

Response of soil respiration to simulated N deposition in a disturbed and a rehabilitated tropical forest in southern China

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Abstract Responses of soil respiration (CO_2 emission) to simulated N deposition were studied in a disturbed (reforested forest with previous understory and litter harvesting) and a rehabilitated (reforested forest with no understory and litter harvesting) tropical forest in southern China from October 2005 to September 2006. The objectives of the study were to test the following hypotheses: (1) soil respiration is higher in rehabilitated forest than in disturbed forest; (2) soil respiration in both rehabilitated and disturbed tropical forests is stimulated by N additions; and (3) soil respiration is more sensitive to N addition in disturbed forest than in rehabilitated forest due to relatively low soil nutrient status in the former, resulting from different previous human disturbance. Static chamber and gas chromatography techniques were employed to quantify the soil respiration, following different N treatments (Control, no N addition; Low-N, $5 \text{ g N m}^{-2} \text{ year}^{-1}$; Medium-N, $10 \text{ g N m}^{-2} \text{ year}^{-1}$), which had been applied continuously for 26 months before the respiration measurement. Results showed that soil respiration

exhibited a strong seasonal pattern, with the highest rates observed in the hot and wet growing season (April–September) and the lowest rates in winter (December–February) in both rehabilitated and disturbed forests. Soil respiration rates exhibited significant positive exponential relationship with soil temperature and significant positive linear relationship with soil moisture. Soil respiration was also significantly higher in the rehabilitated forest than in the disturbed forest. Annual mean soil respiration rate in the rehabilitated forest was 20% lower in low-N plots ($71 \pm 4 \text{ mg CO}_2\text{-C m}^{-2} \text{ h}^{-1}$) and 10% lower in medium-N plots ($80 \pm 4 \text{ mg CO}_2\text{-C m}^{-2} \text{ h}^{-1}$) than in the control plots ($89 \pm 5 \text{ mg CO}_2\text{-C m}^{-2} \text{ h}^{-1}$), and the differences between the control and low-N or medium-N treatments were statistically significant. In disturbed forest, annual mean soil respiration rate was 5% lower in low-N plots ($63 \pm 3 \text{ mg CO}_2\text{-C m}^{-2} \text{ h}^{-1}$) and 8% lower in medium-N plots ($61 \pm 3 \text{ mg CO}_2\text{-C m}^{-2} \text{ h}^{-1}$) than in the control plots ($66 \pm 4 \text{ mg CO}_2\text{-C m}^{-2} \text{ h}^{-1}$), but the differences among treatments were not significant. The depressed effects of experimental N deposition occurred mostly in the hot and wet growing season. Our results suggest that response of soil respiration to elevated N deposition in the reforested tropical forests may vary depending on the status of human disturbance.

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Introduction

Fossil fuel burning, forest disturbance, and land conversion are major anthropogenic activities that have elevated the atmospheric concentration of CO₂ and increased the deposition of reactive nitrogen (N)—(all kinds of N compounds except for N₂) (Matson et al. 2002; Galloway et al. 2003). Industrial development and agricultural intensification are projected to increase in the humid tropics over the next few decades in Asia, causing extensive changes to natural ecosystem in the region (Galloway et al. 2003). Over 40% of all N fertilizers are now used in the tropics and subtropics and over 60% will be used there by 2020 (Galloway et al. 2003). At the same time, fossil fuel use is expected to increase by several folds in many areas of the tropics over the coming decades (Hall and Matson 1999; Galloway et al. 2003). Forest soil is an important source and sink of CO₂ in atmosphere (e.g. Bowden et al. 2004). Nitrogen additions to forest soils have shown variable effects on soil respiration rates, including increases, decreases, or no change (Bowden et al. 2000, 2004; Burton et al. 2004; Micks et al. 2004; Cleveland and Townsend 2006). However, most studies of the consequences of enhanced N deposition on sources and sinks of CO₂ have been performed in temperate forests. There are very few studies of soil respiration responses to N deposition in subtropical and tropical forests (Cleveland and Townsend 2006) and to our knowledge there is no such information from China.

In Asia, the use and emissions of reactive N increased from 14 Tg N year⁻¹ in 1961 to 68 Tg N year⁻¹ in 2000 and is expected to reach 105 Tg N year⁻¹ in 2030 (Zheng et al. 2002). Currently, this leads to high atmospheric N deposition (30–73 kg ha⁻¹ year⁻¹) in some forests of southern tropical China where industry and agriculture activities have recently been increasing rapidly (Ren et al. 2000; Mo et al. 2005). In addition, most of the land originally covered with primary forests in China has been degraded by human activities during the past several centuries (Wang et al. 1982). In extreme cases, the land became so degraded, with barely any vegetation cover (He and Yu 1984). Deforestation in China is estimated to be on the order of 0.61 million ha per year during the 1990s and the remnant mature native forest area now is less than 9% of the total territory (Liu et al. 2000). Attempts to reverse this

process of land degradation have been initiated in many subtropical and tropical regions of China. Over the last few decades, large areas have been reforested with a native pine species (*Pinus massoniana* Lamb), to prevent further degradation of the landscape. Cutting of the trees is usually prohibited, but harvesting of understory and litter is often allowed to satisfy local fuel needs (Brown et al. 1995; Mo et al. 1995, 2003). Thus, these reforested forests can be divided into disturbed forests (understory and litter disturbance occurred) and rehabilitated forests (reforested with no understory and litter harvesting) (Mo et al. 2003). These reforested forests cover more than half of the total forested area in subtropical and tropical China (Brown et al. 1995; Mo et al. 2003, 2004). However, the effects of these major land-use changes on ecosystem processes and structures are poorly known (Mo et al. 2003, 2006, 2007), and information regarding soil respiration and its response to increased N deposition is non-existent.

It was hypothesized that chronic N additions to N-limited forests would initially stimulate soil microbial activity (and increase soil respiration), but over time would result in a carbon-limited state after microbial demand for N was satisfied (Aber et al. 1989). We have reported previously that both rehabilitated and disturbed forests in tropical China are N limited, and that N addition increased both mass loss and C release from the decomposing litter (Mo et al. 2006, 2007). The objective of this study was to examine the effects of N addition on soil respiration and compare this effect between the forest sites of different land-use history. We hypothesize that: (1) soil respiration is higher in rehabilitated forest than in disturbed forest; (2) soil respiration in both forests is stimulated by N additions; (3) soil respiration is more sensitive to N addition in disturbed forest than in the rehabilitated forest due to relatively low soil nutrient status in the former forest resulting from constant human disturbance.

Methods

Site description

This study was conducted in the Dinghushan Biosphere Reserve (DHSBR). The reserve lies in the middle part of Guangdong Province in southern

Table 1 Indices^a of the tree layer in a disturbed and a rehabilitated tropical forest in southern China

Species	Stem density (tree ha ⁻¹)	Mean height (m)	Mean DBH ^b (cm)	Mean age ^c (years)	Basal Area (m ² ha ⁻¹)	Relative basal area (%)
Disturbed forest						
<i>Pinus massoniana</i>	456	6.9	17.5	38.3	13.3	95.1
Other plants	311	4.3	4.4		0.7	4.9
Total	767				14	100
Rehabilitated forest						
<i>Pinus massoniana</i>	133	10.2	22	48.8	5.6	41
<i>Schima superba</i>	1567	5.2	6.4		7.4	53.6
Other plants	233	4.2	5.1		0.8	5.4
Total	1933				13.8	100

^a Data is cited from Fang et al. 2006

^b DBH, Diameter at breast height

^c Mean age was calculated based on the linear relationship between DBH and age of pine trees in the pine forest of the Dinghushan Biosphere Reserve (Brown et al., 1995)

China (112°10' E longitude and 23°10' N latitude) and occupies an area of approximately 1,200 ha. In the reserve, we have identified two types of forest: a mixed pine and broadleaf forest (rehabilitated) and a pine forest (disturbed). The rehabilitated forest, at about 200 m asl occupies approximately 50% of the reserve, and the disturbed forest, at about 50–200 m asl occupies approximately 20% of the reserve (Mo et al. 2003). These two types of forest are approximately 4 km from each other. Both rehabilitated and disturbed forests originated from the 1930s clear-cut and the following pine plantation. The original sites of both forests were badly eroded and degraded (Wang et al. 1982; Mo et al. 1995, 2003). However, the disturbed forest was under continuous human disturbances (generally the harvesting of understory and litter) during 1930–1998 and the tree layer remained dominated by *P. massoniana* (Brown et al. 1995; Mo et al. 1995, 2003). Conversely, colonization from natural dispersal of regional broadleaf species has changed plant composition in the rehabilitated forest (Mo et al. 2003).

The reserve has a monsoon climate and is located in a tropical moist forest life zone, (*sensu* Holdridge 1967). The mean annual rainfall of 1,927 mm has a distinct seasonal pattern, with 75% of it falling from March to August and only 6% from December to February (Huang and Fan 1982; Fang et al. 2006). Nitrogen deposition in rainfall was measured as 36–38 kg ha⁻¹ year⁻¹ in 1990s (Huang et al. 1994; Zhou and Yan 2001). The survey conducted in June 2003

(before the start of N addition) showed that the major species in the canopy layer of the rehabilitated forest were *P. massoniana*, *Schima superba* Chardn. & Champ., and *Castanopsis chinensis* Hance. Disturbed forest was dominated by *P. massoniana*. Stem density, tree height and diameter at the breast height in the two forests are given in Table 1 (data from Fang et al. 2006). Standing floor litter measured in June 2003 was 23.7 ± 4.8 and 20.0 ± 0.4 Mg ha⁻¹ (mean ± standard error, *n* = 3) in disturbed and rehabilitated forests, respectively (Fang et al. 2006).

The soils in both types of forest are oxisols with variable depths. In the rehabilitated forest, depth ranges from 30 to 60 cm (to the top of the C horizon), in the disturbed forest the depth is generally less than 30 cm (Brown et al. 1995; Mo et al. 2003). General soil properties were given in Table 2 (data from Mo et al. 2006).

Experimental treatments

Nitrogen addition experiments were initiated in both types of forest in 2003, 2 years before the current soil respiration study (Mo et al. 2007). Three N addition treatments (each in three replicates) were established in both rehabilitated and disturbed forests: Control (no added N), Low-N (5 g N m⁻² year⁻¹), and Medium-N (10 g N m⁻² year⁻¹). Total 18 plots of 20 m × 10 m dimension were established—9 in rehabilitated and 9 in disturbed forest,—each surrounded by a 10-m wide buffer strip. Field plots and

Table 2 Soil properties (0~10 cm depth) of the control plots in disturbed and rehabilitated tropical forests in southern China*

Forest type	PH (H ₂ O)	Total C (mg g ⁻¹)	Total N (mg g ⁻¹)	C/N	Available P (mg kg ⁻¹)	Soil bulk density (g cm ⁻¹)
Disturbed	3.93 (0.08)	22.7 (3.1)	1.3 (0.1)	17.01 (1.35)	3.59 (0.28)	1.16 (0.05)
Rehabilitated	3.91 (0.03)	17.3 (1.2)	1.2 (0.1)	14.39 (1.03)	4.21 (0.30)	1.22 (0.01)

* Data are cited from Mo et al., 2006. Values are means with 1 SE in parentheses, n = 3 for all samples; measured in July 2004

treatments were laid out randomly. NH₄NO₃ solution was sprayed monthly by hand onto the forest floor as 12 equal applications over the entire year beginning in July 2003 and continued since then. In each plot, fertilizer was weighed, mixed with 20 l of water, and applied using a backpack sprayer below the canopy. Two passes were made across each plot to ensure an even distribution of fertilizer. The Control plots received 20 l water with no N added.

Field sampling and measurements

Soil respiration measurements began 26 months after the initial experimental N application. Soil respiration was monitored using the static chamber and gas chromatography techniques. One static chamber was established in each plot at the start of the experiment (15 September 2005), yielding a sample size of three for each N treatment (and total sample size of 18 for this study). The chamber was a 25-cm-diameter ring permanently anchored 5 cm into the soil. A fan (5–10 cm in diameter) was installed on the top wall of each chamber to make turbulence when air was collected. During flux measurements, a 30-cm-high chamber top was attached to the ring. Air was sampled from each chamber from 09:00 to 10:00 at each sampling date. Diurnal studies in the adjacent forests demonstrated that green house gas fluxes measured from 09:00 to 10:00 were close to daily means (Tang et al. 2006). Soil respiration was measured once a week during the hot and wet growing season (April–September) and once every other week in the other time. Gas samples were collected with 100 ml plastic syringes at 0, 10, 20 and 30 min after the chamber closure and analyzed for CO₂ within 24 h using gas chromatography (Agilent 4890D, Agilent Co. USA). Gas flux was calculated from the linear regression of concentration versus time using the data points from each chamber to minimize the negative effect of close chamber on

CO₂ production (Keller and Reiners 1994; Magill et al. 1997; Tang et al. 2006). Coefficients of determination (r^2) for all linear regression were greater than 0.98.

Soil temperature and moisture at 5 cm below surface were monitored at each chamber while gas samples were collected. Soil temperature was measured using a digital thermometer. Volumetric soil moisture (cm³ H₂O cm⁻³ soil) was measured simultaneously using a PMKit (Tang et al. 2006).

Three litterfall traps (0.5 m × 0.5 m) with a mesh size of 1 mm were placed randomly in each plot about 0.5 m above the ground surface. The traps were emptied once every month during the year. Litterfall was separated into three components: leaf, small woody material (branches and bark), and miscellaneous (mainly reproductive parts).

Statistical analysis

Repeated measure ANOVA with Tukey's HSD test was performed to examine the soil respiration rate, soil temperature, soil moisture content and the quantity of litterfall among treatments for the study period from October 2005 to September 2006 in each type of the forest. Standard *t*-test was performed to examine the above measurements in the control plots between rehabilitated forest and disturbed forest. Relationship between soil respiration rates and soil moisture contents was examined with linear regression. After log-transforming the data of soil respiration, the least square regression analysis was used to examine the relationship between soil respiration rates and soil temperatures. One-way ANCOVA test was also used to compare the regression slopes among treatments.

The Q₁₀-value was obtained from a coefficient, β , in the exponential regression equation (Eq. 1) between the soil temperature and respiration rate (Lloyd and Taylor 1994):

$$R = \alpha e^{\beta T} \quad (1)$$

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

where R is the soil respiration rate, T the soil temperature, and α and β are regression coefficients.

All analyses were conducted using SPSS 10.0 (SPSS, Chicago, III) for windows. Statistical significant differences were set with P -values < 0.05 unless otherwise stated.

Results

Soil temperature and moisture

Soil temperature and moisture (Fig. 1a–d) exhibited clear seasonal patterns in all treatment plots in both forests. Soil was hot and wet from April to September (growing season) and became cool and dry from December to February (winter season). There was no significant difference in the annual mean soil temperature between disturbed ($23.9 \pm 0.5^\circ\text{C}$) and rehabilitated ($23.7 \pm 0.7^\circ\text{C}$) forests ($P = 0.831$) in the control plots. Mean soil moisture was also similar between disturbed ($16.1 \pm 1.0 \text{ cm}^3 \text{ H}_2\text{O cm}^{-3} \text{ soil}$) and rehabilitated ($15.4 \pm 1.3 \text{ cm}^3 \text{ H}_2\text{O cm}^{-3} \text{ soil}$) forests ($P = 0.503$) in the control plots. There were no treatment effect on soil temperatures and soil moisture in both forests during the study period (Fig. 1a–d).

Soil respiration in control plots

Soil respiration in control plots followed a clear seasonal pattern in both forests, with the highest rates observed in the hot and wet growing season and the lowest rates in winter (Fig. 1e, f). In control plots of both disturbed and rehabilitated forests, the average soil respiration rates in the growing season were about three times of those in the winter. The seasonal pattern seemed more pronounced in the disturbed forest (highest to lowest ratio of 4) than in the rehabilitated forest (ratio of 3). However, annual mean soil respiration rate was significantly higher in the rehabilitated forest ($89 \pm 4 \text{ mg CO}_2\text{-C m}^{-2} \text{ h}^{-1}$) than in the disturbed forest ($66 \pm 4 \text{ mg CO}_2\text{-C m}^{-2} \text{ h}^{-1}$) ($P < 0.001$).

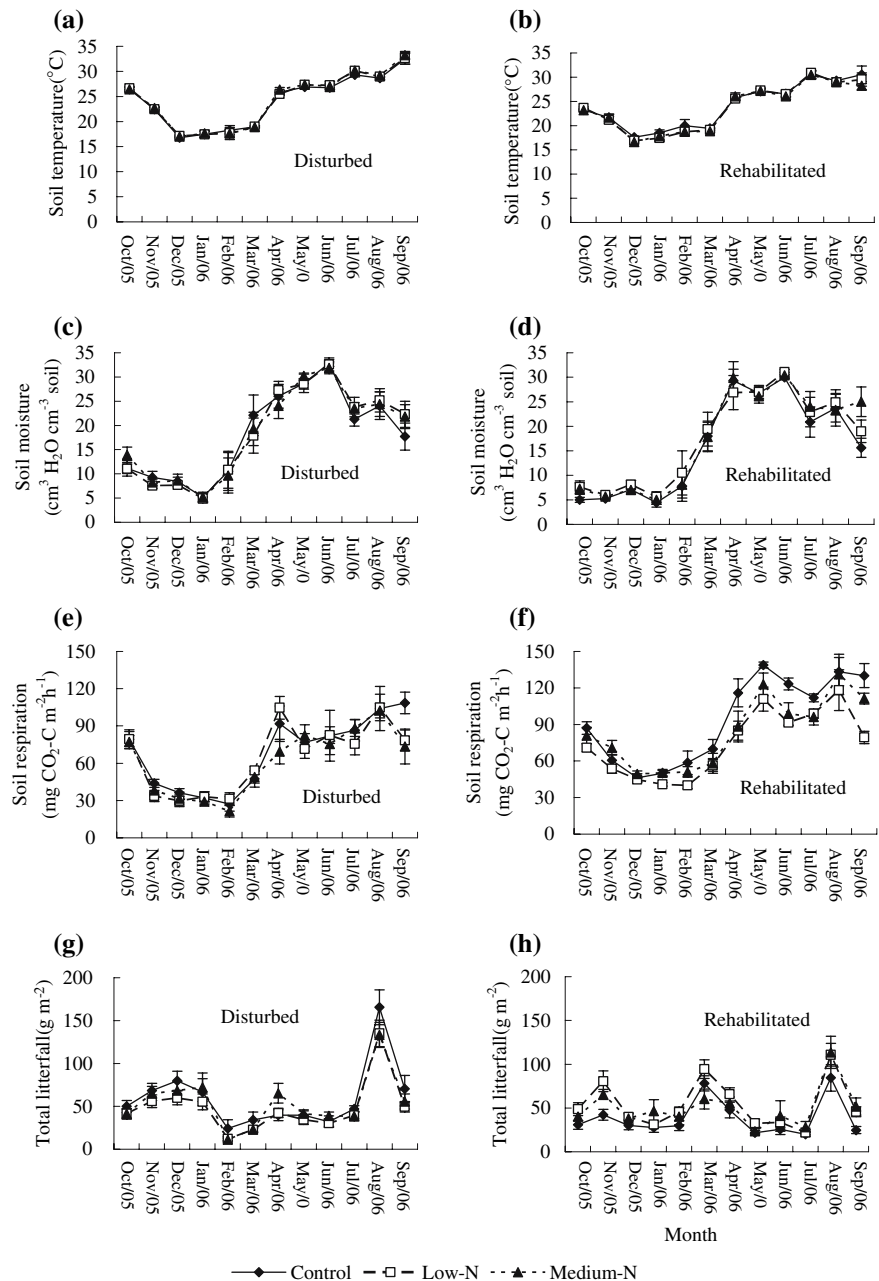
Soil respiration in the disturbed forest exhibited significant positive exponential relationship with soil temperature ($P < 0.001$, $r^2 = 0.74$, Fig. 2a) and significant positive linear relationship with soil moisture ($P < 0.001$, $r^2 = 0.43$, Fig. 2b). The similar relationships were also found in the rehabilitated forest (exponential relationship with temperature, $P < 0.001$, $r^2 = 0.76$, Fig. 2g; linear relationship with moisture, $P < 0.001$, $r^2 = 0.70$, Fig. 2h). The linear relationship between soil respiration and soil moisture was more pronounced in rehabilitated forest ($r^2 = 0.70$) than in disturbed forest ($r^2 = 0.43$). However, the mean temperature coefficient for the respiration rate was slightly higher in disturbed forest ($Q_{10} = 2.3$) than in rehabilitated forest ($Q_{10} = 2.1$).

Effects of N addition on soil respiration

Soil respiration in plots receiving experimental N inputs in both forests followed similar seasonal patterns, exhibited significant positive exponential response to soil temperature ($P < 0.001$, r^2 ranging from 0.56 to 0.81) and significant positive linear to soil moisture ($P < 0.001$, r^2 ranging from 0.45 to 0.68) (Figs. 1, 2). The mean temperature coefficient in rehabilitated forest decreased with increasing level of N addition: control plots ($Q_{10} = 2.1$) $>$ low-N ($Q_{10} = 1.9$) $>$ medium-N plots ($Q_{10} = 1.8$), and the difference between control and low-N or medium-N plots was significant ($P < 0.05$). Whereas in disturbed forest, the mean temperature coefficient was similar across N treatments (Q_{10} was 2.3, 2.2 and 2.3 for control, low-N and medium-N plots, respectively) ($P = 0.427$).

Effects of N addition on soil respiration varied depending on the level of N addition, season and forest type (Fig. 1e, f). In rehabilitated forest, annual mean soil respiration rate was 20% lower in the low-N plots ($71 \pm 4 \text{ mg CO}_2\text{-C m}^{-2} \text{ h}^{-1}$) and 10% lower in the medium-N plots ($80 \pm 4 \text{ mg CO}_2\text{-C m}^{-2} \text{ h}^{-1}$) than in the control plots ($89 \pm 5 \text{ mg CO}_2\text{-C m}^{-2} \text{ h}^{-1}$), and the differences were statistically significant ($P = 0.003$ and 0.043 for low-N and medium-N treatments respectively). The depression of soil respiration by N additions mostly occurred in the growing season (Fig. 1f). The mean soil respiration rate in the growing season was 27% lower in low-N plots ($P = 0.001$) and 9% lower in medium-N plots ($P = 0.098$) than in the control plots, whereas there

Fig. 1 Seasonal variations of soil temperature, soil moisture, soil respiration rate and total litterfall in experimental plots in a disturbed and a rehabilitated tropical forest in southern China during the monitoring period from October 2005 to September 2006. Bars indicate ± 1 SE. (a, b) soil temperature at 5 cm below surface; (c, d) volumetric soil moisture in the 0–5 cm soil layer; (e, f) soil respiration rate; (g, h) total litterfall. Monthly applications of NH_4NO_3 began in July 2003



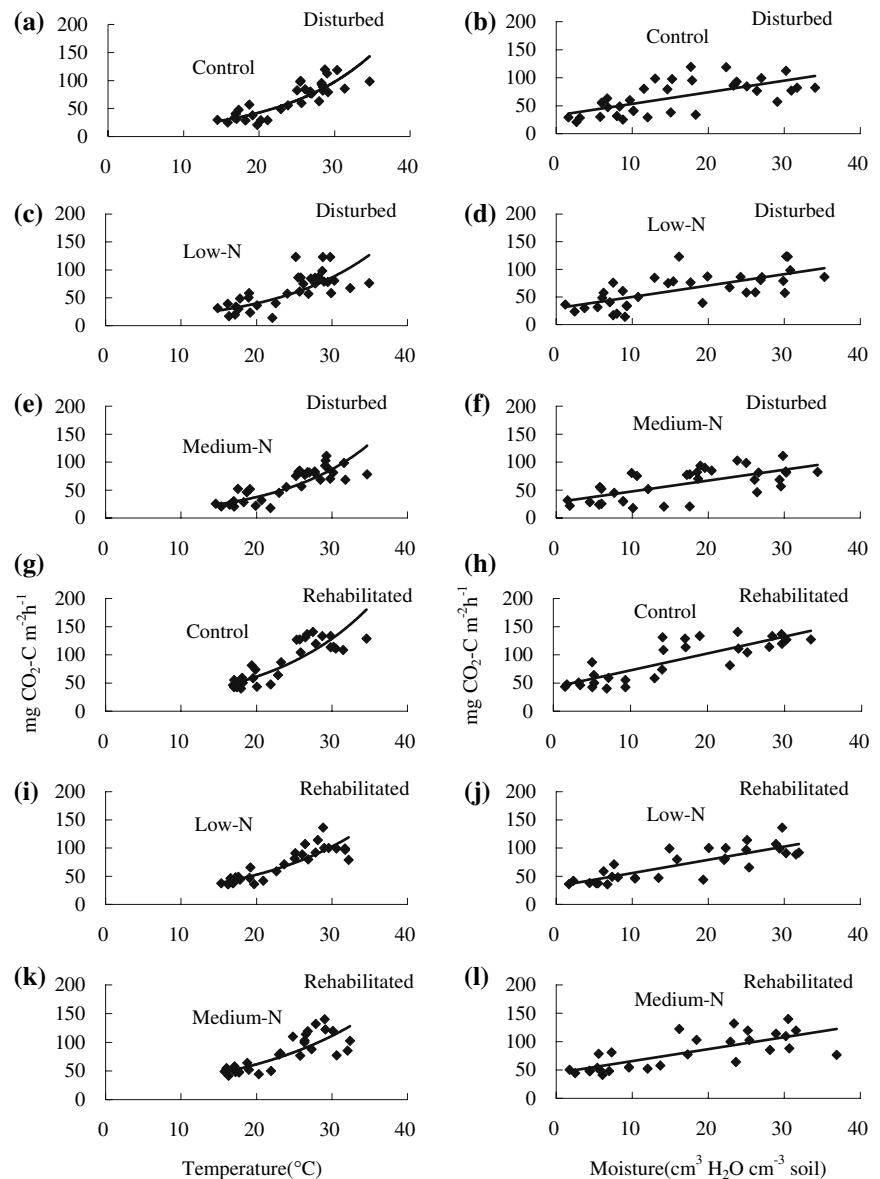
were no significant differences ($P = 0.165$) in soil respiration among treatments in winter (Fig. 1f). In disturbed forest, although annual mean soil respiration rate was 5% lower in low-N plots ($63 \pm 3 \text{ mg CO}_2\text{-C m}^{-2} \text{ h}^{-1}$) and 8% lower in medium-N plots ($61 \pm 3 \text{ mg CO}_2\text{-C m}^{-2} \text{ h}^{-1}$) than in the control plots ($66 \pm 4 \text{ mg CO}_2\text{-C m}^{-2} \text{ h}^{-1}$), the

differences among treatments were not statistically significant ($P = 0.870$) (Fig. 1e).

Litterfall

The mass of total litterfall in all treatments showed a strong seasonal pattern, with the highest value

Fig. 2 Relationships between soil respiration rates and soil temperature (measured 5 cm below surface) and volumetric soil moisture (0–5 cm soil) in experimental plots in a disturbed and a rehabilitated tropical forest in southern China



observed in August in both forests (Fig. 1g, h). In disturbed forest, annual total litterfall in the control, low-N and medium-N plots was: 685 ± 46 , 600 ± 49 and 664 ± 49 $\text{g m}^{-2} \text{year}^{-1}$, respectively, and was not significantly different among treatments ($P = 0.493$). In rehabilitated forest, however, annual total litterfall was significantly higher in low-N plots ($P = 0.009$) and marginally significantly higher in medium-N plots ($P = 0.053$) than in the control plots. Annual total litterfall for control, low-N and medium-N plots

in rehabilitated forest was: 464 ± 33 , 651 ± 40 and 605 ± 43 $\text{g m}^{-2} \text{year}^{-1}$, respectively.

Discussion

Soil respiration in both disturbed and rehabilitated tropical forests followed a similar seasonal pattern, with the highest rates observed in the hot and wet growing season (April–September) and the lowest

Table 3 Annual total soil CO₂ flux, litter input, and estimated total root allocation (mean, SE in parentheses)

	Control	Low-N	Medium-N
Disturbed forest			
Total soil respiration (g CO ₂ -C m ⁻²)	578(35)	552(26)	534(26)
Aboveground Litter input (g m ⁻²)	685(46)	600(49)	664(49)
Rehabilitated forest			
Total soil respiration (g CO ₂ -C m ⁻²)	780(44)	622(35)	701(35)
Aboveground Litter input (g m ⁻²)	464(33)	651(40)	605(43)
*TRA (g C m ⁻²)	571(27)	329(7)	429(26)

* TRA was calculated as: “total soil respiration (g CO₂-C m⁻²)-0.45 × aboveground litter input (g m⁻²)”. Assuming steady state status between soil heterotrophic respiration and litter input and that 45% of the litter decomposition released as CO₂-C

rates in winter (Fig. 1e, f). This is consistent with many results reported in temperate forests (Dong et al. 1996; Zhang et al. 2001; Bowden et al. 2004). In some of these temperate forest studies, the seasonality of soil respiration was interpreted as an effect of temperature only, with no effect of soil moisture (Dong et al. 1996; Zhang et al. 2001). However, our results showed that soil respiration rates in both forests and under different N treatments exhibited significant positive exponential relationships with soil temperature and significant positive linear relations with soil moisture ($P < 0.001$, Fig. 2a–l). Our results are consistent with the results found in three adjacent forests (Tang et al. 2006), a tropical forest in the central Amazon (Sotta et al. 2004), and a lowland tropical rain forest in southwest Costa Rica (Cleveland and Townsend 2006). The dual temperature and moisture controls on soil respiration in this study likely reflect the monsoon tropical climate of our study region, with a distinct separation of hot and wet season and cool and dry season.

The mean temperature coefficient (Q_{10}) for the respiration rate in the control plots was 2.3 and 2.1 in disturbed and rehabilitated forests, respectively. These values are similar to that reported in a tropical forest ($Q_{10} = 2.1 \pm 0.03$, $n = 3$) but lower than that reported in a temperate forest ($Q_{10} = 2.9 \pm 0.26$, $n = 3$) (Bekku et al. 2003). The annual mean soil respiration rates in the control plots were 66 ± 4 and 89 ± 5 mg CO₂-C m⁻² h⁻¹ in disturbed and rehabilitated forests, respectively (Fig. 1e, f). These values are in the same range as those found in adjacent forests in the same region ($45\text{--}87$ mg CO₂-C m⁻² h⁻¹, Tang et al. 2006), in an evergreen tropical forest (82 mg CO₂-C m⁻² h⁻¹, Townsend et al. 1995)

on the island of Hawaii, and in the same order as those found in tropical forests of South America ($51\text{--}115$ mg CO₂-C m⁻² h⁻¹, Davidson et al. 2004; Sotta et al. 2004).

Contrary to our original hypotheses, we found soil respiration tended to decrease with increasing level of N addition, and the responses to N input were more profound in rehabilitated forest (statistically significant) than in disturbed forest (Fig. 1e, f). No significant effect of N addition on litter production was found in disturbed forest (Fig. 1g). However, N addition tended to increase litter production in rehabilitated forest and this increase was statistically significant in low-N plots ($P = 0.009$) and marginally significant in medium-N plots ($P = 0.053$) (Fig. 1h). Soil respiration can be separated as heterotrophic (microbial and fungal) respiration and autotrophic (root) respiration (Sotta et al. 2004). Raich and Nadelhoffer (1989) proposed that under steady state condition, annual above- and below-ground litter C input should equal soil heterotrophic respiration, thus subtracting above-ground litter C input from total soil respiration equals C flux from root respiration + root production, which they termed as total root allocation (TRA). It is unlikely a steady state condition can be assumed for our disturbed forest, which has been under continuous litter removal from 1930 to 1998 (see Method). Assuming steady state condition in our rehabilitated forest, we calculated annual TRA (Table 3). Nitrogen additions significantly reduced TRA in rehabilitated forest. Thus the reduction of total soil respiration under N additions found in the rehabilitated forest was mainly due to the reduction of root-affiliated C flux, even though N additions had increased above-ground litter input to the system (and

likely have increased microbial mediated CO₂ flux from litter decomposition, Mo et al. 2006). Many studies have found chronic N additions could reduce belowground root input (Haynes and Gower 1995; Boxman et al. 1998), and that could be an important mechanism reducing total soil respiration under elevated N input. If however, experimental N additions in our study increased only above-ground litter production but not soil microbial respiration (thus departure from the steady state), then the TRAs calculated in Table 3 for low-N and medium-N treatments would be underestimated, but should still lower than in the control plots.

We suspect that the different responses of soil respiration to N additions in rehabilitated and disturbed forests may be influenced by the degree of initial soil nutrient status. Bowden et al. (2004) attributed the observed decrease of soil respiration to the changes in root activity associated with nutrient uptake in their study site. A large fraction of root respiration is allocated to N assimilation in N-limited system, but with larger doses of N readily available for uptake, energetic costs of N assimilation may have been reduced (Bowden et al. 2004). Our previous study showed that N additions significantly increased litter decomposition in both disturbed and rehabilitated forests, indicating that N was a limiting factor for litter decomposition (Mo et al. 2006, 2007). However, initial nutrient status was higher in rehabilitated forest than in disturbed forest (Mo et al. 2003, 2006, 2007; Fang et al. 2006). For example, concentration of soil extractable inorganic N (NH₄⁺-N, NO₃⁻-N, from the upper 10 cm soil) was higher in rehabilitated forest (6.4 mg kg⁻¹) than in disturbed forest (5.9 mg kg⁻¹) (Fang et al. 2006). The higher soil N availability in the rehabilitated forest relative to the disturbed forest was also reflected in the N concentration of pine needles. The N concentration of pine needles was significantly higher in the rehabilitated forest (13.1 ± 0.04 mg g⁻¹) than in the disturbed forest (12.5 ± 0.05) (*P* < 0.05, Mo et al. 2007). Similarly, the soil available P was higher in the rehabilitated forest (4.21 mg kg⁻¹) than in the disturbed forest (3.59 mg kg⁻¹) (Table 2), so was the P concentration of pine needles (*P* < 0.01, Mo et al. 2007). The difference in initial nutrient status corresponded significantly to higher decomposition rate of pine needles in the rehabilitated forest compare with

that in the disturbed forest (Mo et al. 2007). The interpretations above suggest that rehabilitated forest may takes less time or less amount of N to eliminate N limitation compare to the disturbed forest.

Thus, the continuous experimental N inputs in the previous 26 months could have reduced total C flux belowground in the rehabilitated forest (Table 3), a response to the more favorable soil nutrient condition, despite that N additions in this study period still stimulated aboveground litter fall production. In disturbed forest where soil nutrient condition is less favorable, continuous N addition may stimulate root growth, benefited from the overall positive effect of N additions on plant growth, or have positive effect on belowground C flux. This interpretation is consistent with the hypothesis that chronic N additions to N-limited forest soil would initially stimulate soil microbial activity, but over time would result in a carbon-limited state after microbial demand for N was satisfied (Aber et al. 1989). The decreased respiration in rehabilitated forest was similar to the results found in several studies in temperate forests, in those studies soil respiration rates were found to decrease significantly in N addition plots after one or two years of N fertilization (Bowden et al. 2000, 2004; Maier and Kress, 2000; Burton et al. 2004; Micks et al. 2004).

Conclusions

In summary, soil respiration exhibited a strong seasonal pattern, with the highest rates observed in the hot and wet growing season and the lowest rates in winter season for both rehabilitated and disturbed forests. Both soil temperature and soil moisture were driving factors on soil respiration in our study forests. Soil respiration was significantly higher in rehabilitated forest than in disturbed forest. Nitrogen additions had no significant effect on soil respiration in disturbed forest, but significantly decreased soil respiration in rehabilitated forest. The depressed effects occurred mostly in the hot and wet growing season and may due to the significant reduction of root allocation of C. Our results suggest that response of soil respiration to elevated N deposition in the reforested tropical forests may vary depending on the status of human disturbance and associated change of belowground processes.

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