

Dependence of Soil Respiration on Soil Temperature and Soil Moisture in Successional Forests in Southern China

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Abstract

The spatial and temporal variations in soil respiration and its relationship with biophysical factors in forests near the Tropic of Cancer remain highly uncertain. To contribute towards an improvement of actual estimates, soil respiration rates, soil temperature, and soil moisture were measured in three successional subtropical forests at the Dinghushan Nature Reserve (DNR) in southern China from March 2003 to February 2005. The overall objective of the present study was to analyze the temporal variations of soil respiration and its biophysical dependence in these forests. The relationships between biophysical factors and soil respiration rates were compared in successional forests to test the hypothesis that these forests responded similarly to biophysical factors. The seasonality of soil respiration coincided with the seasonal climate pattern, with high respiration rates in the hot humid season (April–September) and with low rates in the cool dry season (October–March). Soil respiration measured at these forests showed a clear increasing trend with the progressive succession. Annual mean (\pm SD) soil respiration rate in the DNR forests was (9.0 ± 4.6) Mg CO₂-C/hm² per year, ranging from (6.1 ± 3.2) Mg CO₂-C/hm² per year in early successional forests to (10.7 ± 4.9) Mg CO₂-C/hm² per year in advanced successional forests. Soil respiration was correlated with both soil temperature and moisture. The T/M model, where the two biophysical variables are driving factors, accounted for 74%–82% of soil respiration variation in DNR forests. Temperature sensitivity decreased along progressive succession stages, suggesting that advanced-successional forests have a good ability to adjust to temperature. In contrast, moisture increased with progressive succession processes. This increase is caused, in part, by abundant respirators in advanced-successional forest, where more soil moisture is needed to maintain their activities.

Key words: Dinghushan Nature Reserve; moisture sensitivity; Q₁₀; soil CO₂ efflux; soil respiration; subtropical forests; successional forests; temperature sensitivity; Tropic of Cancer.

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Soil respiration, also referred to as soil CO₂ efflux, is a major pathway of global carbon cycling. The flux of carbon from soils to the atmosphere in the form of CO₂ is estimated to have a magnitude of 68–100 Pg C/yr (Musselman and Fox 1991; Raich and Schlesinger 1992). It is second only to gross primary productivity (100–120 Pg C/yr; Houghton and Woodwell 1989). Even a small change in soil respiration could significantly exacerbate or mitigate atmospheric increases in CO₂, resulting in

effects on climate change. Nevertheless, despite its global significance, as well as considerable scientific commitments to studies in this field over the past decades, there is still limited understanding of the factors controlling temporal and spatial variability of soil respiration (Reichstein et al. 2003). Soil temperature and soil moisture are two of the most important environmental parameters controlling variations in soil CO₂ efflux (Raich and Schlesinger 1992; Davidson et al. 1998, 2000; Fang and Moncrieff 1999, 2001; Kirschbaum 2000; Liu et al. 2002; Risk et al. 2002; Joffre et al. 2003; Reichstein et al. 2003). However, the relationships between soil respiration and these two environmental parameters vary in different ecosystems (Moiser 1998; Buchmann 2000; Rustad et al. 2000). This variability calls for more measurements of soil respiration to explore its environmental dependence on a regional scale.

Most of the studies on soil CO₂ efflux have been conducted in temperate forests (Raich and Schlesinger 1992; Davidson et al. 1998; Dong et al. 1998; Buchmann 2000; Reichstein et al. 2003) and tropical forests (Conant et al. 2000; Davidson et al. 2000; Kiese and Butterbach-Bahl 2002; Epron et al. 2004). To our knowledge, there are few reports available on the variation of soil respiration and its dependence on environmental factors in forests close to the Tropic of Cancer. This is partly because there are few forests in this region (Tang et al. 2006). Favored by the unique subtropical monsoon climate with an abundance of heat, light, and water resources (Ding et al. 2001), moist subtropical forests spread out in southern China, although a large area near the Tropic of Cancer is covered by deserts (Kong et al. 1993). Therefore, forests in this region deserve more attention with respect to climate change. Do the forests near the Tropic of Cancer behave differently from forests in other regions in terms of soil respiration because of the unique climate regimens? Does soil respiration in forests near the Tropic of Cancer respond to biophysical factors, such as soil temperature and soil moisture, in the same way as forests in other biomes? Forests in the Dinghushan Nature Reserve (DNR), including common forests in southern China from early, to mid-, to advanced-successional stages, provide an excellent opportunity to answer these questions. Furthermore, for successional forests within similar edaphic and regional climate conditions, we are interested in succession-related issues. How does soil respiration vary within forests at different successional stages? Do successional forests respond to biophysical factors similarly or differently? We hypothesized that the seasonal patterns of soil respiration among these forests were the same, without dependence on succession stages. Soil temperature and moisture were measured together with

soil respiration rate. Based on the data, the dependence of soil respiration on controlling biophysical factors was analyzed. Sensitivities of soil respiration to biophysical factors were compared in these forests to test the hypothesis that successional forests responded similarly to biophysical factors. The specific aims of the present study were to: (i) observe seasonal variations of soil respiration by forests; (ii) evaluate the relationship between soil respiration and soil temperature and moisture; and (iii) compare the dependence of soil respiration on soil temperature and soil moisture among successional forests.

Results

Variations in microenvironmental factors and soil respiration

Seasonal patterns of precipitation and temperature during the study period were consistent with the long-term climate regimen in DNR. Annual mean precipitation from March 2003 to February 2005 was 1 293 mm, less than the long-term average annual precipitation of 1 927 mm (Wu et al. 1982). Intense rainstorms occurred frequently in summer (June–September). Precipitation during this period accounted for more than 60% of total rainfall throughout the observation period. Winter was relatively dry, with less precipitation. The annual mean air temperature was 20.0 °C, ranging from 10.6 °C (in January 2005) to 27.6 °C (in July 2003; Figure 1).

Soil respiration, together with soil temperature and soil moisture, showed strong seasonal variations, with higher rates

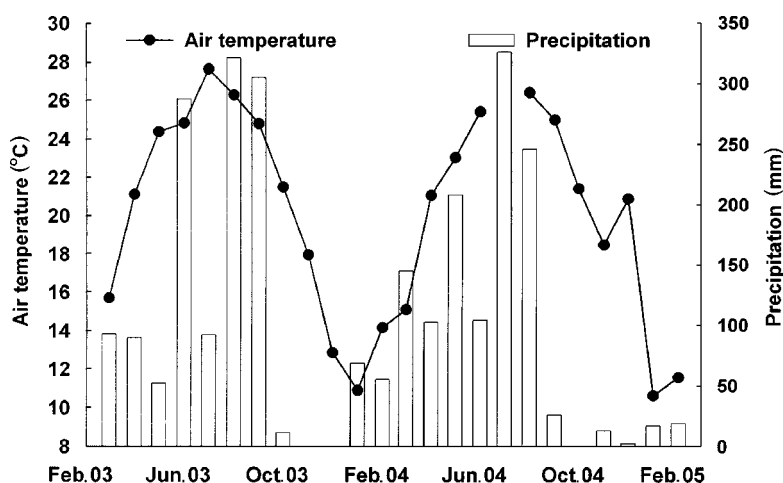


Figure 1. Monthly mean air temperature (°C) and precipitation (mm) from March 2003 to February 2005 in Dinghushan Nature Reserve.

No air temperature was recorded in August 2004 owing to instrument failure.

in the hot humid seasons (April–September) and lower values in the cool dry seasons (October–March; Table 1). The seasonality of soil respiration was consistent with the seasonal patterns of temperature and precipitation (Figure 1).

Soil in the pine forest was consistently drier and warmer than that in the conifer and broadleaf mixed forest (hereafter referred to as mixed forest) and evergreen broadleaf forest (hereafter referred to as broadleaf forest; Table 1). Soil temperature and soil moisture in the mixed forest did not differ from those in the broadleaf forest (Table 1). Soil respiration varied among the three forests. A clear increasing trend of soil respiration along positive successional stages was observed. Soil respiration rate was consistently the highest in the broadleaf forest, followed by the mixed forest and the pine forest, when both seasonal and annual means were compared (Table 1).

Effects of soil temperature and moisture on soil respiration rate

Soil respiration correlated with both soil temperature and soil moisture. The relationship between soil temperature and soil respiration rate was fitted with an exponential model and the results are given in Table 2. The T models (equation 1) explain approximately 50% of the variations in soil respiration (Table 2A; Figure 2). The fitted Q_{10} values, known as the multiplier to the respiration rate for a 10 °C increase in temperature, ranged from 1.78 to 2.44 in these forests, with the highest Q_{10} value in the pine forest and the lowest in the broadleaf forest. Soil moisture also affected soil respiration (Table 2A). Unlike the exponential relationship between soil respiration and soil temperature, soil respiration and soil moisture had a positive linear relationship (Figure 2). The M models (equation 2) explain

Table 1. Comparisons of annual and seasonal mean soil temperature, soil moisture, and soil respiration rate among forests

Variable	Season	Broadleaf forest	Mixed forest	Pine forest
Soil respiration rate (mg CO ₂ ·m ⁻² ·h ⁻¹)	Cool dry	288.7 ± 14.6 ^{ab}	235.7 ± 10.5 ^{ba}	137.4 ± 6.0 ^{ca}
	Hot humid	616.1 ± 22.8 ^{ab}	521.2 ± 16.0 ^{ba}	370.0 ± 18.4 ^{ca}
	Annual	450.5 ± 22.3 ^a	381.8 ± 18.2 ^b	250.9 ± 20.2 ^c
Soil moisture (% WFPS)	Cool dry	31.0 ± 1.7 ^{ab}	28.8 ± 2.0 ^{ab}	12.2 ± 1.8 ^{ba}
	Hot humid	55.5 ± 1.7 ^{ab}	51.9 ± 1.8 ^{ab}	36.5 ± 3.4 ^{ba}
	Annual	43.2 ± 1.8 ^a	40.7 ± 1.9 ^a	23.4 ± 2.7 ^b
Soil temperature (°C)	Cool dry	16.2 ± 0.6 ^{ab}	16.3 ± 0.6 ^{ab}	19.4 ± 0.9 ^{ba}
	Hot humid	24.9 ± 0.4 ^{ab}	25.1 ± 0.3 ^{ab}	26.4 ± 0.5 ^{ba}
	Annual	20.5 ± 0.6 ^a	20.8 ± 0.6 ^a	22.8 ± 0.7 ^b

Mean (± SE) values within a row with different lowercase letters have significant forest differences at $\alpha = 0.05$ level. Means within each column indicated by the asterisk show significant seasonal differences at $\alpha = 0.05$ level. WFPS, water-filled pore space.

Table 2. Regression models for the relationship between soil respiration rate, soil temperature (T), in °C and taken 5 cm below soil surface, and moisture (θ) or % water-filled pore space

(A) $R_s = \beta_0 e^{\beta_1 T}$							
Forest	β_0	β_1	<i>P</i>	Pseudo <i>R</i> ²	RMSE	Q_{10}	
Broadleaf forest	107.1 (22.1)	0.067 (0.009)	<0.000 1	0.53	140.4	1.96 (1.80–2.14)	
Mixed forest	80.9 (14.7)	0.072 (0.007)	<0.000 1	0.64	104.6	2.05 (1.90–2.20)	
Pine forest	44.9 (18.3)	0.073 (0.016)	<0.000 1	0.44	101.2	2.08 (1.78–2.44)	
(B) $R_s = \beta_2 + \beta_3 \theta$							
Forest	β_2	β_3	<i>P</i>	<i>R</i> ²	RMSE		
Broadleaf forest	64.9 (43.9)	9.4 (1.0)	<0.000 1	0.56	137.07		
Mixed forest	31.0 (39.2)	8.1 (0.9)	<0.000 1	0.55	117.5		
Pine forest	107.5 (22.6)	5.9 (0.8)	<0.000 1	0.61	84.6		
(C) $R_s = \beta_0 e^{\beta_1 T} \theta^{\beta_2}$							
Forest	β_0	β_1	β_2	<i>P</i>	Pseudo <i>R</i> ²	RMSE	Q_{10}
Broadleaf forest	17.7 (5.6)	0.044 (0.007)	0.617 (0.085)	<0.000 1	0.74	104.9	1.56 (1.45–1.67)
Mixed forest	17.1 (5.2)	0.048 (0.007)	0.551 (0.089)	<0.000 1	0.77	85.1	1.61 (1.51–1.72)
Pine forest	19.2 (5.6)	0.055 (0.010)	0.415 (0.056)	<0.000 1	0.80	60.7	1.73 (1.57–1.92)

Data are mean values, with the SE given in parentheses, Q_{10} values are means with 95% CI given in parentheses.

RMSE, root mean squared error; Q_{10} , the multiplier to the respiration rate for a 10 °C increase in temperature.

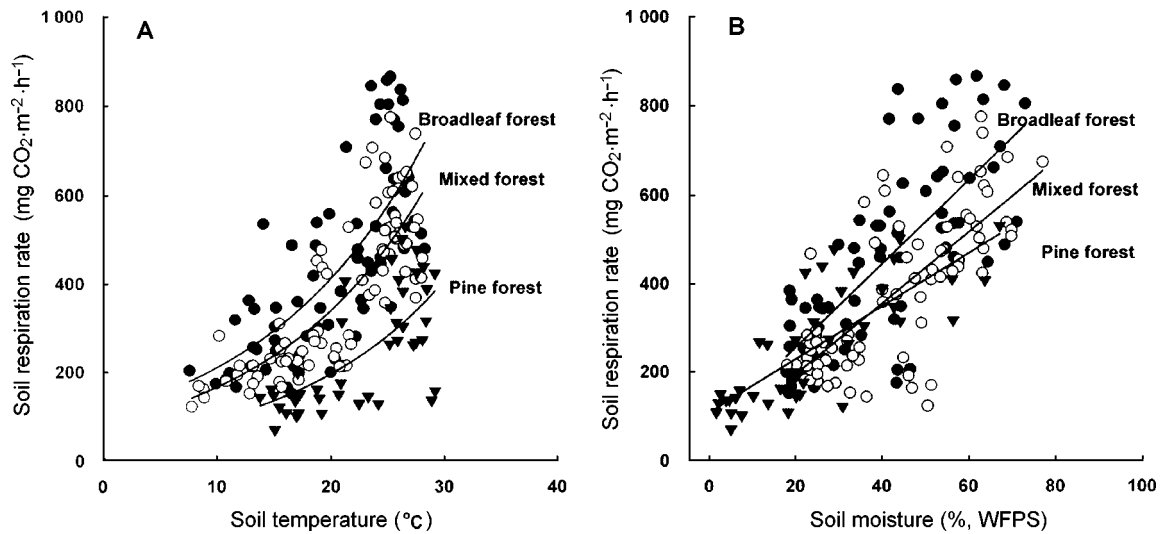


Figure 2. Relationship between soil respiration rate and environmental factors in Dinghushan Nature Reserve forests.

55%–61% of variations in soil respiration (Table 2B). Note the soil temperature covaried with soil moisture through seasons (Figure 3). These two factors affect soil respiration simultaneously. The T/M model combined soil temperature and soil moisture together (equation 3) and yielded higher R^2 values and lower root mean squared error (RMSE) values than univariate models alone (Table 2C). Coupling soil temperature and soil moisture explained 74%–80% of the temporal variation in soil respiration in the three forests. Mean Q_{10} values based on the T/M models are 1.56, 1.61, and 1.73 for broadleaf forest, mixed forest, and pine forest, respectively (Table 2C).

Discussion

Forest succession stages and soil respiration

Annual mean (\pm SD) soil respiration strengths were (10.7 ± 4.9), (9.1 ± 4.1), and (6.0 ± 3.2) $\text{Mg CO}_2\text{-C/hm}^2$ per year from the broadleaf forest, the mixed forest, and the pine forest, respectively. On average, soils in the DNR released approximately (9.0 ± 4.6) Mg C/hm^2 per year (arithmetic average of the three forest plots) in the form of CO_2 to the atmosphere. The results presented herein fall in the range of soil respiration

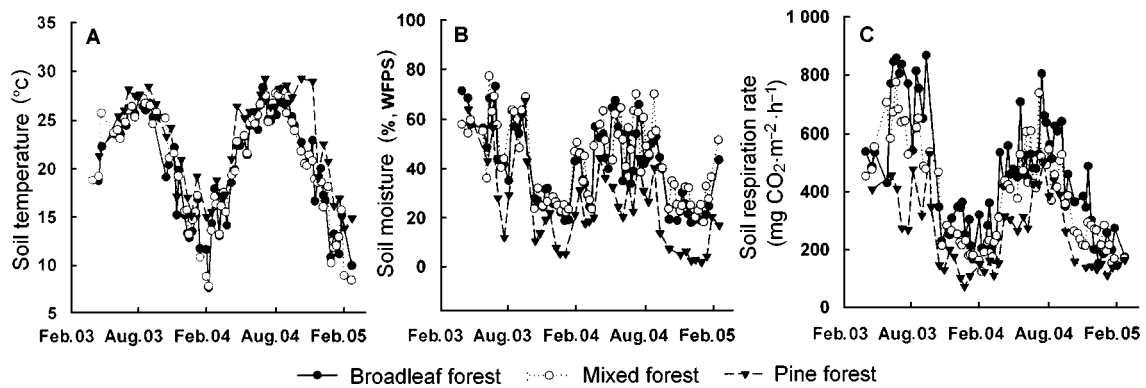


Figure 3. Seasonal variations of soil temperature ($^{\circ}\text{C}$), soil moisture (% water-filled pore space (WFPS)), and soil respiration rate ($\text{mg CO}_2\text{-m}^{-2}\text{-h}^{-1}$) in Dinghushan Nature Reserve forests from March 2003 to February 2005.

(A) Soil temperature.

(B) Soil moisture.

(C) Soil respiration rate.

BF, broadleaf forest; MF, mixed forest; PF, pine forest.

rates reported by a number of similar studies worldwide (Raich 1998; Granier et al. 2000; Longdoz et al. 2000; Raich and Tufekcioglu 2000; Davidson et al. 2002; Giardina and Ryan, 2002; Salimon et al. 2004; Sotta et al. 2004).

Soil respiration presented a clear increase trend with progressive succession (Table 1). This is consistent with similar studies in temperate and tropical forests (Buchmann 2000; Wiseman et al. 2004). Soil respiration generates mainly from autotrophic (root) and heterotrophic (microbial) activities (Janssens et al. 2001). Autotrophic respiration depends strongly on the amount of living root biomass, whereas heterotrophic respiration depends on the quantity of dead roots and soil organic matter (Rustad et al. 2000). Soil respiration in the present study was positively correlated with biomass and litter input (Table 3), suggesting carbon allocation and detritus input affected the quality and quantity of substrate. As a result, both auto- and heterotrophic respiration were affected. Other site-specific characteristics, such as soil organic carbon (SOC), fine root biomass, leaf area index (LAI), and microbial biomass, were also positively correlated with soil respiration, although the correlations were not statistically significant (Table 3). Decreasing top soil C/N ratios from pine forest to broadleaf forest indicated that the substrate quality in advanced-successional forest favored more decomposition than that in the early and mid-successional forests. The aforementioned evidence suggests that the increasing soil respiration strength in DNR successional forests is the result of enhanced auto- and heterotrophic respiration with progressive succession (Table 3).

Relationships between soil respiration and biophysical factors

Soil temperature and soil moisture are considered to be two of the most important biophysical parameters controlling the temporal variation of soil respiration in a given site (Lloyd and Taylor 1994; Davidson et al. 1998, 2000; Buchmann 2000; Fang et al. 2001; Xu et al. 2001; Kiese and Butterbach-Bahl 2002;

Gough et al. 2004). The T/M model, which combined soil temperature and soil moisture (Table 2C), explained a considerable fraction of the variation in soil respiration, suggesting that these two biophysical variables are driving factors in soil respiration in DNR forests. Studies in Mediterranean (Castro et al. 2000; Rey et al. 2002; Joffre et al. 2003) and semi-arid (Xu et al. 2001; Tang et al. 2004) ecosystems also highlighted that soil respiration is controlled by both temperature and moisture. However, the way in which these two factors affected soil respiration in those forests is quite different from the way they affected soil respiration in DNR forests. Soil temperature alone accounted for a major fraction of the variation in soil respiration when soil moisture was within a site-specific threshold value in these arid and semi-arid regions (Davidson et al. 1998; Xu et al. 2001; Rey et al. 2002). However, soil moisture in DNR forests covaried with the soil temperature regimen (Figure 3). Therefore, soil moisture in the present study showed a positive rather than negative relationship with temperature, as in the other studies. This is partly caused by the fact that the soil moisture measurements were often lower than the field capacity of the soil (Table 4) and not high enough to reach the point when soil respiration becomes limited by reduced oxygen diffusion into the soil. Moreover, because of the covariation of soil moisture and temperature driven by the simultaneous seasonal patterns of precipitation and air temperature, it is difficult, if not impossible, to distinguish the relative importance of moisture and temperature in controlling soil respiration based on current field observations (Davidson et al. 1998; Illeris et al. 2004).

Sensitivities of soil respiration to biophysical factors in successional forests

Soil respiration increased exponentially with temperature in DNR forests (Figure 2; Table 2). The slopes of temperature dependency regressions (Figure 2) for each forest were similar, suggesting common responses across these forests. However,

Table 3. Correlation matrix for soil respiration rate and site variables from Table 4

	R_s	SOC	Biomass	Fine root biomass	Litter input	Microbial biomass	LAI	C : N ratio in top soil
R_s		0.82NS	0.99*	0.92NS	0.99 *	0.88NS	0.86 NS	-0.99 NS
SOC	0.82NS		0.79NS	0.98NS	0.85NS	0.99NS	0.99NS	-0.76NS
Biomass	0.99*	0.79NS		0.89NS	0.99NS	0.86NS	0.84NS	-0.99*
Fine root biomass	0.92NS	0.98NS	0.89NS		0.94NS	0.99NS	0.99NS	-0.88NS
Litter input	0.99*	0.85NS	0.99NS	0.94NS		0.90NS	0.89NS	-0.99NS
Microbial biomass	0.88NS	0.99NS	0.86NS	0.99NS	0.90NS		0.99*	-0.83NS
LAI	0.86NS	0.99NS	0.84NS	0.99NS	0.89NS	0.99*		-0.81NS
C : N ratio in top soil	-0.99NS	-0.76NS	-0.99*	-0.88NS	-0.99NS	-0.83NS	-0.81NS	

The level of significance is indicated as follows: *significant at $\alpha = 0.05$ level; NS, not significant at the $\alpha = 0.05$ level.

R_s , soil respiration rate; SOC, soil organic carbon; LAI, leaf area index.

Table 4 Stand characteristics of three forests in Dinghushan Nature Reserve

Forest	Pine forest	Mixed forest	Broadleaf forest
Successional stage	Early	Mid	Advanced
Biomass (mg C/hm ²) ^a	40.6	116.2	147.8
Microbial biomass ($\times 10^6$ /g dry soil) ^b	1.2	1.4	2.1
Fine root biomass in top soil (mg C/hm ²) ^c	1.9 (1.1)	2.8 (1.1)	4.9 (3.0)
Litter input (mg C·h ⁻¹ ·yr ⁻¹) ^d	1.8	4.3	4.2
SOC (mg C/hm ²) ^e	105.2	111.3	164.1
Bulk density (g/cm ³) ^f	1.495	1.220	1.093
Leaf area index (m ² /m ²) ^f	4.5	5.0	7.2
C : N ratio in top soil ^f	15.7	18.4	25.9
Field capacity (% WFPS) ^g	64.7	61.3	83.4

^aFrom Peng and Zhang (1994), Peng and Fang (1995) and Wen et al. (1998).

^bFrom Zhou et al. (2002).

^cFine root in top soil refers to root (diameter less than 6 mm) biomass in a 0–20 cm depth of soil. Means from eight soil drills, 10 cm in diameter, are given with standard deviations in parentheses. Unpublished data from Dinghushan Forest Ecosystem Research Station (2003).

^dFrom Zhou et al. (2006).

^eFrom Zhou et al. (2005).

^fUnpublished data from Dinghushan Forest Ecosystem Research Station (2003–2004).

^gCalculated from field capacity (cm³ H₂O/cm³ soil) reported by Zhang and Zhuo (1985).

do all forests react similarly or differently to temperature? Which forest is more sensitive if soil respiration responds differently to temperature? To answer these questions, temperature dependence parameters, denoted as β_1 in the T models, were compared (Table 2A). Note how the range of soil temperature varied among these forests; therefore, we compared temperature dependency within the same range from 15 °C to 30 °C. For a straightforward comparison, exponential T models were logarithmically transformed into linear functions. The logarithmically transformed soil respiration rate (ln Rs) and soil temperature in three forests were plotted together (Figure 4). Slopes of linear functions represented temperature dependence parameters in T models. The higher slope of the regression line in pine forest suggested that soil respiration in this forest is more sensitive to soil temperature than in the other two forests. The Q_{10} values, derived from T and T/M models, varied among successional forests in the present study (Table 2). Higher Q_{10} values in the pine forest and the mixed forest compared with the broadleaf forest suggested that early and mid-successional forests are more sensitive to soil temperature than advanced-successional forest. Relatively low Q_{10} values in the broadleaf forest indicated that the advanced-successional forest has good self-adjustment in response to changes in temperature. Therefore, in light of rising temperatures caused by global warming, soil respiration in advanced-successional forests will be maintained at a relatively constant rate owing to so-called “temperature acclimation” (Luo et al. 2001). Temperature acclimation in the advanced-successional forest may possibly be caused by differences in substrate

quantity and quality, as suggested by Luo et al. (2001). Early studies found microbial communities varied among successional forests (Zhou et al. 2002); such variation could also affect the soil respiration rate by regulating the responses of soil respiration to temperature.

Recent studies have suggested that the Q_{10} values derived from different models are different (Fang and Moncrieff 2001). The Q_{10} values derived from T/M models (Table 2C) were lower than those calculated from T models (Table 2A). Taking soil moisture into consideration in the T/M models caused the differences in the Q_{10} values. Because soil moisture and temperature

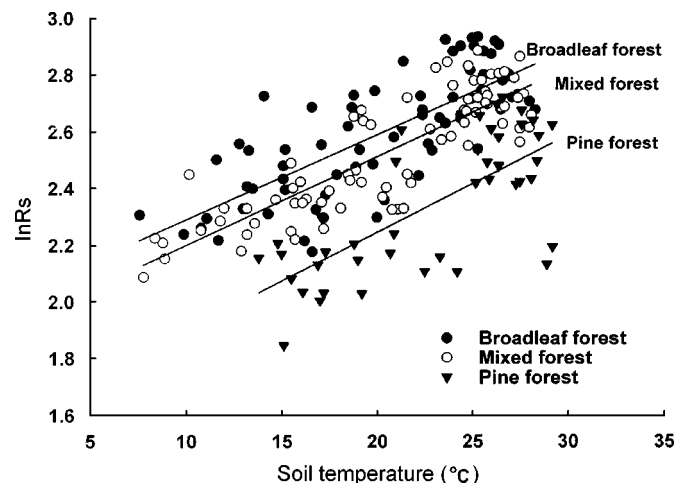


Figure 4. Dependence of soil respiration (logarithmic soil respiration rate; lnRs) on soil temperature in Dinghushan Nature Reserve forests.

covariates across seasons, it is possible that the relationship between soil respiration and soil temperature is confounded by soil moisture. That is, the Q_{10} values may be masked by the correlation between soil moisture and soil respiration. Because soil moisture varied with temperature in DNR forests, high moisture occurring simultaneously with high temperature is common (Figure 1). Numerous studies have verified that high soil water content reduces soil CO_2 efflux by inhibiting aerobic respiration (Davidson et al. 1998, 2000; Liu et al. 2002; Joffre et al. 2003; Reichstein et al. 2003; Illeris et al. 2004). Therefore, Q_{10} values derived from the T/M models, which included the confounding effect of soil moisture, are more accurate in representing the temperature dependence of soil respiration than those derived from T models in DNR forests.

Similar slopes of soil moisture dependence regressions for each forest (Figure 2) suggest that soil respiration in successional forests responds similarly to soil moisture. The similar trends of soil respiration to soil moisture can be explained, in part, by the similar seasonality of soil moisture, which is driven by the same climate conditions in these forests. In contrast, differences in soil moisture dependency can be explained by the heterogeneity of respirators among these forests. The stronger dependency of soil respiration on moisture in the broadleaf forest can be explained, in large part, by the diverse respirators in this forest. Compared with other forests, the broadleaf forest has abundant respirators in the soil, including roots and microbes (Table 4). It is evident that different respirators have various soil moisture dependencies (Joffre et al. 2003). More soil water may be needed in the broadleaf forest to maintain the activities of abundant respirators in this forest.

Conclusions

Soil respiration within each of the forests was strongly correlated with soil temperature and soil moisture. Driven by the seasonality of temperature and precipitation, soil CO_2 efflux showed a clear seasonal pattern, with fluxes significantly higher in the hot humid season than in the cool dry season. Soil respiration increased along with forest successional stage, with a consequence of enhanced auto- and heterotrophic respiration. Forests at different succession stages responded similarly to soil temperature and soil moisture but to different extents. Relatively weak temperature sensitivity in the broadleaf forest suggested a good self-adjustment of the advanced-successional stage. This indicates that, in light of rising temperatures caused by global warming, soil respiration in advanced-successional forests will be maintained at a relatively constant rate owing to the temperature acclimation effect. The increasing moisture dependency of soil respiration along succession stages can be explained, in part, by increased auto- and heterotrophic

respirators, which need more soil water to maintain their activities. Acknowledging the covariance of soil temperature and soil moisture in DNR forests, Q_{10} values derived from the T/M models are more accurate than those derived from the T model when the effects of temperature on soil respiration are examined.

Methods

Site description

The DNR, with an area of 1 133 hm^2 and an elevation ranging from 10 to 1 000 m above sea level, is located in the mid-part of Guangdong Province in southern China (112°30'39"–112°33'41" E, 23°09'21"–23°11'30" N). The region is characterized by a typical south subtropical monsoon climate, with annual average precipitation of 1 927 mm, of which nearly 80% falls in the hot humid season (April–September) and 20% in the cool dry season (October–March). The annual mean temperature is 21.4 °C and the relative humidity is 80%. Bedrocks are classified as Devonian sandstone and shale (Wu et al. 1982). Soils are classified as lateritic red earth (oxisol), loamy in texture, and acidic (the pH value of the top 20-cm soil layer was approximately 3.9), with low base saturation (He et al. 1982).

In the present study, three plots, each representing a common forest type, were chosen within the DNR. The three forests, including pine forest, conifer and broadleaf mixed forest (mixed forest), and evergreen broadleaf forest (broadleaf forest), represent forests in the early-, mid-, and advanced-successional stages in the region, respectively (Peng and Wang 1985, 1995). During natural succession, heliophytes (e.g. *Schima superba* and *Castanopsis chinensis*) gradually invade pine forests to form mixed forests and mesophytes (e.g. *Cryptocarya concinna* and *Cryptocarya chinensis*) subsequently invade mixed forests, eventually transforming them into broadleaf forests.

The pine forest, which was originally planted by local people in the 1930s, is distributed primarily in the hilly lands of the eastern, southern, and northern portions of the reserve, at an elevation of 50–200 m above sea level. The pine forest is dominated by *Pinus massoniana* in the tree layer and *Rhodomyrtus tomentosa*, *Dicranopteris linearis*, and *Baeckea frutescens* in the shrub and herb layers.

The mixed forest was developed from artificial pine forest with a gradual invasion of some pioneer broadleaf species through natural succession. Dominant species in the mixed forest include *Pinus massoniana*, *S. superba*, *Ca. chinensis* and *Craibiodendron kwangtungense*.

The broadleaf forest is the regional climax of vegetation. It is distributed in the Erbao Peak and the Sanbao Peak, at an elevation that varies from 250 to 350 m. Dominant species in the broadleaf forest include *Ca. chinensis*, *Cr. chinensis*, *Cr.*

concinna, *Erythrophleum fordii* and *Cyathea podophylla* (Kong et al. 1993). The main characteristics of the forests are listed in Table 4.

Soil respiration measurement

Soil respiration rate was measured using static chamber and gas chromatography techniques (Wang et al. 2003). Three chambers were installed in each forest site in February 2003. The static chamber was made of stainless steel and consisted of two parts: a square box (without a top and bottom, length \times width \times height = 0.5 m \times 0.5 m \times 0.1 m) and a removable cover box (without a bottom, length \times width \times height = 0.5 m \times 0.5 m \times 0.5 m). The square box was inserted directly into the forest floor approximately 10 cm below the floor surface, and the cover was placed on top during sampling and removed afterwards. A white adiabatic cover was added outside the stainless steel cover to avoid direct radiative heating during sampling. A typical experiment started at 09:00 h and lasted for approximately 30 min. Gas samples were collected every 10 min using 100-mL plastic syringes. Our diurnal studies demonstrated that the soil respiration rate measured at 09:00 h was close to the daily mean (Figure 5). Field measurements were performed weekly in the broadleaf forest and the mixed forest, and biweekly in the pine forest. Because the pine forest plot was located far away from the broadleaf forest and the mixed forest plots, we were unable to collect field data with the same frequency from the pine forest plot as in the other forests.

The CO₂ concentrations of samples were analyzed in the

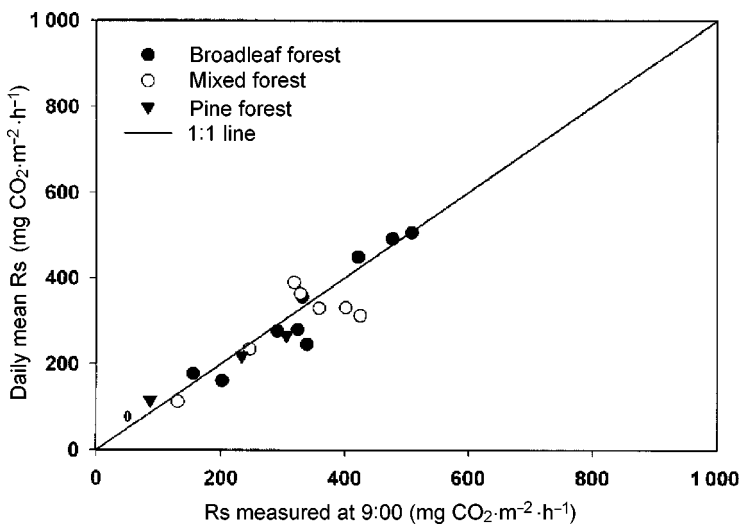


Figure 5. Correlations between soil respiration rates measured at 09.00 h and daily means in the pine (\blacktriangle), mixed (\circ), and broadleaf (\bullet) forests.

Daily means were calculated by averaging soil respiration rates from 10 measurements in diurnal observations.

laboratory within 24 h after sampling using gas chromatography (HP 4890D; Agilent Technologies, Palo Alto, CA, USA). The gas chromatograph was with an equipped flame ionization detector for CO₂ analysis. Fluxes were calculated from the rate of change in concentration in the chamber during the sampling interval, determined by linear regression based on four samples. All the coefficients of determination (r^2) of the linear regression were greater than 0.98 in the present study.

Soil temperature and moisture measurements

Soil temperature and moisture 5 cm below the surface were monitored at each chamber simultaneously when the gas samples were collected. Soil temperature ($^{\circ}$ C) was measured using digital thermometers. Soil moisture, measured as volumetric soil water content (% cm^3/cm^3) was determined using an MPKit (ICT Australia; <http://www.ictinternational.com.au/soils.htm>), which consists of three amplitude domain reflectometry (ADR) moisture probes (MP406) and a data logger (MPM160 meter). Water-filled pore space (% WFPS) was calculated using volumetric soil water content, soil bulk density, and particle density (Salimon et al. 2004). Climatic data (precipitation and air temperature) were obtained from the weather station at the Dinghushan Forest Ecosystem Research Station, part of the Chinese Ecosystem Research Network (CERN).

Statistical analysis

Seasonal means of soil respiration rate, soil temperature, and soil moisture were calculated by grouping the measured data into hot humid season (April–September) and a cool dry season (October–March). Analysis of variance (ANOVA) was performed to test the significance of differences in soil respiration rate, soil temperature, and soil moisture according to forest and season at the $\alpha = 0.05$ level.

Relationships between soil respiration and biophysical factors were examined by using regression models. Three types of regression models were used. The first model is exponential and involves only soil temperature (T , $^{\circ}$ C), referred to as the T model):

$$R_s = \beta_0 e^{\beta_1 T} \quad (1)$$

where T is soil temperature, the coefficient β_0 is the intercept of soil respiration when the temperature is zero, and the coefficient β_1 represents the temperature sensitivity of soil respiration. The second model is linear, where soil moisture (θ) was used as the indicator variable (referred to as the M model):

$$R_s = \beta_2 + \beta_3 \theta \quad (2)$$

where θ is the soil moisture (% WFPS) and β_2 and β_3 are the model coefficients. In the third model, the soil respiration rate is the function of both soil temperature

and moisture (referred to as the T/M model):

$$R_s = \beta_0 e^{\beta_1 T} \theta^{\beta_2} \quad (3)$$

The RMSE, R^2 (for linear models), pseudo R^2 (for non-linear models; Helland 1987; Motulsky and Christopoulos 2003), and 95% confidence intervals of the parameters are used to determine the significance and goodness-of-fit of the models.

The Q_{10} values were calculated as follows:

$$Q_{10} = e^{10\beta_1} \quad (4)$$

where β_1 is taken from the T model (equation 1) and the T/M model (equation 3).

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