to test the treatment difference in annual or semiannual soil respiration, as well as root biomass and soil organic matter.

Both linear and nonlinear regression models were used to examine the relationship between soil respiration rates and soil temperature and moisture (Tang et al., 2006; Li et al., 2008). Simple models with soil temperature and soil moisture were performed. An exponential equation and a linear equation were used:

$$R = a\,exp(bT) \tag{2}$$

$$R = aM + b \tag{3}$$

Where R is soil respiration rate (μmol CO_2 m^{-2} s^{-1}), T is soil temperature (°C), M is soil moisture (%) and a, b are constants fitted to the regression equation.

The index of soil respiration response to temperature was also described by the Q_{10} value, defined as the difference in respiration rates over a 10 °C interval. Q_{10} value was calculated using the exponential relationship between soil respiration and soil temperature (Lloyd and Taylor, 1994; Buchmann, 2000; Xu and Qi, 2001):

$$Q_{10} = \exp(10b) \tag{4}$$

Where b is the constant fitted into Eq. 2. One-way ANOVA test was used to compare b values among treatments.

All analyses were conducted using SPSS 10.0 (SPSS, Chicago, Ill) for Microsoft Windows.

Table 2. Significance of the impacts of CO_2 (effect of individual elevated [CO_2]), N (effect of individual N addition), CO_2*N (the interactive effect between elevated [CO_2] and N addition) and season on soil respiration (R), soil temperature (T) and soil moisture (M) in the repeated measures ANOVA.

		R		T		M	
		F	p	F	p	F	p
Annual	CO_2	121.45	< 0.001	0.21	0.643	30.45	< 0.001
	N	10.31	0.003	0.04	0.846	7.20	0.024
	CO_2*N	7.24	0.006	0.01	0.930	1.95	0.263
	Season	261.58	< 0.001	520.86	< 0.001	276.11	< 0.001
Wet season	CO_2	75.25	< 0.001	1.03	0.312	10.01	0.002
	N	7.26	0.008	0.02	0.898	3.26	0.073
	CO_2*N	0.41	0.524	0.08	0.782	0.39	0.535
Dry season	CO_2	54.30	< 0.001	0.01	0.906	21.38	< 0.001
	N	3.47	0.064	0.02	0.881	5.00	0.026
	CO_2*N	18.55	< 0.001	0.01	0.936	1.82	0.179

Table 3. Mean soil respiration rate, mean soil temperature at 5 cm below the soil surface and mean soil moisture of the top 5 cm soil layer under different CO_2 and N treatments (mean ± standard deviations). Standard deviation within each treatment showed the dispersion among open–top chambers employed for each treatment. $n = 3$ for the CN and CC treatments, $n = 2$ for the NN treatment and CK. Mean values within a row with different lowercase letter have significant treatment differences at α=0.05 level. Means values within each column indicated by the asterisk show significant seasonal differences at α=0.05 level. The treatments are: CK = control, NN = high N, CC = elevated CO_2, CN = elevated CO_2 + high N.

treatment	Time	CN	CC	NN	CK
Soil respiration rate (μmol CO_2 m^{-2} s^{-1})	Wet season	4.61 ± 0.10a*	4.12 ± 0.08b*	3.34 ± 0.03c*	2.94 ± 0.05d*
	Dry season	2.91 ± 0.05a*	2.36 ± 0.03b*	1.89 ± 0.03c*	2.10 ± 0.04bc*
	Annual means	3.76 ± 0.07a	3.24 ± 0.04b	2.56 ± 0.04c	2.52 ± 0.02c
Soil temperature (°C)	Wet season	24.20 ± 0.15a*	25.23 ± 0.17a*	25.28 ± 0.11a*	25.25 ± 0.21a*
	Dry season	17.26 ± 0.08a*	17.31 ± 0.09a*	17.35 ± 0.13a*	17.33 ± 0.11a*
	Annual means	21.23 ± 0.12a	21.18 ± 0.11a	21.29 ± 0.07a	21.25 ± 0.19a
Soil moisture (%)	Wet season	24.31 ± 0.60a*	25.52 ± 0.36a*	22.51 ± 0.76b*	23.48 ± 0.82ab*
	Dry season	17.77 ± 0.64ab*	18.80 ± 0.24a*	14.72 ± 0.50c*	17.35 ± 0.95b*
	Annual means	20.84 ± 0.56b	22.16 ± 0.22a	18.58 ± 0.90c	20.42 ± 0.896b

3 Results

3.1 Soil temperature and moisture

Soil temperature and moisture exhibited clear seasonal patterns ($p < 0.001$ for both). Soil was warm and wet from April through September (the wet season) and became cool and dry from October to the March of the next year (the dry season) (Tables 2 and 3; Fig. 1). The seasonality of soil temperature and moisture was consistent with the seasonal patterns of air temperature and precipitation (Liu et al, 2008). Annual mean soil temperature and soil moisture were 21.25 ± 0.19 °C and 20.42 ± 0.90%, respectively in the CK chambers. There was no treatment effect on soil temperature ($p > 0.05$ for all treatments). However, elevated

[CO_2] significantly increased soil moisture ($p < 0.001$), and N addition significantly decreased soil moisture ($p = 0.024$). The CN treatments did not alter the regimes of soil moisture ($P = 0.263$) (Tables. 2 and 3).

3.2 Soil respiration

Soil respiration also exhibited a clear seasonal pattern with the maximum respiration rates occurred during the summer when soil temperature and moisture were high; the minimum respiration rates occurred during the winter when soil temperature and moisture were low ($p < 0.001$ for both) (Table 3; Fig. 1). In all treatments, significant exponential relationships between soil respiration rate and soil temperature
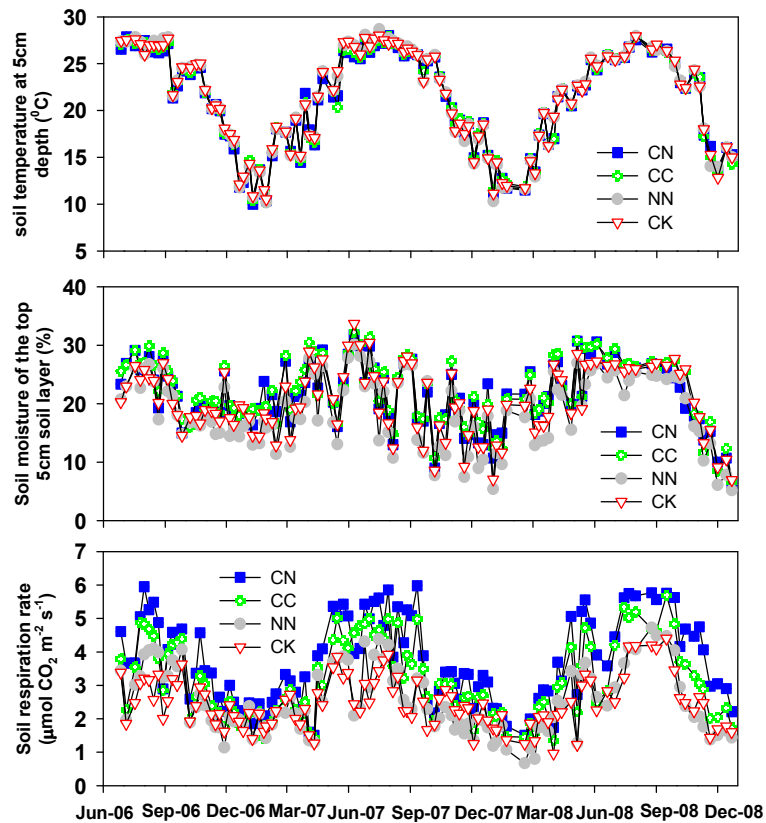
Fig. 1. Seasonal dynamics of soil temperature at 5 cm below the soil surface, soil moisture of the top 5 cm soil layer and soil respiration rate under different CO_2 and N treatments. The treatments are: CK=control, NN=high N, CC=elevated CO_2, CN=elevated CO_2 + high N.

were found ($p < 0.001$ for both) (Table 4; Fig. 2). Temperature sensitivity (Q_{10}) was estimated as 1.87, 1.90, 1.86 and 1.57 in the CN, CC, NN and CK treatments, respectively. By analyzing subsets of data with low and high soil moisture content we found a significant positive linear relationship between soil respiration rate and soil moisture when soil moisture was below 15% (Table 4; Fig. 3).

The repeated measures ANOVA showed that both CO_2, N treatments and their interaction affected soil respiration significantly ($F = 121.45$, $p < 0.001$; $F = 10.31$, $p = 0.003$; and $F = 7.24$, $p = 0.006$, respectively) (Table 2). Soil respiration rate was the highest in the CN chambers ($3.76 \pm 0.07\,\mu\text{mol CO}_2\,\text{m}^{-2}\,\text{s}^{-1}$), followed by the CC chambers ($3.24 \pm 0.04\,\mu\text{mol CO}_2\,\text{m}^{-2}\,\text{s}^{-1}$), NN and the control chambers (CK) (2.56 ± 0.04 and $2.52 \pm 0.02\,\mu\text{mol CO}_2\,\text{m}^{-2}\,\text{s}^{-1}$, respectively) for the experimental period (Table 3). In addition, CO_2 treatment affected soil respiration significantly in both wet and dry season ($p < 0.001$, for both), but N treatment affected soil respiration significantly only in wet season ($p = 0.008$) and their interaction affected soil respiration significantly only in dry season ($p < 0.001$) (Table 2).

The mean value of annual soil respiration was 5.32 ± 0.08, 4.54 ± 0.10, 3.56 ± 0.03 and $3.53 \pm 0.03\,\text{kg CO}_2\,\text{m}^{-2}\,\text{yr}^{-1}$ in the CN, CC, NN and CK treatments, respectively (Table 5). By analyzing each treatment's annual or semiannual soil respiration in the latter half of 2006, 2007 and 2008, we observed that annual or semiannual soil respiration in the CN and CC treatments increased by 49.24–51.38% and 27.24–28.45%, respectively (Table 5). It seems that the stimulatory effect of the CN and CC treatments on soil respiration was sustained over our study period. However, the effect of the NN treatment on soil respiration was increased in 2006 (8.17%), with no change in 2007 and 2008 (2.32% and −0.55%, respectively) (Table 5). Obviously, the effect of the NN treatment on soil respiration had been weakened over time.

3.3 Above-ground biomass, root biomass and soil organic matter

Both of above- and below-ground biomass in the CN CC and NN treatments was significantly higher than that in the CK chambers at our study sites. Mean above-ground biomass was 4.37, 3.11, 3.41 and 2.62 kg m^{-2} in the CN, CC, NN and CK treatment in January 2008, respectively (Fig. 4). Mean

Table 4. Model for relationships between the soil respiration (R) and soil temperature at 5 cm below the soil surface (T) and soil moisture of the top 5 cm soil layer (M) (mean $\pm$ standard deviations). Standard deviation within each treatment showed the dispersion among open-top chambers employed for each treatment. $n = 3$ for the CN and CC treatments, $n = 2$ for the NN treatment and CK. Mean values of b in the exponential equation ($R = a\exp(bT)$) within a column with different lowercase letter have significant treatment differences at $\alpha = 0.05$ level. R^2 is the determination of coefficient. The treatments are: CK = control, NN = high N, CC = elevated CO_2, CN = elevated CO_2 + high N. Unit: $\mu mol\, CO_2\, m^{-2}\, s^{-1}$ for R; $°C$ for T and % for M.

| Treatment	a	b	Q_{10}	p	R^2
a) Soil moisture > 15%: $R = a\exp(bT)$					
CN	1.0155 ± 0.027	0.0627 ± 0.001 a	1.87	< 0.001	0.68
CC	0.8085 ± 0.061	0.0641 ± 0.001 a	1.90	< 0.001	0.69
NN	0.66 ± 0.017	0.062 ± 0.002 a	1.86	< 0.001	0.67
CK	0.9904 ± 0.030	0.0449 ± 0.001 b	1.57	< 0.001	0.57
Treatment	a	b	n	p	R^2
b) Soil moisture < 15%: $R = aM + b$					
CN	0.1545 ± 0.007	1.1638 ± 0.071	13	< 0.001	0.61
CC	0.1389 ± 0.008	0.701 ± 0.044	10	< 0.001	0.63
NN	0.1332 ± 0.011	0.5926 ± 0.058	37	< 0.001	0.60
CK	0.1651 ± 0.010	0.3893 ± 0.055	20	< 0.001	0.54
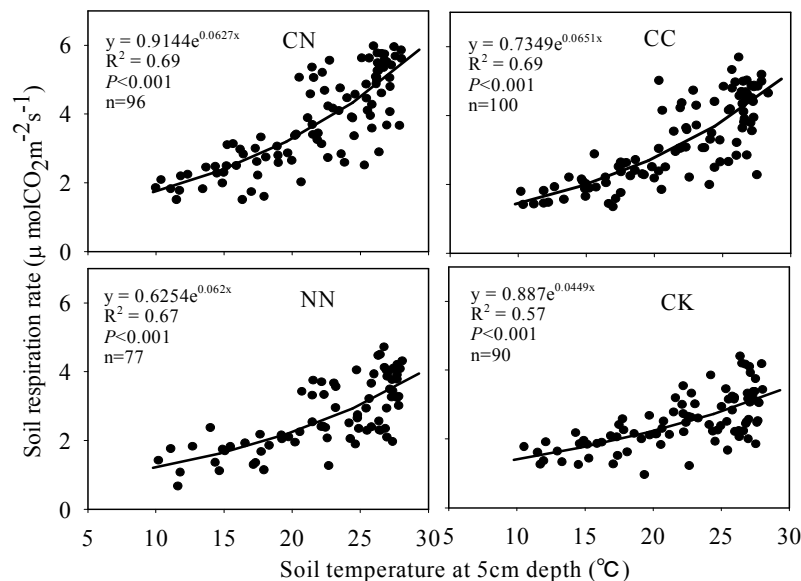
Fig. 2. Relationships between soil respiration rate and soil temperature at 5 cm depth when soil moisture was larger than 15% under different CO_2 and N treatments. Each datum in panels CN and CC is the mean of three replications. Each datum in panels NN and CK is the mean of two replications. The treatments are: CK = control, NN = high N, CC = elevated CO_2, CN = elevated CO_2 + high N.

root biomass was 1.43, 1.29, 1.17 and 0.91 kg m^{-2} in the CN, CC, NN and CK treatment in January 2008, respectively (Fig. 4). Higher SOM was observed only in the CN treatment ($p < 0.05$). There was no significant difference of SOM among the CC, NN and CK chambers ($p > 0.05$). Mean SOM was 2.68, 2.17, 2.41 and 2.21%, respectively in the CN, CC, NN and CK treatment in November 2008 (Fig. 4).

4 Discussion

4.1 Effect of soil temperature and moisture on the seasonality of soil respiration

Soil respiration in all treatments showed strong seasonal patterns with higher value observed in the wet season (April–September) compared to the dry season (October–March) (Fig. 1). This is consistent with other results reported in
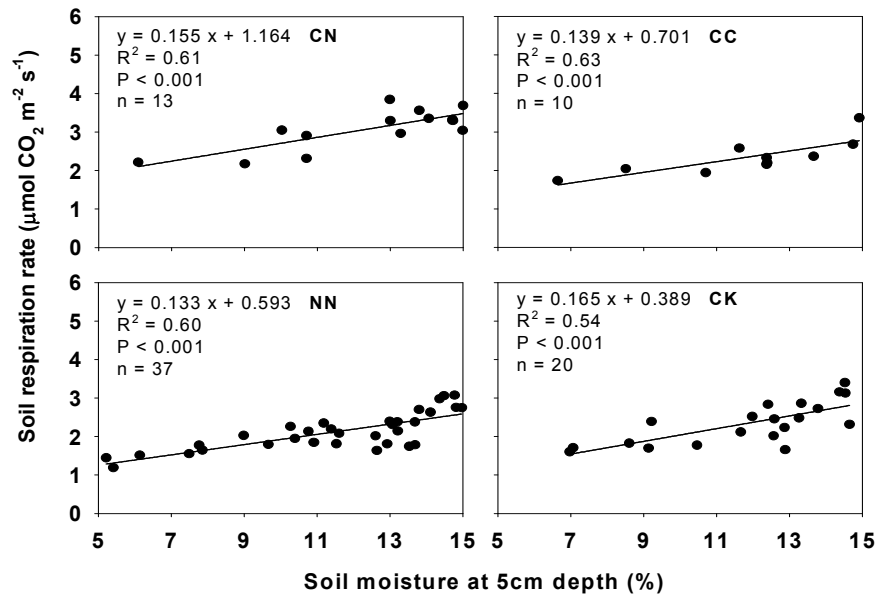
Fig. 3. Relationships between soil respiration rate and soil moisture of the top 5 cm soil layer (below 15%) under different CO_2 and N treatments. Each datum in panels CN and CC is the mean of three replications. Each datum in panels NN and CK is the mean of two replications. The treatments are: CK = control, NN = high N, CC = elevated CO_2, CN = elevated CO_2 + high N.

subtropical forests in China (Tang et al., 2006; Zhang et al., 2006; Mo et al., 2007, 2008). This area is characterized by a typical subtropical monsoon climate, where nearly 80% of annual precipitation falls in the wet season (April to September). Besides, air temperature in the wet season is significantly higher than that in the dry season. Therefore, high plant growth and soil microbial activity in the wet season can stimulate greater soil respiration rate. Positive exponential relationships between soil respiration and soil temperature, as well as positive linear relationships between soil respiration and soil moisture have been found in some warm and moist forests (Sotta et al., 2004; Cleveland and Townsend, 2006; Tang et al., 2006; Zhang et al., 2006; Mo et al., 2007, 2008). In our study, significant exponential relationships between soil respiration rates and soil temperatures were developed when soil moisture was higher than 15% (Fig. 2). We found that soil respiration linearly increased with soil moisture when soil moisture was below 15% (Fig. 3). A similar result was reported by Mo et al. (2008) in a mature tropical forest in southern China. Inclan et al. (2007) believed soil moisture effects on soil respiration might occur below a certain threshold varying with soil texture (Dilustro et al., 2005). Our result suggested that soil moisture may play a more important role in soil respiration rate as the soil becomes drier.

4.2 Temperature sensitivity of soil respiration

The temperature sensitivity (Q_{10}) of soil respiration was significantly higher in the CN, CC and NN treatments when compared to the CK chambers (Table 4 and Fig. 2), suggesting that elevated [CO_2] and N would increase temperature

sensitivity. This is probably because the CN, CC and NN treatments increased the allocation of carbon to the roots. Higher SOM was also observed in the CN treatment. Soil respiration is thought to be controlled primarily by temperature (Lloyd and Taylor, 1994). This is based on the assumption that enzymatic rates control soil physiological processes to a greater extent than resource supply rates (Skopp et al., 1990; Craine et al., 1998). Zheng et al. (2009) also reported that Q_{10} of soil respiration was primarily determined by soil temperature during measurement periods, soil organic carbon (SOC) content, and ecosystem type. So the respiratory substrate availability plays a crucial role in the response of soil respiration to soil temperature (Liu et al., 2006). When substrate supply is low, the temperature sensitivity of soil respiration is low. Otherwise, increased substrate supply can elevate the temperature sensitivity of soil respiration. Therefore, these additional substrates of root biomass and SOM (Fig. 4) for autotrophic and heterotrophic respiration in our study could result in high temperature sensitivity (Dhillion et al., 1996; Lin et al., 2001; Pendall et al., 2004).

4.3 Effect of elevated [CO_2] on soil respiration

Many studies indicated that elevated [CO_2] increased soil respiration significantly (Lin et al., 2001; King et al., 2004; Astrid et al., 2004; Bernhardt et al., 2006; Pregitzer et al., 2008). Our results also demonstrated that elevated CO_2 resulted in a considerable increase of carbon release (about 29% on average) from the forest floor. The increase was comparable to an open-top chamber study in eastern Finland which reported about a 30% increase (Sini et al., 2004).

Table 5. Aannual or semiannual soil respiration (R) and its % increased for each year of the experiment (mean ± standard deviations). Standard deviation within each treatment showed the dispersion among open-top chambers employed for each treatment. $n = 3$ for the CN and CC treatments, $n = 2$ for the NN treatment and CK. R within a row with different lowercase letter have significant treatment differences at $\alpha = 0.05$ level. The treatments are: CK = control, NN = high N, CC = elevated CO_2, CN = elevated CO_2+ high N. % increased = 100 ((R of each treatment – R of the CK)/R of the CK) % (in the same year). Unit: $kg\,CO_2\,m^{-2}$ 6-months^{-1} for R in the latter half of 2006; $kg\,CO_2\,m^{-2}\,yr^{-1}$ for R in 2007 and 2008.

Year*	CN		CC		NN		CK
	R	% increased	R	% increased	R	% increased	R
2006	2.72 ± 0.9a	49.24	2.22 ± 0.12b	27.24	1.97 ± 0.10c	8.17	1.83 ± 0.03d
2007	5.16 ± 0.10a	49.57	4.43 ± 0.18b	28.41	3.53 ± 0.10c	2.32	3.45 ± 0.07c
2008	5.48 ± 0.12a	51.38	4.65 ± 0.06b	28.45	3.60 ± 0.05c	-0.55	3.62 ± 0.01c
mean	5.32 ± 0.09a	50.07	4.54 ± 0.10b	28.61	3.56 ± 0.03c	0.01	3.53 ± 0.03c

* Because the measurement of soil respiration begun in 26 June 2006, we only estimate semiannual soil respiration from July to December in 2006 and estimate the mean value of all year from 2007 to 2008.

However, it was higher than the Duke Forest Free Air CO_2 Enrichment (FACE) Experiment (about 16% on average) (Bernhardt et al., 2006) and the FACE Experiment of the Federal Agricultural Research Centre (about 17% on average) (Astrid et al., 2004). The increased soil respiration in the CC chambers may be due to the following two reasons. Firstly, increased soil moisture under elevated [CO_2] may increase SOM decomposition rate and stimulate soil microbial respiration. Many studies showed that CO_2 enrichment increased soil moisture (Amthor, 2001; Bunce 2004). Higher soil moisture in the CC treatment was revealed at our study sites (Tables 2 and 3), which would stimulate soil microbial processes (Niklaus et al., 1998) by improving litter decomposition and nutrient mineralization. Secondly, increased root biomass may increase root respiration and rhizosphere microbial respiration. Most studies showed that elevated [CO_2] increased fine root biomass and in most cases higher fine turnover resulted in higher C input into soil via root necromass (Edwards and Norby, 1999; Norby and Luo, 2004; Lukac et al., 2009). In our study, elevated [CO_2] increased root biomass (Fig. 4) that was also accompanied by increased CO_2 loss from the soils.

By analyzing each treatment's annual or semiannual soil respiration in the latter half of 2006, 2007 and 2008, we observed that the stimulatory effect of elevated [CO_2] on soil respiration was maintained throughout the experimental period (Table 5). This is not consistent with some other reports which showed that soil respiration gradually declined over time because of the N limitation (e.g., Bernhardt et al., 2006). Increases in photosynthetic carbon gain under elevated [CO_2] need to be matched by increases in nutrient supply and/or increases in plant nutrient-use efficiency, otherwise the effect of CO_2 enrichment on plant growth may weaken due to N-limitation (Norby et al., 1986; Murray et al., 2000). At our study area, the rapid expansion of industrial and agricultural activities in subtropical regions has resulted in high atmospheric N deposition (NH_4^+-N, NO_3^--

N) in forests of southern China (30–73 kg N ha^{-1} yr^{-1}) (Ma, 1989; Ren et al., 2000; Xu et al., 2001). It seems that plant growth is not limited by N under elevated [CO_2] in the long term. This may be the reason that the stimulatory effect of elevated [CO_2] on soil respiration might be sustained over time, at least during the current experimental period.

4.4 Effect of N addition on soil respiration

Some other studies showed that soil respiration would be suppressed under N addition (Boxman et al., 1998; Mo et al., 2008). However, the repeated measures ANOVA in our study showed that a positive effect on soil respiration existed in the NN treatment, which may primarily owe to N addition stimulating soil respiration rate at the very start of the experiment. This is similar to the pattern observed by Bowden et al. (2004) that N addition could increase soil respiration significantly in the first 2 years. The response of soil respiration to elevated N deposition was influenced by the degree of initial soil nutrient status (Mo et al., 2007). We also believed that young seedlings used in this study grew quickly and required more soil N, which would lead to a transitory and slight N limitation at our study sites. Increased aboveground biomass and increased root biomass (Fig. 4) was obtained in the N treatment (Duan et al., 2009). As Bowden et al. (2004) suggested, it is likely that added soil carbon from above- and below-ground litter would stimulate heterotrophic respiration, and greater root biomass enhanced autotrophic respiration under N addition. Lu et al. (1998) also reported that the root respiration rate for seedlings grown at 50 mg L^{-1} N concentration due to increased root biomass was significantly higher than for seedlings grown at 10 mg L^{-1} N.

By analyzing each treatment's annual or semiannual soil respiration in the latter half of 2006, 2007 and 2008, we observed that the positive effect of N addition treatment existed in the year 2006 and it had been weakened over time. Aber et al. (1989) reported that N additions would initially stimulate
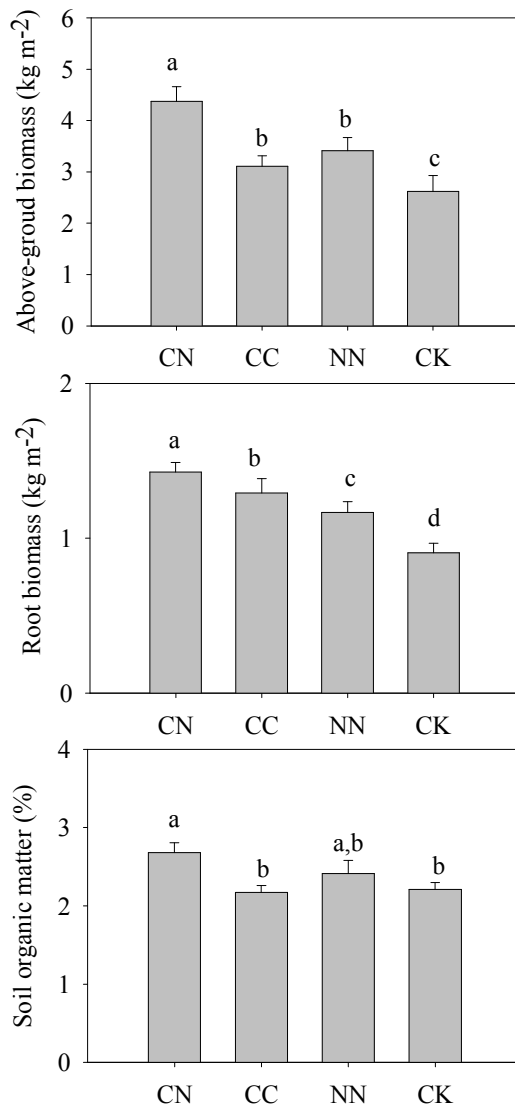
Fig. 4. Above-ground biomass and root biomass in January 2008, and soil organic matter in November 2008 under different CO_2 and N treatments. Error bars are standard deviations, which showed the dispersion among open-top chambers employed for each treatment. $n = 3$ for the CN and CC treatments, $n = 2$ for the NN treatment and CK. Different letters denote significant difference between treatments. Significant level is set at $\alpha = 0.05$. The treatments are: CK = control, NN = high N, CC = elevated CO_2, CN = elevated CO_2 + high N.

soil microbial activity, but would lead to a carbon limitation state after microbial demand for N was satisfied over time. In addition, plant growth would become slow over time and needed to assimilate less N from soil. Meanwhile, with larger doses of N readily available for uptake, energetic costs of N assimilation may have been reduced. Since a large fraction of root respiration is allocated to N assimilation (Bloom et al., 1992), root activity and autotrophic respiration would weaken (Bowden et al., 2004). Here we have not direct data

to prove that the root activity and soil microbial activity were weakening under N addition in our study. However, soil microbial activity was closely related to soil moisture (Kucera et al., 1971). In our study, N addition significantly decreased soil moisture (Table 3), which might be due to the increased plant growth (Duan et al., 2009) and the increased diffusive conductance and stomatal conductance of the leaves in the NN chambers (Li et al., 2004; Duan, H. L., unpublished data). Since there was a significant positive linear relationship between soil respiration rates and soil moisture when soil moisture was below 15% (Fig. 3), soil respiration would gradually be suppressed with drier soil under N addition (Table 2). Especially in the dry season, for which mean soil moisture was below 15%, mean soil respiration rate in the NN chambers had a little decrease compared to the CK chambers (Table 3). This gradually weakening trend suggested that the responses of soil respiration might reverse in the future under the continued N addition at our study sites.

4.5 Interactive effect of elevated [CO_2] and N addition on soil respiration

Increasing atmospheric CO_2 and N deposition are two primary and concurrent changes in subtropical China. Elevated [CO_2] could maintain increasing plant growth under N addition (Finzi et al., 2002). Elevated [CO_2] and N addition affected each other in stimulating plant growth (Hungate et al., 2003; Luo et al., 2004; de Graaff et al., 2006), which could result in potential and complex interactive effects on soil respiration. Allen and Schlesinger (2004) reported that N addition could increase soil respiration in FACE soil cores due to accelerated litter decomposition. However, experimental results in the FACE prototype plot (Oren et al., 2001) showed that adding N fertilizer led to reduced soil respiration response to elevated [CO_2] (Butnor et al., 2003). In addition, Astrid et al. (2004) found that different levels of N fertilization generally had no effect on soil respiration in ambient and elevated [CO_2] rings, because N seemed not to be a controlling factor in their study sites.

At our studies sites, although there was high ambient N deposition, a significant interactive effect between elevated [CO_2] and N addition ($F = 7.24$, $p = 0.006$) was found, and the combined effect of them increased soil respiration by 50% compared to that in the CK chambers (Table 5). This may be because young seedlings used in this study grew quickly and required more soil N. A positive effect on soil respiration was revealed in the N treatment (Tables 2 and 3), which indicated a transitory and slight N limitation. This N limitation would be intensified and prolonged to a certain extent under elevated [CO_2], because [CO_2] led to greater photosynthetic assimilation rates, and required more N from soil for plant growth. As a result, the greatest above-ground biomass, root biomass and SOM were also revealed in the CN treatment at our study sites (Fig. 4). In several OTC

studies with CO_2 and N manipulations, poplar seedlings and saplings ($\approx$1–5 years old) had greater plant growth stimulation by elevated [CO_2] at high rather than at low N supply after two years in Michigan (Zak et al., 2000) and Italy (Liberloo et al., 2005) and three years in Iceland (Sigurdson et al., 2001). Higher root biomass could increase root respiration and rhizosphere microbial respiration. Higher SOM would provide additional carbon supplies to decomposers (Zak et al., 2000), which would stimulate heterotrophic respiration. This might be the reason that the response of soil respiration in young subtropical forest ecosystems to elevated [CO_2] under high N deposition was much stronger than under low N deposition.

In addition, varied soil moisture due to CO_2 treatment may affect soil respiration response to N addition. Soil microbial processes such as litter decomposition and nutrient mineralization were stimulated by soil moisture (Niklaus et al., 1998). At our study, soil respiration was gradually suppressed when soil moisture was below 15% (Table 2). We found that soil moisture was significantly reduced by N addition alone (Tables 2 and 3), particularly in dry season (all below 15%), which also led to reduced soil respiration. But this decreased soil moisture was offset by elevated [CO_2]. As a result, soil moisture in the CN treatment was significantly higher than that in the NN treatment (Table 3). Thus, the effect of N on soil respiration was enhanced by CO_2 treatment, further indicating a strong interactive effect of these two factors on soil respiration.

5 Conclusions

By measuring soil respiration in open-top chambers with young subtropical trees under different CO_2 and N treatments, we estimated main and interactive effects of CO_2 and N on soil respiration. Soil respiration displayed strong seasonal patterns, with higher values observed in the wet season and lower values in the dry season in all treatments, which were primarily driven by soil temperature and soil moisture. Both CO_2 and N treatments significantly affected soil respiration, and there were significant interactions between elevated [CO_2] and N addition. Soil respiration was the highest in the chambers exposed to elevated [CO_2] and high N deposition (CN), followed by the chambers exposed to elevated [CO_2] and ambient N deposition (CC), ambient [CO_2] and high N deposition (NN), and ambient [CO_2] and ambient N deposition (CK as a control). However, the stimulatory effect of elevated [CO_2] on soil respiration was sustained over time because of a high ambient N deposition in subtropical China, even under no N addition. In addition, we found the positive effect of N addition alone had been weakened over time. These two different trends of CO_2 and N on soil respiration could lead to a potential and more complex interactive effect of elevated [CO_2] and N addition on soil respiration

in the future. Studies on source components of soil respiration and multiple aspects of soil carbon cycling are needed in long-term experiment under different CO_2 and N treatments.

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