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

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Abstract

Global climate change in the real world always exhibited 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 the subtropical China. We assessed the main and interactive effects of elevated [CO_2] and nitrogen addition on soil respiration by growing tree seedlings in ten large open-top chambers under CO_2 [ambient CO_2 and 700 μmol 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 root biomass and soil organic matter. 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 28% increased) was maintained throughout the experimental period. The positive effect of N addition was found only in 2006 (9.91% increased), and then had been weakened over time. The combined effect of them on soil respiration (about 50% increased) was greater than the impact of either one alone. Mean value of annual soil respiration was 5.24±0.10, 4.47±0.06, 3.62±0.05 and 3.51±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. The greater root biomass was obtained in the CN, CC and NN treatments, and higher soil organic matter

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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

Due to anthropogenic activities such as fossil fuel burning, deforestation, and land conversion, 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). Simultaneously, in Asia, 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). Due to the rapid expansion of industrial and agricultural activities, atmospheric nitrogen (N) deposition (NH_4^+-N and NO_3^--N) in southern China also has 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] and N deposition would influence the subtropical forests in China has not been well investigated.

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 caused by 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). Thus, understanding regulations of soil respiration by [CO_2] increase and nitrogen addition is a critical step to project global carbon cycling in the future.

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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 led 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, increased the above- and belowground biomass production. The increase in belowground 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 a higher soil respiration under elevated [CO_2] (Zak et al., 2000).

Nitrogen supply plays an important role in plant photosynthesis, plant growth and may influence the effect of elevated [CO_2] on soil respiration. Under the elevated CO_2 treatments, plants require more nutrients for plant growth. 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 (including soil respiration) may decline or weaken over time (Norby et al., 1986; Murray et al., 2000; Bernhardt et al., 2006). Adding mineral nutrients such as N can sustain increasing plant growth and provide greater soil carbon inputs under elevated [CO_2] in the long term (Luo et al., 2004; de Graaff et al., 2006). 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 now quite unclear. Increases, decreases, and unchanged in soil respiration with N additions to forest soils have been reported (Bowden et al., 2000, 2004; Burton et al., 2004; Micks et al., 2004; Clevel and Townsend, 2006; Mo et al., 2007). 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 would N deposition and elevated [CO_2] interactively influence soil respiration in subtropical forests remains unclear.

The major objective of this study was to assess the individual and interactive effects of elevated [CO_2] and N addition on soil respiration in subtropical forest. We measured soil respiration, soil temperature and soil moisture for 30 months, as well as root biomass and soil organic matter in an open-top chamber experiment. Elevated [CO_2] and N addition increased plant growth and soil carbon inputs, and they need to be matched each other. Thus we tried to examine: 1) whether elevated [CO_2] would stimulate soil respiration and the stimulatory effect would be sustained over time under high ambient N deposition; 2) whether N addition would positively affect soil respiration and the effect of N addition treatment would be weakened over time; and 3) whether the combined effect of them on soil respiration would be greater than the impact of either one alone.

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 ranged 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 radiations reach 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 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 either. 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 controlled

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using a Licor-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 in February 2005. 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 collected the soil) was shown in Liu et al. (2008). One to two years 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. and 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 the widely distributed tree species in southern China.

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 a concentration of ca. 700 μmol mol^{-1} CO_2 in the chambers. The N addition treatments were achieved by spraying seedlings one time 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 below-ground 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 Licor-6400 infrared gas analyzer (Li-COR, Inc., Lincoln, Nebraska, USA) connected with a Licor-6400-09 soil respiration chamber (9.55 cm diameter) (Li-COR, Inc., Lincoln, Nebraska, USA). The measurements were made between 09:00 a.m. and 12:00 p.m. 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 the 5 cm below 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 being taken.

2.5 Annual soil respiration calculation

Annual 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 09:00 a.m. and 12:00 p.m. can represent the daytime averages, which 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 begun in 26 June 2006, we could only estimate semiannual soil respiration from July to December in 2006. However, the seasonal variations in soil respiration were

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closely related to environment factors. There was no significant difference between the seasonal variations in environment factors among 2006, 2007 and 2008 in our study site ($p<0.001$ for air temperature and $p<0.05$ for precipitation), which indicated that seasonal variations in soil respiration are similar among the three years. In addition, the proportions of semiannual soil respiration (July–December) in annual soil respiration in 2007 and 2008 were estimated, and we found that the margin of the proportion values between 2007 and 2008 were less than 5%. Thus, in order to have a whole picture of 2006 so as to compare the effects among our three measured years, we calculated annual soil respiration in 2006 by following methods. Based on the mean proportion of semiannual soil respiration (July–December) in 2007 and 2008 (53.72%, 53.63%, 52.55% and 53.21% for the CN, CC, NN and CK treatment, respectively), we applied it for 2006. That's to say, the soil respiration from July to December in 2006 is proportional to the whole year as the behaviors showed in 2007 and 2008. Finally, we inversed the annual soil respiration estimated in 2006.

2.6 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-stem surface to the tip of the apical bud and the basal diameter was assessed at the soil surface. To measure plant biomass, one plant of each species in every chamber was harvested in January 2008. The plant was separated into roots, stems and leaves. Plant samples were oven-dried at 60 ˚C before weighed. A traditional plant growth function was developed for different components biomass estimation (Whittake and Woodwell, 1986; Wen et al., 1997):

$$W = a(D^2H)^b \quad (1)$$

Where W is dry biomass of plant components including roots, stems and leaves, D is plant basal diameter, H is height, and a, b are regression coefficients. The whole tree

biomass was the sum of root, stem and leave biomass.

Soil samples were collected on November 2008 to determine soil organic matter (SOM). Three samples of nine cores (0–20 cm depth) were collected randomly in each chamber 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 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, soil 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 the soil moisture (%) and a, b are constants fitted to the regression equation.

The index of soil respiration response to temperature was also described by 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):

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

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.

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 1 and 2; 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 1 and 2).

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 2; Fig. 1). In all treatments, significant exponential relationships between soil respiration rate and soil temperature were found ($p<0.001$ for both) (Table 3; Fig. 2). Temperature sensitivity (Q_{10}) was estimated as 1.79, 1.84, 1.82 and 1.50 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 3; Fig. 3).

The repeated measures ANOVA showed that both CO_2, N treatments and their interaction affected soil respiration significantly ($p<0.001$, $p=0.003$, and $p=0.006$, respectively) (Table 1). Soil respiration rate was the highest in the CN chambers ($3.76\pm0.07\,\mu mol\,CO_2\,m^{-2}\,s^{-1}$), followed by the CC chambers ($3.24\pm0.04\,\mu mol\,CO_2\,m^{-2}\,s^{-1}$), NN and the control chambers (CK) (2.56 ± 0.04 and $2.52\pm0.02\,\mu mol\,CO_2\,m^{-2}\,s^{-1}$, respectively) for the experimental period (Table 2). 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 1).

Mean value of annual soil respiration was 5.24 ± 0.10, 4.47 ± 0.06, 3.62 ± 0.05 and $3.51\pm0.03\,kg\,CO_2\,m^{-2}\,yr^{-1}$ in the CN, CC, NN and CK treatments, respectively (Table 4). By analyzing each treatment's annual soil respiration of the year 2006, 2007 and 2008, we observed that annual soil respiration in the CN and CC treatments increased by 47.81–51.38% and 26.24–28.45%, respectively (Table 4). 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

increase in 2006 (9.91%), with turned to no change in 2007 and 2008 (2.32% and −0.55%, respectively) (Table 4). Obviously, the effect of the NN treatment on soil respiration had been weakened over time.

3.3 Root biomass and soil organic matter

Root biomass in the CN chamber was the highest, followed by CC, NN and CK treatments at our study sites. Mean 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 that in the dry season (October–March) (Fig. 1). This is consistent with other results reported in subtropical forests (Tang et al., 2006; Zhang et al., 2006; Mo et al., 2007, 2008). This area is characterized by a typical subtropical monsoon climate, with 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 (Fig. 2). We also found that soil respiration linearly increased with soil moisture when soil moisture was below 15% (Fig. 3). 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 supports 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 higher in the CN, CC, NN treatments than that in CK, suggesting that elevated [CO_2] and N increased temperature sensitivity (Table 3). This is probably because that 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 Q_{10} of soil respiration were 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; Cardon et al., 2001; 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 sol 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 increased considerable amount of carbon release (about 28% on average) from the forest floor. The increase was comparable to an open-top chamber study in eastern Finland which reported an about 30% increase (Sini et al., 2004). 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 stimulated 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 1 and 2), 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; Martin 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 soil.

By analyzing each treatment's annual soil respiration of the year 2006, 2007 and 2008, we observed that the stimulatory effect of elevated [CO_2] on soil respiration was maintained throughout the experimental period (Table 4). This is not consistent with some reports that it gradually declined over time because of the N limitation (Bernhardt et al., 2006). Increases in photosynthetic carbon gain under elevated [CO_2] need to be matched by the 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-limited (Norby et al., 1986; Murray et al., 2000). At our study area, due to the rapid expansion of industrial and agricultural activities in subtropical regions, it results 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 a 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

In our study, the repeated measures ANOVA showed that a positive effect on soil respiration existed in the N treatment. This is similar with the pattern observed by Bowden et al. (2004) that N addition could increase soil respiration significantly in the first 2 years. However, some studies showed that soil respiration would be suppressed under N addition (Boxman et al., 1998; Mo et al., 2007, 2008). The different responses of soil respiration under N addition might reflect changes in root activity associated with nutrient uptake (Bowden et al., 2004). Mo et al. (2007) also believed that response of soil respiration to elevated N deposition might be influenced by the degree of initial soil nutrient status. We believe that young seedlings used in this study grew quickly under N addition and needed higher soil N, which would lead to a transitory and slight N limitation at our study sites. Increased aboveground biomass was observed by Duan et al. (2009) and increased root biomass (Fig. 4) was obtained in the N treatment. As Bowden et al. (2004) suggested, it is likely that added soil carbon from aboveground and belowground litter would stimulate heterotrophic respiration, greater roots biomass and root exudation enhanced autotrophic respiration under N addition.

However, 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). Aber et al. (1989) also reported that N additions would initially stimulate soil microbial activity, but would lead to a carbon limitation state after microbial demand for N was satisfied over time. By analyzing each treatment's annual soil respiration of the year 2006, 2007 and 2008 in our study, we observed that the positive effect of N addition treatment existed in the first year and it had been weakened over time. We have no data to prove that the root activity and soil microbial activity was 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 2), which might 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 soil drier under N addition. Especially in the dry season, for mean soil moisture was below 15%, mean soil respiration rate in the NN chambers had a little decrease compared to that in the CK chambers (Table 2). This gradually weakening trend suggested that the responses of soil respiration might reverse in the feature under the continued N addition at our study sites.

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

Unlike common single-factor experiments, global climate change in the real world always exhibited concurrent changes in multiple factors (Shaw et al., 2002; Norby and Luo, 2004). Increasing atmospheric CO_2 and N deposition were two primary and concurrent changes in the 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 (Luo et al., 2004; Hungate et al., 2003; 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. 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] (Bowden et al. 2004). 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. At our studies sites, a significant interactive effect between elevated [CO_2] and N addition (P=0.006) was found, and the combined effect of them increased soil respiration by 50% compared to that in the CK chambers. The increased soil respiration may be due to both increased root biomass and SOM in the CN treatment (Fig. 4). Soil respiration is due to root activity and microbial decomposition of organic material. Increased root biomass could increase root respiration and rhizosphere microbial respiration. Increased SOM would provide additional carbon supplies to decomposers (Zak et al., 2000), which would stimulate heterotrophic respiration. Elevated [CO_2] led to greater photosynthetic assimilation rates, and required more N from soil for plant growth. In addition, adding mineral nutrients such as N could sustain increasing plant growth and provide greater soil carbon inputs under elevated [CO_2] (Luo et al., 2004; de Graaff et al., 2006). As a result, the greatest root biomass and SOM were revealed in the CN treatment at our study sites (Fig. 4). This may be the reason that CO_2 effect on soil respiration increased under high N than ambient N and the effect of N was also enhanced by CO_2 treatment. This indicated that response of soil respiration in the subtropical forest to elevated [CO_2] under high N deposition could be much stronger than under low N deposition.

5 Conclusions

By measuring soil respiration in subtropical forests 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 CN chambers, followed by the CC, NN and CK chambers for the experimental period. However, this increase of soil respiration under different CO_2 and N treatments might be due to both/either of increased root biomass and SOM. It seemed that high soil C input accompanied high soil carbon output simultaneously in our experiment. In addition, elevated [CO_2] consistently increased soil respiration during current study period, but the positive effect of N addition treatment had been weakened. These two different trends could lead to a potential and more complex interactive effect of elevated [CO_2] and N addition on soil respiration in the feature. Prediction of the net result under different CO_2 and N treatments on the soil carbon balance remains unclear. 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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Table 1. 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.

	Annual			Wet season			Dry season		
	R	T	M	R	T	M	R	T	M
CO_2	<0.001	0.643	<0.001	<0.001	0.312	0.002	<0.001	0.906	<0.001
N	0.003	0.846	0.024	0.008	0.898	0.073	0.064	0.881	0.026
CO_2*N	0.006	0.930	0.263	0.524	0.782	0.535	<0.001	0.936	0.179
Season	<0.001	<0.001	<0.001						

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Table 2. Mean soil respiration rate, mean soil temperature at the 5 cm below 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

Table 3. Relationships between the soil respiration (R) and soil temperature at the 5 cm below soil surface (T) and soil moisture of the top 5 cm soil layer (M) (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 of b in the exponential equation ($R=a\exp(bT)$) within a column with different lowercase letter have significant treatment differences at α=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: μmol CO_2 m^{-2} s^{-1} for R; °C for T and % for M.

Treatment	a	b	Q_{10}	p	R^2
	a) $R=a\ \exp(bT)$				
CN	1.0155±0.027	0.0581±0.001 a	1.79	<0.001	0.64
CC	0.8085±0.061	0.0607±0.001 a	1.84	<0.001	0.66
NN	0.66±0.017	0.0596±0.001 a	1.82	<0.001	0.60
CK	0.9904±0.030	0.0406±0.001 b	1.50	<0.001	0.50
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

Table 4. Annual 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. Mean values of R within a row with different lowercase letter have significant treatment differences at α=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} yr^{-1} for R.

Year	CN		CC		NN		CK
	R	% increased	R	% increased	R	% increased	R
2006	5.07±0.17a	47.81	4.33±0.18b	26.24	3.77±0.35c	9.91	3.43±0.01d
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	5.24±0.10a	49.29	4.47±0.06b	27.64	3.62±0.05c	3.13	3.51±0.03c

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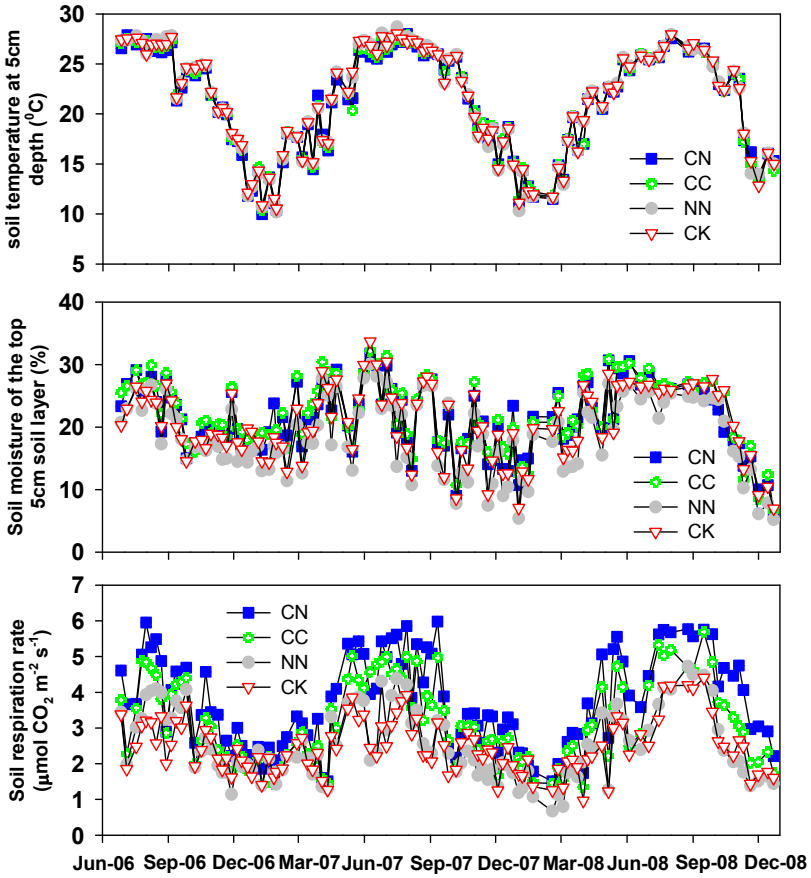

Fig. 1. Seasonal dynamics of soil temperature at the 5 cm below soil surface, soil moisture of the top 5 cm soil layer and soil respiration rate under different CO_2 and N treatments. The treatments are: CK=control, NN=high N, CC=elevated CO_2, CN=elevated CO_2+high N.

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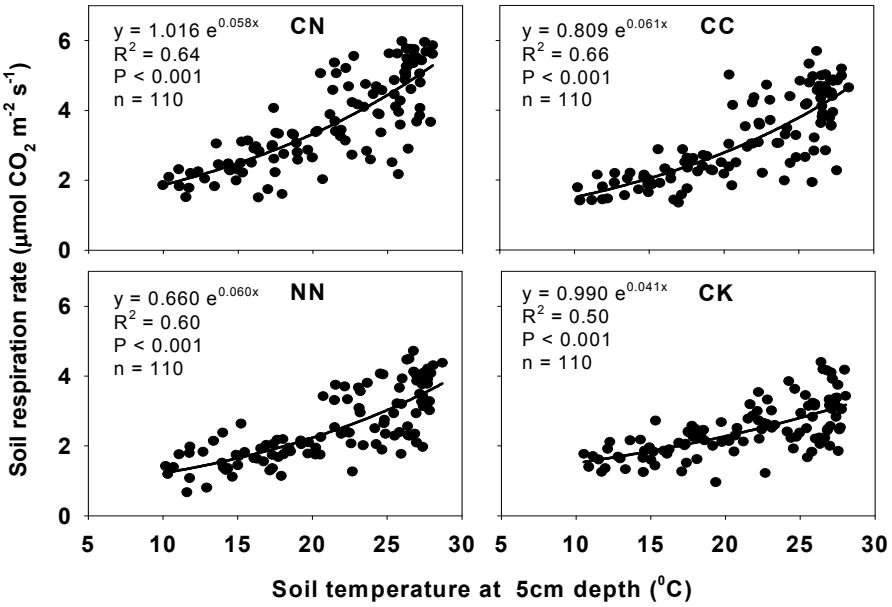

Fig. 2. Relationships between soil respiration rate and soil temperature at 5 cm depth under different CO_2 and N treatments. Each datum in panels CN and CC is the mean of three replications. Each datum in panels NN and CK is the mean of two replications. The treatments are: CK=control, NN=high N, CC=elevated CO_2, CN=elevated CO_2+high N.

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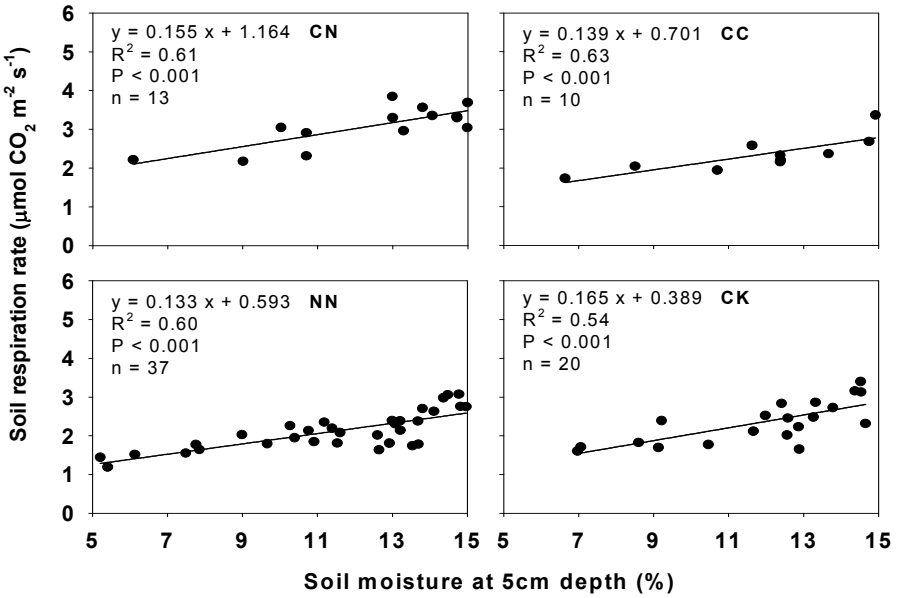

Fig. 3. Relationships between soil respiration rate and soil moisture of the top 5 cm soil layer (below 15%) under different CO_2 and N treatments. Each datum in panels CN and CC is the mean of three replications. Each datum in panels NN and CK is the mean of two replications. The treatments are: CK=control, NN=high N, CC=elevated CO_2, CN=elevated CO_2+high N.

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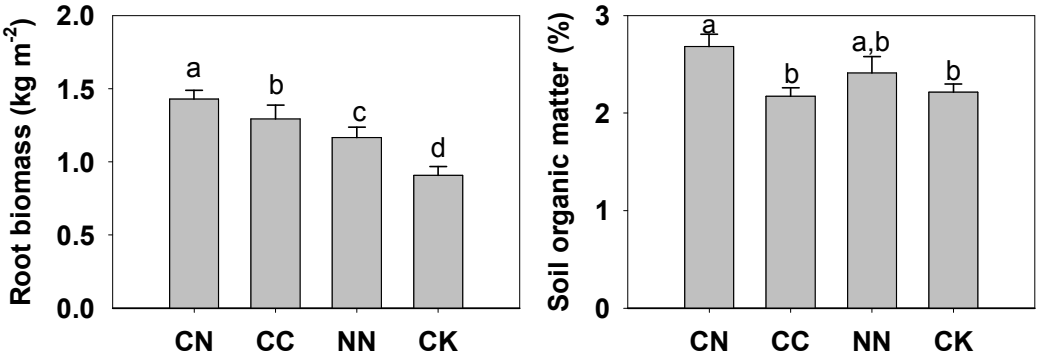

Fig. 4. Root biomass (January 2008) and soil organic matter (November 2008) under different CO_2 and N treatments. Error bars are standard deviations, which showed the dispersion among open-top chambers employed for each treatment. n=3 for the CN and CC treatments, n=2 for the NN treatment and CK. Different letters denote significant difference between treatments. Significant level is set at α=0.05. The treatments are: CK=control, NN=high N, CC=elevated CO_2, CN=elevated CO_2+high N.

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