

Research Paper

Will nitrogen deposition mitigate warming-increased soil respiration in a young subtropical plantation?



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ARTICLE INFO

Keywords:

Chinese fir nitrogen addition
Plantation
Soil respiration
Soil warming
Subtropical forest

ABSTRACT

Global change such as climate warming and nitrogen (N) deposition is likely to alter terrestrial carbon (C) cycling, including soil respiration (Rs), the largest CO₂ source from soils to the atmosphere. To examine the effects of warming, N addition and their interactions on Rs, we conducted a two-way factorial soil warming (control, 5 °C warming) and N addition (control, 40 and 80 kg N ha⁻¹ yr⁻¹) mesocosm experiment in subtropical China. We measured Rs and nutrient availability. We found warming alone increased Rs by 15%, but warming plus high N addition treatment appeared to have offsetting effects as these plots were not significantly different from unheated and unfertilized controls. Warming alone increased soil available phosphorus (P) but availability declined in response to warming plus N additions. N additions alone had no effect on Rs in this study. Our results suggest that future increases in N deposition could mitigate warming-increased Rs in P-limited and relatively N-saturated subtropical forest ecosystems.

1. Introduction

Climate change models predict that atmospheric temperature and N deposition will continue to increase within sub-tropical regions (Kanakidou et al., 2016; Knutti and Sedláček, 2013; Reay et al., 2008). It is estimated that air temperature in subtropical regions will increase by 1.3–5.0 °C within the next 100 years, which is greater than the global average of 1–3.7 °C (Field et al., 2014; The Committee of China's National Assessment Report on Climate Change, 2015). In the coming 20 years, worldwide N deposition is anticipated to increase by between 50% and 100% by 2030 relative to 2000, with the largest absolute increases occurring over East and South Asia (Reay et al., 2008). Atmospheric wet/bulk N deposition in subtropical China ranges from 26 to 55 kg N ha⁻¹ yr⁻¹ (Du et al., 2016; Shen et al., 2013). It is widely appreciated that increasing temperature and N deposition have major impacts on C process rates in the tropics and subtropics (Lu et al., 2013; Luo, 2007; Reay et al., 2008). Tropical forests store approximately 25% of all terrestrial C, support one-third of the terrestrial biosphere's net primary productivity, and may play an important role in mitigating future global warming (Bonan, 2008). The extent to which tropical

forests might mitigate future warming is uncertain, however, because the independent and interactive effects of warming and nutrient additions on C process rates are poorly understood.

While there have been many manipulative warming experiments in the mid to high latitudes (Aguilos et al., 2011; Luo et al., 2001; Noh et al., 2016; Schindlbacher et al., 2009; Suseela and Dukes, 2013), few studies have tackled the effects of rising temperature on tropical and subtropical forests (Giardina et al., 2014; Wu et al., 2016). This lack of detailed information about tropical and subtropical forest response to warming points to an urgent need for warming experiments in the tropics and subtropics (Cavaleri et al., 2015; Zuidema et al., 2013).

Compared with wide-spread N limitations to forest productivity in temperate regions, nutrient limitations to productivity in older soils of tropical and subtropical regions are typically driven by P (Cleveland and Townsend, 2006; Cleveland et al., 2002). Thus, effects of high rates of N deposition on ecosystem processes in the tropical and subtropical regions may be expressed very differently than in temperate regions. Many studies have examined the effects of elevated N deposition on soil C cycles of forest ecosystems in tropical and subtropical forests (Gao et al., 2014; Mo et al., 2008; Ramirez et al., 2012). Some studies

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indicate that responses of soil C cycles of tropical and subtropical forests to N deposition are significantly different between N-enriched and N-limited forests (Gao et al., 2014; Mo et al., 2008). There is little information on the effects of N deposition on subtropical forests in southeastern China.

Soil respiration (R_s) is the largest source of CO_2 from terrestrial ecosystems to the atmosphere (Metcalf et al., 2011). Many studies indicate that both increased temperature and N deposition have major impacts on R_s (Melillo et al., 2011; Noh et al., 2016; Schindlbacher et al., 2009; Sun et al., 2014; Suseela and Dukes, 2013). In addition, warming often stimulates forest net N mineralization and thus increases N availability in soils (Butler et al., 2012; Melillo et al., 2011), which in turn can affect R_s rates through altered plant allocation schemes, changes to plant litter decomposition, or reduced mycorrhizal colonization rates (Giardina et al., 2004; Giardina et al., 2003).

The independent effects of warming and N deposition on R_s have been studied across a diversity of forest types, but few studies have examined both independent and interactive effects and underlying mechanisms of warming and N deposition on R_s (Contosta et al., 2011; Graham et al., 2014). Research in tropical and subtropical regions is largely absent despite the fact that these regions are facing substantial increases in both temperature and N deposition (Field et al., 2014; Kanakidou et al., 2016). These knowledge gaps are important because for larger areas of the terrestrial biosphere, both temperature and N deposition are increasing, the tropics and subtropics account for a large fraction of the Earth's primary productivity, and their interactive effects cannot be fully understood from single factor experiments (Bonan, 2008; Cavaleri et al., 2015; Zhou et al., 2013; Zuidema et al., 2013).

China's forests represent an important sink for atmospheric C, storing 4.75 Pg C per year (Fang et al., 2001) and taking up 0.19–0.26 Pg C per year (Piao et al., 2009). Approximately 65% of Chinese forests and associated C occur in the southeastern subtropical provinces of Fujian, Hunan and Zhejiang (Piao et al., 2009). More than 32% of these forests are plantations, the dominant species being Chinese fir (*Cunninghamia lanceolata*), which accounts for most commercial plantations with respect to acreage and timber production (Lu et al., 2015; SFA, 2009). We used Chinese fir plantation as a model system to understand R_s responses to the independent and combined effects of artificial soil warming and N enrichment through fertilization. A thorough understanding of R_s responses of Chinese fir to both warming and N enrichment and their interactions is critical for accurately predicting belowground C dynamics of subtropical forest ecosystems with future climate change. Our multi-factorial experiment allowed us to quantify the effects of soil warming, N addition and their interactions on R_s .

We used our experimental design to address the following questions: (1) how do soil warming and N addition affect R_s of a subtropical plantation? (2) will temperature sensitivity of R_s change with warming and N addition? and (3) how will soil warming interact with N addition in affecting R_s ?

2. Materials and methods

2.1. Study area

The study was conducted in the Chenda Observation Study Site (26° 19'55" N, 117° 36'53" E, 300 m a.s.l.) of Sanming Forest Ecosystem and Global Change Research Station in Fujian Province, China. This study site borders the Daiyun Mountains on the south-east and the Wuyi Mountains on the northwest. This area is 10 km northwest of the small industrial city of Sanming. Average annual wet N deposition (NO_3^- plus NH_4^+) from precipitation in Sanming region is $36.3 \text{ kg N m}^{-2} \text{ yr}^{-1}$ (Zhang, 2013). The study site is characterized by a typical maritime subtropical monsoon climate. The mean annual temperature (MAT) is 19.1 °C with low temperatures occurring in January and high temperatures occurring in July. Mean annual relative humidity is 81% and the mean annual precipitation (MAP) is 1750 mm.

Approximately 75% of total precipitation occurs from March to August. The mean annual potential evapotranspiration is 1585 mm. The soil at the study site is sandy in texture and granite in parent material. It is classified as red soil from the China soil classification systems, and is equivalent to Oxisol in the USDA Soil Taxonomy (State Soil Survey Service of China, 1998; Soil Survey Staff of USDA, 2014).

2.2. Experimental design

In this experiment, a randomized block design was used with soil warming and N addition as the main treatments. There were five blocks and each block included control (CT), soil warming (W), low N addition (LN, $40 \text{ kg N ha}^{-1} \text{ yr}^{-1}$), soil warming plus low N addition (WLN), high N addition (HN, $80 \text{ kg N ha}^{-1} \text{ yr}^{-1}$), and soil warming plus high N addition (WHN). This experimental design resulted in a total of 30 plots and each plot had a size of $2 \text{ m} \times 2 \text{ m}$. The plots were separated with PVC boards inserting into soils at a depth of 0.7 m. Each plot was divided into four $1 \text{ m} \times 1 \text{ m}$ subplots and one-year-old Chinese-fir seedling was planted in each subplot. The seedlings were selected from a local nursery to be uniform in plant height, basal diameter and fresh weight. The average plant height and basal diameter of the seedlings were $25.7 \pm 2.5 \text{ cm}$ and $3.4 \pm 0.4 \text{ mm}$, respectively. In November 2013, four healthy seedlings were randomly selected and transplanted into the center of each subplot.

Soil temperatures in the warmed plots (W, WLN and WHN) were maintained at a constant 5 °C above the ambient temperature of the unwarmed control plots. The warming treatment was conducted by using buried heating cables placed 10 cm below the soil surface with an interval of 20 cm. The heating cables (TXLP/1, Nexans, Norway) contained a resistance wire with an output of 17 W m^{-1} at 230 V. The heating cables were installed in August 2013 and soil warming started on 1 March 2014, approximately 4 months after planting. We used "disturbance control" in this study (i.e., with cables buried but no heating). The temperature sensors (T109 from Campbell Scientific Inc., Logan, UT, USA) were placed between two cable lines in the soils at a depth of 10 cm. Three temperature sensors were installed in each warming plot and two in each control plot. Soil moisture in each plot was measured by using 2 ECH₂O-5 soil moisture probes (Decagon, Pullman, Washington, USA) placed between two cable lines in the soils at a depth of 10 cm.

2.3. Nitrogen addition

Nitrogen additions began at the time of the warming treatments in March 2014 and were applied monthly using an aqueous solution of NH_4NO_3 to achieve a total application rate of 40 and $80 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ for the low N (LN and WLN) and high N (HN and WHN) treatments, respectively. The solutions were mixed with 800 mL of deionized water and applied evenly to each subplot of each treated plot using a watering can. The control and warming plots received 800 mL of deionized water without N. Nitrogen addition rate was only slightly higher than the local N deposition rate which averages $36.3 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Zhang et al., 2013).

2.4. R_s measurements

Two PVC collars (20 cm in diameter) were installed at a soil depth of 5 cm for R_s measurements at the center of two seedlings in each plot. R_s measurements started in March 2014. R_s was measured biweekly using two automatic soil CO_2 flux systems (LI-8100A, LI-COR, USA) from 09:00 to 12:00 a.m. Soil temperatures were measured at 5-cm depth using a hand-held probe (Model SK-250WP, Sato Keiryoki Mfg. Co. Ltd, Tokyo, Japan) and soil moisture at 0–12 cm depth using time domain reflectometry (TDR 300 Soil Moisture Meter, Spectrum, USA). Measurements continued for one year until February 2015.

2.5. Soil sampling and analysis

Soils were sampled for physical and chemical analyses in April of 2015, one year after treatments were imposed. Five soil cores (2 cm in diameter) were taken at a soil depth of 10 cm from each plot. The soil samples were immediately stored in an icebox and then transported to the laboratory for analyses, which occurred no more than 7 days after sampling. Each soil sample was passed through a 2 mm sieve, and roots, organic debris and rocks were removed. The sieved soils were then stored in a refrigerator at a temperature of 4 °C until processing, when each processed sample was divided into two sub-samples for analysis. One subsample was used for analysis of nitrate, ammonium and available P. The other subsample was used for total soil C and N determination under high-temperature oxidation using a CN analyzer (Elementar Vario MAX, Germany). Soil pH was measured using a mixture of soil and water with a ratio of 1:2.5. Microbial biomass C was estimated using the fumigation-extraction technique adapted from Vance et al. (1987). A 25-g moist soil sample was fumigated with chloroform for 24 h and then extracted with 100 mL 0.5 M K₂SO₄. The samples were shaken for 30 min and then filtered through a membrane filter with 0.45-μm pores. The non-fumigated soil samples were also extracted using the same procedure. These filtrates were analyzed for organic C using a TOC analyzer (Shimadzu Corporation, Japan). Microbial biomass C was calculated from the difference in extractable C before and after fumigation using a conversion factor (kc) of 0.45. For nitrate and ammonium analyses, five grams of fresh soil from each sample were extracted using a 2-mol/L KCl solution. The solutions were shaken for 40 min and then filtered for nitrate and ammonium determination using a Continuous Flow Analyzer (SKALAR San + +, Holland). Available P was determined by the Mehlich-3 method (Carter and Gregorich, 2006). A 3 g soil sample was put into a 150 mL disposable plastic cup to make a solution at a ratio of 1:10 (soil:M3), then shaken for 5 min on a 200-rpm orbital shaker before being filtered through Whatman No. 42 filter paper. The supernatant was used to determine the available P by using the Continuous Flow Analyzer (SKALAR San + +, Holland).

2.6. Fine root sampling and biomass measurement

For the fine root sampling, five soil cores were taken randomly in each plot with a soil corer (3.5 cm in diameter) in April of 2015. The big roots (> 2 mm) were carefully removed from the soil samples with forceps and then the soils were wet-sieved with a mesh size of 0.5 mm. The sieved soils were put into a beaker with deionized water at a temperature of 1 °C and stirred repeatedly to float the fine root segments to water surface for collection. Fine roots were placed into an oven at a temperature of 65 °C for 48 h and then weighed. The total C and N concentrations of the fine root were measured with high-temperature oxidation using a CN analyzer (Elementar Vario, MAX, Germany).

2.7. Data analysis

Annual Rs for each treatment was estimated by summing daily Rs multiplied the number of days between sampling points (Li et al., 2013). The temperature sensitivity of Rs was determined by fitting the data collected from March 2014 to February 2015 to the following equation:

$$R_s = ae^{bt} \quad (1)$$

where Rs is the measured CO₂ efflux (μmol m⁻² s⁻¹), t is the soil temperature (°C) at 5 cm depth, a is the respiration rate at a reference temperature of 0 °C and b is the temperature sensitivity of soil CO₂ efflux. Respiratory quotient (Q₁₀) is calculated as:

$$Q_{10} = e^{10b} \quad (2)$$

A total of 24 data sets from biweekly measurements were used to calculate Q₁₀ of Rs for each plot. Linear mixed-effects models restricted maximum likelihood (REML) repeated measures ANOVA were used to assess the effects of warming, N addition and their interactions on Rs, soil temperature and soil moisture. The effects of warming, N addition and their interactions on soil property, fine root biomass, fine root C, fine root N and microbial biomass C were analyzed using a mixed-model restricted maximum likelihood (REML) ANOVA. In the models warming and N addition were treated as fixed factors and block was treated as a random factor. The significance threshold was pre-established at α = 0.05. Significant differences between the treatments for Rs, soil temperature, soil moisture, soil properties, fine root biomass and Q₁₀ were tested using the Tukey's multiple comparison post hoc method. Treatment effects were interpreted as significant if p < 0.05. Regression models were used to examine the relationships between Rs and soil moisture and soil available P. The statistical analyses were performed using SPSS 20 (SPSS Inc., Chicago, IL, USA).

3. Results

3.1. Warming effects on soil temperature and soil moisture

The soil warming treatments (W, WLN and WHN) increased the annual mean soil temperatures at a depth of 10 cm by 5.1 ± 0.3 °C (Fig. 1b). The soil temperature in all the warming plots constantly followed the seasonal pattern of air temperature in the study area (r² = 0.96, p < 0.001, Fig. 1a, b). Soil warming significantly (p < 0.01) decreased the annual mean soil moisture (in volume) by 4.6% in W, 4.9% in WHN, and 4.2% in WLN compared to the CT plots (Table 1, Fig. 1c). Nitrogen addition (LN or HN) or interaction of warming and N addition had no effects on both soil temperature and moisture (Table 1).

3.2. Warming and N addition effects on Rs dynamics

Across the year, Rs generally tracked soil temperature, ranging from a minimum of 0.7 μmol m⁻² s⁻¹ in winter to a maximum of 2.8 μmol m⁻² s⁻¹ in summer in all plots (Fig. 1d). There was a trend that Rs was higher in all warming plots (W, WHN, WLN) than non-warming plots (CT, LN, HN) from March to September (wet season). From October to February (dry season) there was no such trend between warming plots and non-warming plots. Within the warming treatments, W and WLN plots had higher Rs than the WHN plots throughout the one-year period of study (Fig. 1d).

3.3. Warming and N addition effects on annual efflux Rs

Among all the treatments, the annual cumulative Rs ranged from 473 to 578 g C m⁻² yr⁻¹ (Fig. 2). Compared to the CT plots, annual Rs was significantly greater in the W and WLN treatments. There were no significant differences in Rs between the CT and the WHN, LN or HN treatment (Fig. 2). The Rs increased by 15% and 8% in the W and the WLN treatments, respectively.

3.4. Temperature sensitivities of Rs

Soil respiration was positively correlated to soil temperature at a soil depth of 5 cm. The temperature sensitivities of Rs are shown in Table 2. Soil temperature explained 35–72% of the variation in Rs for the warming treatments and 21–54% for the non-warming treatments (Table 2). The Q₁₀ values of Rs did not differ between all the warming treatments (W, WLN and WHN) and the CT plots (Table 2). However, the Q₁₀ values of N addition treatments (LN and HN) were lower than all the warming treatments (W, WLN and WHN).

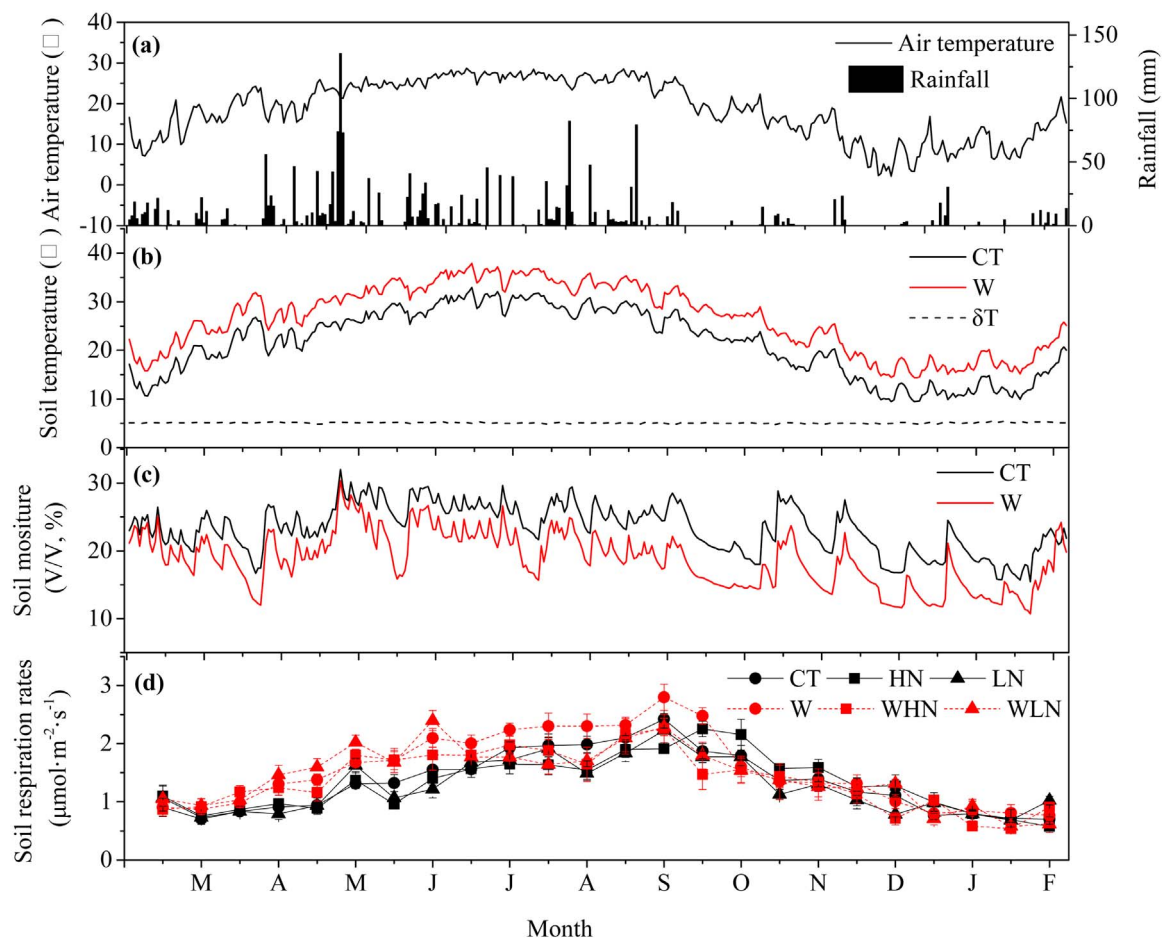


Fig 1. Daily rainfall and air temperature (a), seasonal variation soil temperature (b), soil moisture (c) at 10 cm under CT and W plots and seasonal variation in R_s (d) from March 2014 to February 2015 averaged by warming treatment and N addition treatment ($n = 5$ samples, mean ± 1 SE). δT means difference value of soil temperature between W and CT plots. CT: control, LN: low N addition, HN: high N addition, W: warming, WLN: warming plus low N addition, WHN: warming plus high N addition.

3.5. Soil properties, microbial C and fine root biomass

Total soil organic C, N and C:N were not significantly altered by either warming or N addition treatments (Table 3). Microbial biomass C in the W plots ($185 \pm 28 \text{ mg kg}^{-1}$) was not significantly different from the CT plots ($163 \pm 14 \text{ mg kg}^{-1}$) but it was significantly lower in the WHN plots. Warming reduced microbial biomass C from $243 \pm 17 \text{ mg kg}^{-1}$ in the LN plots to $120 \pm 10 \text{ mg kg}^{-1}$ soil in the WLN plots and from $197 \pm 23 \text{ mg kg}^{-1}$ in the HN plots to $87 \pm 6 \text{ mg kg}^{-1}$ soil in the WHN plots. Microbial biomass C increased in the LN but not in the HN plots (Table 3).

Soil NH_4^+ content in the W plots ($5.6 \pm 0.3 \text{ g kg}^{-1}$) did not differ from the CT plots ($5.3 \pm 0.4 \text{ g kg}^{-1}$) but it was higher in the WHN plots ($7.3 \pm 0.5 \text{ g kg}^{-1}$) and the HN plots ($9.2 \pm 1.0 \text{ g kg}^{-1}$) (Table 3).

Soil NO_3^- content increased in the W, WLN and WHN compared to

the CT plots, with the values of 7.3 ± 1.0 , 6.7 ± 1.0 , 9.5 ± 0.9 and $3.1 \pm 0.3 \text{ g kg}^{-1}$ in the W, WLN, WHN and CT plots, respectively. Soil NO_3^- contents did not differ between the CT and either LN ($3.8 \pm 0.6 \text{ g kg}^{-1}$) or HN ($4.8 \pm 1.2 \text{ g kg}^{-1}$).

Soil available P increased in the W plots ($1.9 \pm 0.1 \text{ mg kg}^{-1}$) compared to the CT plots ($1.6 \pm 0.1 \text{ mg kg}^{-1}$). Soil available P in the W plots was also higher than the WLN ($1.3 \pm 0.1 \text{ mg kg}^{-1}$) and WHN plots ($1.5 \pm 0.1 \text{ mg kg}^{-1}$). Relative to the CT plots ($1.6 \pm 0.1 \text{ mg kg}^{-1}$), soil available P was lower in the HN plots ($1.1 \pm 0.1 \text{ mg kg}^{-1}$) (Table 3).

Fine root biomass (Table 3) was significantly lower in W, WLN and WHN plots relative to CT plots. There were no differences among the non-warming treatments either, with values of 12.7 ± 3.2 , 7.5 ± 1.7 and $9.6 \pm 3.2 \text{ g m}^{-2}$ in the LN plots, HN plots and CT plots, respectively (Table 3). The W, LN and HN, and WLN and WHN plots all reduced fine root C:N compared with CT. Soil pH was not affected by the

Table 1

Soil temperature at the depth of 0–10 cm and soil moisture (means \pm SE) at the depth of 0–12 cm. Sample size for both soil temperature and soil moisture is 5. The numbers in the columns under “treatment effects” mean F-values generated by linear mixed-effects models testing the effects of warming (W), Nitrogen addition (N) and their interactions on soil temperature and soil moisture. CT: control; LN: low N addition; HN: high N addition; W: warming; WLN: warming plus low N addition; WHN: warming plus high N addition. WE: warming effect; NE: N addition effect; WE*NE: interaction effect of warming and N addition. Different lower letters mean significantly different at 0.05 significance level in difference treatment; Bold font indicates a significant effect ($p < 0.05$). *: $p < 0.05$, **: $p < 0.01$ and ***: $p < 0.001$.

Parameter	Treatments						Treatment effects		
	CT	HN	LN	W	WLN	WLN	WE	NE	WE*NE
Soil temperature ($^{\circ}\text{C}$)	$20.1 \pm 0.1\text{b}$	$20.1 \pm 0.2\text{b}$	$20.5 \pm 0.2\text{b}$	$24.7 \pm 0.1\text{a}$	$24.7 \pm 0.1\text{a}$	$24.5 \pm 0.1\text{a}$	1252***	0.69	5.47
Soil moisture (vol, %)	$22.7 \pm 0.7\text{a}$	$21.2 \pm 0.3\text{a}$	$21.8 \pm 0.6\text{a}$	$18.1 \pm 0.6\text{b}$	$17.8 \pm 0.6\text{b}$	$18.5 \pm 0.6\text{b}$	70.45***	3.04	0.83

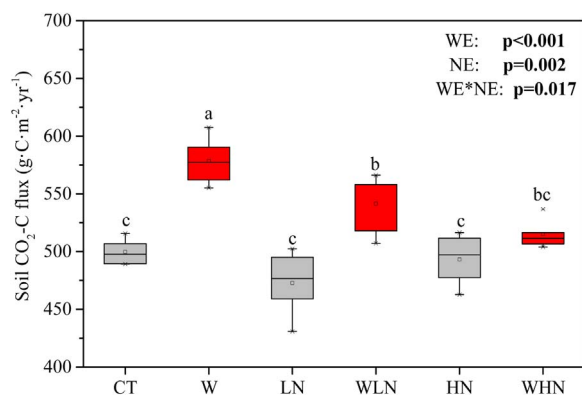


Fig. 2. Soil CO₂-C annual efflux of Rs in the warming and N addition treatments in the first year (n = 5). CT: control, LN: low N addition, HN: high h N addition, W: warming, WLN: warming plus low N addition, WHN: warming plus high N addition. WE: warming effect, NE: N addition effect, WE*NE: interaction effect of warming and N addition. Box plots present the median with an interval of 95% confidence and minimum and maximum values. Different letters indicate significant differences between treatments at p < 0.05.

treatments with the exception that WHN plots showed significantly lower pH values compared to CT plots (Table 3).

3.6. Relationships between Rs and soil moisture and available P

Using all data from combined treatments (n = 30), the linear regressions demonstrated that Rs was negatively correlated to soil moisture (Fig. 3a, $R^2 = 0.22$, $p = 0.008$) but positively correlated to soil available P (Fig. 3b, $R^2 = 0.17$, $p = 0.023$). If only using the data from all warming treatments (W, WLN, WHN) (n = 15), the linear regression demonstrated that warming treatments had a higher correlation between Rs and available P (Fig. 3b, $R^2 = 0.444$, $p = 0.004$) than

the combined treatments.

4. Discussion

4.1. Rs response to warming and N addition

Many studies have reported that soil warming increased Rs in different temperate forests (Melillo et al., 2011; Noh et al., 2016; Schindlbacher et al., 2009). Studies in temperate regions suggest that warming often stimulates net N mineralization and then increased N availability in the temperate forests (Butler et al., 2012; Melillo et al., 2011). Thus, warming could reduce the competition of microbes in relatively N-limited temperate forests.

In the present study, we also found that warming increased Rs and that soil mineral N ($\text{NH}_4^+ + \text{NO}_3^-$) content was higher in all warming treatments (Table 3). However, enhanced soil mineral N content by warming was not significantly correlated with soil heterotrophic respiration (unpublished data). This result indicates that in our study, higher soil temperature increased soil mineral N but the additional mineralized N may not take up by the plants (Zhang et al., 2017) or microbes. This lack of uptake could be due to competing constraints on microbial activity due to lack of available substrate (e.g. C or P), reduced soil moisture (Fig. 1c, Table 1) or that N does not limit the biological processes in these systems (Huygens et al., 2008; Zhang et al., 2013).

Our result that Rs was positively correlated with available P in soils was consistent with the findings by Cleveland and Townsend (2006) and Reed et al. (2011) that many tropical and subtropical forests may be P-limited. Liu et al. (2012) also reported that P addition increased soil microbial biomass and altered microbial communities in subtropical forests. Our results that warming increased both N and P availability but only P was significantly correlated with Rs (Fig. 3b)

Table 2

Exponential relationship between Rs and soil temperature T (°C) and Q₁₀. Data are means ± standard error (n = 5). CT: control, LN: low N addition, HN: high N addition, W: warming, WLN: warming plus low N addition, WHN: warming plus high N addition. Q₁₀ with different letter means a significant difference at p < 0.05.

Treatment	subplots	Formulas	R ²	p	Q ₁₀	Mean of Q ₁₀
CT	CT1	$y = 0.428e^{0.048x}$	0.51	< 0.001	1.54	1.46 ± 0.03ac
	CT2	$y = 0.626e^{0.032x}$	0.28	0.008	1.38	
	CT3	$y = 0.499e^{0.046x}$	0.53	< 0.001	1.52	
	CT4	$y = 0.501e^{0.043x}$	0.45	< 0.001	1.53	
	CT5	$y = 0.663e^{0.032x}$	0.38	0.001	1.38	
HN	HN1	$y = 0.623e^{0.031x}$	0.36	0.002	1.36	1.32 ± 0.03c
	HN2	$y = 0.798e^{0.023x}$	0.21	0.024	1.25	
	HN3	$y = 0.816e^{0.019x}$	0.26	0.038	1.21	
	HN4	$y = 0.666e^{0.032x}$	0.32	0.004	1.37	
	HN5	$y = 0.522e^{0.042x}$	0.51	< 0.001	1.42	
LN	LN1	$y = 0.477e^{0.040x}$	0.47	< 0.001	1.49	1.38 ± 0.04bc
	LN2	$y = 0.525e^{0.039x}$	0.54	< 0.001	1.48	
	LN3	$y = 0.780e^{0.023x}$	0.25	0.012	1.25	
	LN4	$y = 0.637e^{0.025x}$	0.34	0.004	1.29	
	LN5	$y = 0.636e^{0.033x}$	0.47	< 0.001	1.39	
W	W1	$y = 0.343e^{0.053x}$	0.72	< 0.001	1.70	1.57 ± 0.03a
	W2	$y = 0.367e^{0.054x}$	0.68	< 0.001	1.55	
	W3	$y = 0.320e^{0.056x}$	0.67	< 0.001	1.58	
	W4	$y = 0.520e^{0.041x}$	0.62	< 0.001	1.51	
	W5	$y = 0.747e^{0.029x}$	0.55	0.001	1.51	
WHN	WHN1	$y = 0.360e^{0.050x}$	0.57	< 0.001	1.60	1.55 ± 0.03ab
	WHN2	$y = 0.394e^{0.046x}$	0.51	< 0.001	1.58	
	WHN3	$y = 0.389e^{0.046x}$	0.66	< 0.001	1.59	
	WHN4	$y = 0.544e^{0.034x}$	0.45	< 0.001	1.54	
	WHN5	$y = 0.520e^{0.036x}$	0.46	< 0.001	1.43	
WLN	WLN1	$y = 0.440e^{0.047x}$	0.58	< 0.001	1.60	1.51 ± 0.04ab
	WLN2	$y = 0.536e^{0.034x}$	0.35	0.002	1.40	
	WLN3	$y = 0.550e^{0.034x}$	0.41	0.001	1.41	
	WLN4	$y = 0.437e^{0.048x}$	0.61	< 0.001	1.61	
	WLN5	$y = 0.440e^{0.047x}$	0.58	< 0.001	1.53	

Table 3

Soil properties, fine-root biomass, and C and N concentration in the fine roots and top soil (0–10 cm). The numbers in the columns under “treatment effects” mean F-values generated by linear mixed-effects models. CT: control; LN: low N addition; HN: high N addition; W: warming; WLN: warming plus low N addition; WHN: warming plus high N addition. WE: warming effect; NE: N addition effect; WE*NE: interaction effect of warming and N addition. Data are means \pm standard error (n = 5); Different letters mean significantly different at 0.05 significance level. *: $p < 0.05$, **: $p < 0.01$ and ***: $p < 0.001$. Significant results ($p < 0.05$) are bolded.

Parameter	Treatment						Treatment effects		
	CT	HN	LN	W	WLN	WLN	WE	NE	WE*NE
Soil C content (g kg^{-1})	14.2 \pm 0.4a	13.5 \pm 1.1a	13.2 \pm 0.75a	12.7 \pm 1.0a	13.9 \pm 0.4a	13.7 \pm 0.79a	0.16	0.07	1.05
Soil N content (g kg^{-1})	1.4 \pm 0.1a	1.4 \pm 0.2a	1.3 \pm 0.1a	1.2 \pm 0.1a	1.3 \pm 0.1a	1.3 \pm 0.1a	0.58	0.55	0.41
C/N	10.5 \pm 0.2a	9.9 \pm 0.7a	10.5 \pm 0.3a	10.6 \pm 0.3a	10.4 \pm 0.2a	10.5 \pm 0.2a	0.50	0.66	0.37
pH	4.7 \pm 0.1a	4.6 \pm 0.1ab	4.6 \pm 0.1ab	4.6 \pm 0.1ab	4.4 \pm 0.1b	4.5 \pm 0.1ab	5.79*	1.71	0.11
NH_4^+ (g kg^{-1})	5.3 \pm 0.4 cd	7.3 \pm 0.5b	6.2 \pm 0.4bd	5.6 \pm 0.3 cd	9.2 \pm 1.0a	6.8 \pm 0.8bc	3.57	11.37***	0.88
NO_3^- (g kg^{-1})	3.1 \pm 0.3c	4.8 \pm 1.2bc	3.8 \pm 0.6c	7.3 \pm 1.0ab	9.5 \pm 0.9a	6.7 \pm 1.0b	29.89***	2.95	0.51
P availability (mg kg^{-1})	1.6 \pm 0.1b	1.1 \pm 0.1d	1.6 \pm 0.1b	1.9 \pm 0.1a	1.5 \pm 0.1bc	1.3 \pm 0.1 cd	1.45	12.82***	7.83***
Microbial biomass C (mg kg^{-1})	163 \pm 14 cd	197 \pm 23bc	243 \pm 17ab	185 \pm 28c	87 \pm 6e	120 \pm 10d	22.79***	2.73	9.93**
Fine root biomass (g m^{-2})	9.6 \pm 3.2a	7.5 \pm 1.7ab	12.7 \pm 3.2a	3.2 \pm 1.1c	3.0 \pm 1.3c	5.1 \pm 2.2bc	11.02**	1.34	0.23
Fine-root C content (g kg^{-1})	407 \pm 1a	387 \pm 2bc	392 \pm 2b	402 \pm 1a	380 \pm 3d	383 \pm 2 cd	16.51**	50.57***	0.61
Fine-root N content (g kg^{-1})	6.5 \pm 0.3f	9.6 \pm 0.1d	7.8 \pm 0.8e	14.2 \pm 0.2b	23.1 \pm 0.1a	11.5 \pm 0.2c	562***	148***	59.7***
Fine-root C/N	62.4 \pm 2.5a	40.3 \pm 0.4c	52.6 \pm 5.2b	28.3 \pm 0.3d	16.5 \pm 0.1e	33.4 \pm 0.8 cd	172***	29.2***	5.75***

indicates that future global warming may increase Rs in N-limited forests only where mineral nutrient availability is also increased.

The addition of N to temperate and tropical forests has resulted in contrasting effects on Rs. Some studies report reduced Rs caused by the negative effects of N additions on microbial biomass, fine root biomass and/or microbial community structures (Mo et al., 2008; Ramirez et al., 2012; Sun et al., 2014), while other studies report increased Rs caused by the positive effects of N additions on fine root biomass and ectomycorrhizal (EM) fungal communities (Gao et al., 2014; Hasselquist et al., 2012). Our results that N addition increased NH_4^+ and NO_3^- concentrations in soils but did not have a significant effect on Rs indicate that N is not limited in this recently established subtropical plantation. Warming plus high N addition treatments appear to have offsetting effects as these plots were not significantly different from unheated and unfertilized controls. Our results suggest that future increased N deposition could mitigate warming-increased Rs from soils in P-limited and relatively N-saturated subtropical forest ecosystems. With continued atmospheric inputs of N to the system, changes may become apparent if soil chemistry changes in response to high N loads.

4.2. Interaction between warming and N addition

Several recent studies showed that warming plus N addition increased Rs in temperate forests (Contosta et al., 2011) and temperate

grasslands (Graham et al., 2014). In this study, we found that Rs increased by 15% in warming plots but warming had no effect when paired with high N addition (Fig. 2). This result implies that warming-related stimulation of Rs is inhibited by extra N inputs and that the inhibition becomes stronger with higher N inputs in subtropical forests of southeastern China not limited by N.

Burton et al. (2012) reported that root activities typically increase with increasing tissue N concentration. Increased N concentration in root tissues may change microbial community structures and further change root litter inputs into soil C. In our study, we found that the total fine root biomass was quite low compared to mature forests in this region (Guo et al., 2016). This result could be due to an uneven distribution of fine roots which were sampled with only 5 replicates.

The interaction between warming and N addition was also reflected in P availability. Our study showed that available P significantly increased only in the warming plots but not in the warming plus N addition plots (Table 3). This inhibition effect is possibly due to increased soil acidity by N addition (Lu et al., 2014; Tian and Niu, 2015). Typically, soils with low pH mobilize Fe^{3+} and Al^{3+} that precipitate P and thus reduce P availability (Crews et al., 1995; Giesler et al., 2002; Perring et al., 2008).

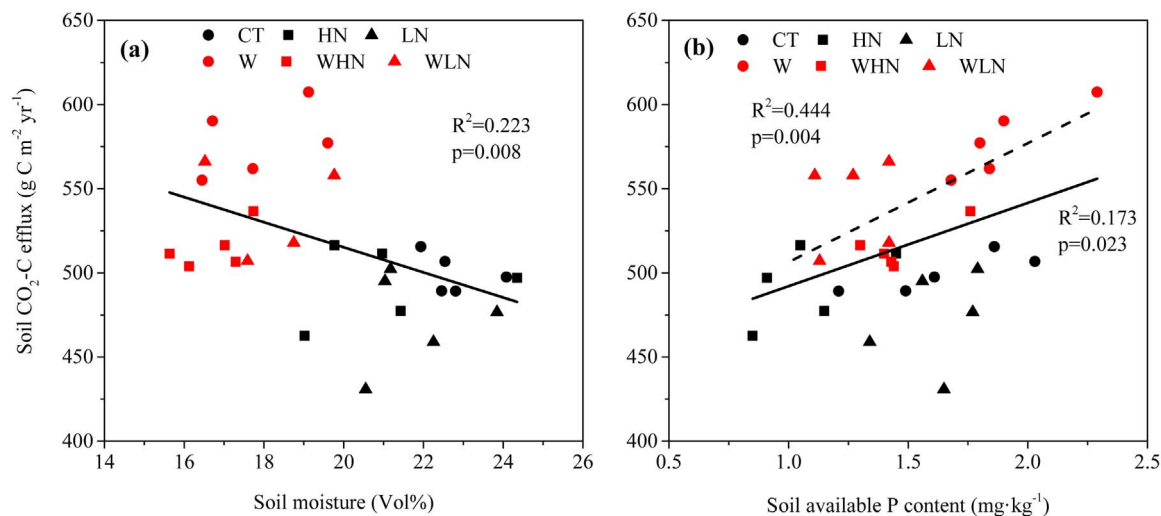


Fig. 3. Relationships between Rs and soil moisture (a), and soil available P content (b). CT: control, LN: low N addition, HN: high N addition, W: warming, WLN: warming plus low N addition, WHN: warming plus high N addition.

4.3. Temperature sensitivities of Rs

The Q_{10} values of Rs in this study were not different among all the warming treatments (W, WLN and WHN) and the CT plots (Table 2). Many studies report that soil warming decreases Q_{10} of Rs in temperate grasslands (Luo et al., 2001) and forests (Noh et al., 2016; Schindlbacher et al., 2009). Temperature sensitivity can be influenced by changes in environmental constraints to SOM decomposition such as soil moisture and substrate availability (Davidson and Janssens, 2006; Giardina and Ryan, 2000; Suseela et al., 2012). Decreased soil moisture induced by warming could decrease substrate availability and become a limiting factor in warmed soils, leading to lower Q_{10} (Davidson and Janssens, 2006; Suseela et al., 2012). In contrast, Giardina et al. (2014) in a whole ecosystem study where soil moisture was controlled found that 5 °C of warming resulted in increased Rs that was driven entirely by increased inputs belowground by a warmed canopy. In the present study, soil moisture reduced by 4.2–4.9 Vol% caused by soil warming but still maintained relatively higher soil moisture (17.8–18.5 Vol%) over the entire experimental period (Table 1). High soil moisture condition in this study area maintained a high Q_{10} during the one-year period of experiment.

Interestingly, we found that correlations between Rs and soil temperature were much weaker in all non-warming plots when compared to the warming plots (Table 2). We did not have supportive data explaining this result. It is likely that under natural conditions microbes acclimate to the local temperature and that their activity was mainly controlled by other factors, such as soil moisture, soil organic C or predators of major decomposers. With the warming treatment, increased soil temperature become the dominant factor affecting decomposers so that a stronger relationship occurred between Rs and soil temperature.

5. Conclusions

Our results that Rs increased in the warming plots but did not change in the two-level N addition plots indicate a strong interaction between warming and N addition in subtropical plantation. Whether this interaction enhances or reduces Rs may depend on soil moisture and available P. Soil moisture is mainly affected by changes of precipitation and drought patterns caused by global warming. Available P may be partially regulated by N deposition through acidifying soils. Our results indicate that the response of subtropical plantation to warming and N deposition could be very different from temperate plantations, especially with the interactions between the two-major influential environmental factors.

There is an urgent need to conduct field warming experiments in tropical and subtropical forests due to the lack of information on forest responses to climate warming (Cavaleri et al., 2015). This field warming experiment conducted in southeastern China is one of the pioneer studies in the subtropics. However, due to limited resources such as high demand for power and topographical constraints in the mountainous study area, the size of measuring plots is too small for such a multifactorial experiment. Although we used a randomized block design five replicates are not enough for measuring fine roots in such small plots and thus our data for separating heterotrophic and autotrophic soil respirations were not included in this paper, which is otherwise valuable to understanding the mechanisms of warming and N addition effects on Rs. Because we studied young tree plantations in this experiment, uncertainties exist for extrapolating our results to mature forests and/or natural forests. With increasing atmospheric temperature and N deposition, more manipulative field experiments in the tropics and subtropics are needed to investigate the effects of warming and N deposition on forest ecosystems. Lack of such information in the tropics and subtropics limits our ability to accurately predict terrestrial ecosystem responses to climate change at a global scale. Further studies are needed to draw rigorous conclusions on the responses of forest

ecosystems to global climate change. In addition, one-year experiment duration for examining the effects of soil warming and N addition and their interactions is too short. Short-term effects of warming and N addition could markedly differ from long-term responses, particularly when the Rs components response to warming and N addition in different mechanisms. For example, autotrophic respiration decreased with experimental duration while heterotrophic respiration did not fully acclimate to warming (Wang et al., 2014).

One important limitation of the present study is the biweekly Rs measurement. Automated chamber systems have the potential to solve this problem. Also, short-term extreme events, such as cold-wave, extreme rainfall and heat wave could be captured if we used high frequent observation technology. Therefore, automated chamber systems with high resolution and continuous observation for soil respiration could provide us valuable data and greatly improve our understanding of Rs response to climate change.

Based on the results of our experiment, we strongly suggest that soil warming experiments in relatively N-saturated subtropical forests should include P as a treatment to manipulate and examine the responses of subtropical forests to global climate warming.

Acknowledgements

This research was jointly supported by the Chinese National Key Development Program for Basic Research (2014CB954003) and the National Natural Science Foundation of China (Nos. 31500407 and 31500408). Dr. Francis Boles helped to design the soil warming experiment. We thank Dr. Laurence Walker and the two anonymous reviewers for their comments which greatly improved the manuscript.

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