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Plant and Soil

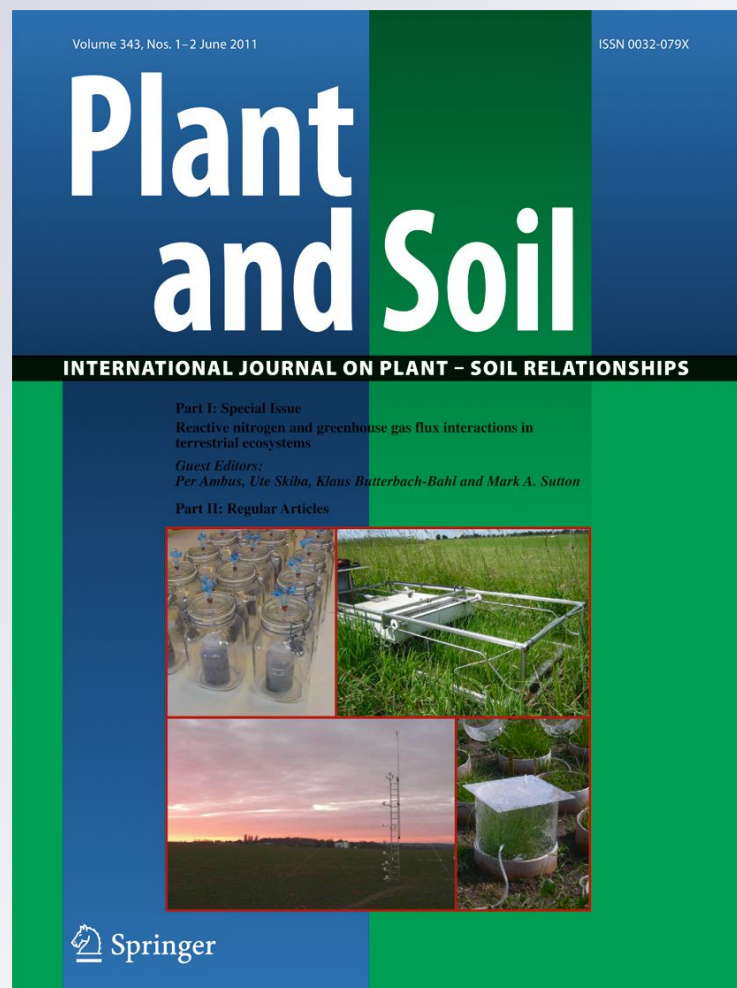
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Soil carbon stocks and fluxes in a warm-temperate oak chronosequence in China

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Abstract Soil respiration (R_S) and soil carbon stocks, as well as stand properties were investigated in a warm-temperate oak chronosequence in order to understand the age effect on soil CO_2 efflux. The chronosequence consisted of three 40-year-old, 48-year-old, 80-year-old, and 143-year-old oak stands, respectively. R_S measurements were conducted using a Li-8100 soil CO_2 flux system from October 2008 to October 2009.

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Temporal variations of R_S of all the four forests largely depended on soil temperature of 5 cm depth (T_5) ($R^2=0.738-0.825$). The mean R_S for 40-year-old, 48-year-old, 80-year-old, and 143-year-old forests were 2.37, 2.59, 2.99, and 3.32 $\mu\text{mol } CO_2 \text{ m}^{-2} \text{ s}^{-1}$ respectively. Both top soil organic carbon (SOC) and light fraction organic carbon (LFOC) stocks were significantly correlated to R_S variation, while only significant different LFOC among stands was found. This indicated that cumulated labile organic carbon was a better indicator on R_S variation, which was further illustrated by a better relationship between R_{10} and LFOC than that of R_{10} and SOC. We found that the variation of mean R_S among stands was well correlated with basal area (BA). Marginal correlation between R_S and fine root biomass (FR) demonstrated the relationship between R_S and belowground metabolism. We also found total porosity (TP) negatively influenced the mean R_S and this negative effect may mainly be attributed to the capillary porosity (CP). Forest growth and yield could be contributed to R_S variation among stands. Forest succession also changed soil labile carbon stock and soil physical properties that influenced the CO_2 efflux.

Keywords Soil respiration · Carbon cycle · Forest age · Oak forest · Spatial variation

Abbreviations

T_5 soil temperature at 5 cm soil depth
SWC soil water content at 0–5 cm soil depth

SOC	soil organic carbon
TN	total nitrogen
LFOC	light fraction organic carbon
BA	basal area
FR	fine root biomass
TP	total soil porosity
CP	capillary porosity
NCP	non-capillary porosity
SD	standard deviation
CV	coefficient variation
R _S	soil respiration
LAI	leaf area index

Introduction

Soil respiration accounts for a large proportion of total ecosystem respiration in forests (Janssens et al. 2001) and it is the second largest terrestrial carbon flux. It is sensitive to climate, vegetation type as well as forest age (IPCC 2001; Pregitzer and Euskirchen 2004; Raich and Potter 1995; Tang et al. 2009). To scale up R_S from chamber based measurements to annual soil CO₂ fluxes at an ecosystem level, we need to quantify R_S variations spatially and temporally (Ryan and Law 2005). Soil temperature and soil water content are recognized as the main factors controlling the temporal variation of soil respiration (Davidson et al. 1998; Janssens et al. 2001). Examining spatial variability of soil respiration is a complex process due to its component origin, such as the spatial distribution of fine roots (Saiz et al. 2006; Tang et al. 2009), plant photosynthesis (Bhupinderpal-singh et al. 2003; Högberg et al. 2001; Tang et al. 2005), leaf area and primary productivity (Högberg et al. 2001; Rey et al. 2002; Yuste et al. 2004), aboveground and belowground litterfall (Ryan and Law 2005), soil organic carbon (Wang and Yang 2007; Xu and Qi 2001), and labile organic carbon concentration (Laik et al. 2009). They all contribute to the spatial and the temporal variations of soil respiration.

To model the long-term forest carbon dynamics and its coupling with the climate system, we need to understand not only the responses of forest ecosystems to the changing climate, but also the successional status of carbon dynamics (Tang et al. 2009). Still, there is a substantial uncertainty regarding the effect of forest age on carbon fluxes, although it plays a

distinguishing role in determining the distribution of carbon pools and fluxes in different forest ecosystems. For example, studies on a loblolly pine plantation (Wiseman and Seiler 2004), and a larch plantation (Jiang et al. 2005) found that soil surface CO₂ flux increased with stand age. In contrast, Wang et al. (2002) reported that the annual soil surface CO₂ flux in a black spruce fire chronosequence decreased as stand age increased from 11 to 130 years old. On the other hand, Klopatek (2002) estimated the annual soil C efflux was 1367, 883 and 1,194 gm⁻² for the sites of 20-, 40- and old-growth stands of Douglas-fir, respectively. Tang et al. (2009) reported an increase of cumulative soil respiration in the growing season from burned stand to 26-years old stand, then declined to mature (73-years old) and old growth (350-years old) stands. Those complex patterns of soil CO₂ flux with forest age may indicate that age effect on soil CO₂ efflux varied with forest origin.

In north China, warm-temperate oak forests occupy large areas of forested land, composed of different succession stages regenerated from harvest sites. Still, knowledge of the effects of forest succession on soil C fluxes is limited, but it is important to determine the national carbon budgets. In this study, a warm-temperate oak chronosequence (40-year-old, 48-year-old, 80-year-old, and 143-year-old) was selected to investigate the role of forest successional status in shaping soil carbon dynamics by examining spatially different stands within the same period. The specific objectives of this study were to: (1) understand the seasonal pattern of soil respiration for different forests and their relationships with environments; (2) examine spatial variation of R_S and its seasonality among forests; and (3) quantify the relationships between mean R_S across stands with stand properties.

Materials and methods

Study sites and experimental design

The study sites were at the Forest Ecological Research Station, located at the Baotianman Nature Reserve (111°47'–112°04' E, 33°20'–33°36' N), Henan Province, China. The average elevation is 1,450 m. The meteorological parameters were collected from a nearby weather station, less than 3 km away from the study sites. The annual mean precipitation and air

temperature were 900 mm and 15.1°C, respectively. Precipitation occurred mainly in summer (55–62%; Liu et al. 1998). Upland soils were dominated by Haplic luvisol (FAO). All plots were dominated by *Quercus aliena* var. *acuteserrata*. In addition to the dominant species, other tree species included *Carpinus cordata*, *Cornus controversa* Hemsl, *Lindera obtusiloba*, and *Tilia mongolica* Maxim. A common set of stand attributes are summarized in Table 1.

In experimental design, the chronosequence of stands consisted of various age classes from 40-year old, 48-year old, and 80-year old to approximately 143-year old, as of year 2008. All forests were naturally regenerated from the former harvest sites with the similar harvest method (all debris and slash were left over on site) as well as site history except the 143-years old forest as an old-growth without site disturbance. These stands were all under the similar climate and soil properties and therefore provide an ideal chronosequence to study the age effect on soil carbon dynamics. Three 20 m×20 m measurement plots for each age class stand were established in September 2008. Three random soil CO₂ efflux sampling PVC collars (19.6 cm inside diameter, ca. 5 cm were inserted from ground surface into the soil, including 1–2 cm litter layer) were installed in each plot (R_S). All the PVC collars were installed permanently throughout the observation phases.

Soil respiration, soil temperature and water content

We measured soil CO₂ efflux from October 2008 to October 2009 using a Li-8100 soil CO₂ flux system (LI-COR Inc., Lincoln, NE, USA). Soil temperature at 5 cm depth (T₅) was measured adjacent to each respiration collar with a portable temperature probe provided with the Li-8100. Soil volumetric water content at 0–5 cm (SWC) was measured with a portable time domain reflectometer MPKit-B soil moisture gauge (NTZT Inc., Nantong, China) at three points close to each chamber. The measurements were taken twice a month in the growing season and once a month in other periods. No measurements were conducted during December 2008, January, and February 2009 due to snow coverage.

Soil and stand properties

Three soil samples were cored and mixed close to each collar (in a radius of 1–2 m from the collar center) where we measured soil CO₂ efflux at each plot with a diameter of 10 cm at 0–10, 10–30, and 30–50 cm of soils in summer 2009. Coarse (> 5 mm), medium (2–5 mm) and fine (< 2 mm) roots were manually separated from 0–30 cm soils (> 80% fine root biomass (FR) was distributed at 0–30 cm soil depth, unpublished data), and dry biomass was

Table 1 Summary of stand characteristics measured in summer 2009

Stand	BA (m ² ha ⁻¹)	Density (trees ha ⁻¹)	DBH (±SD, cm)	LAI (±SD)	BD(±SD) g/cm ³	SOC kg C m ⁻²	TN kg N m ⁻²	PH
40-year-old 1	52.0	1,900	16.2(9.5)	3.34(0.23)	0.88(0.05)	31.10	2.32	4.65
40-year-old 2	46.5	2,100	13.7(9.2)	3.41(0.41)	0.72(0.04)	31.24	2.26	4.43
40-year-old 3	57.3	2,600	15.0(7.7)	3.04(0.40)	0.60(0.08)	25.31	1.78	4.44
48-year-old 1	60.0	2,700	12.4(11.6)	2.43(0.09)	0.60(0.06)	35.91	2.44	4.84
48-year-old 2	53.2	1,900	16.2(10)	2.39(0.17)	0.66(0.06)	34.28	2.79	4.56
48-year-old 3	46.5	2,000	13.7(10.7)	2.36(0.22)	0.69(0.05)	35.81	2.22	5.02
80-year-old 1	65.5	2,000	17.02(11.57)	2.97(0.19)	0.66(0.02)	36.65	2.74	4.49
80-year-old 2	77.6	2,600	16.36(10.11)	3.26(0.25)	0.67(0.03)	35.84	2.39	4.47
80-year-old 3	61.0	2,000	15.03(13.08)	2.84(0.23)	0.62(0.03)	29.58	2.33	4.57
143-year-old 1	80.1	1,200	21.64(20.47)	3.24(0.53)	0.46(0.06)	41.98	2.33	4.66
143-year-old 2	85.4	2,500	12.59(16.44)	3.07(0.44)	0.73(0.08)	51.34	2.94	5.24
143-year-old 3	100.9	2,000	17.83(18.48)	3.11(0.52)	0.53(0.07)	28.45	1.51	4.88

BA, DBH, LAI, BD, SOC and TN stand for basal area, mean tree diameter at breast height, leaf area index, bulk density, soil organic carbon and total nitrogen stock at 0–10 cm of soil depth

Form. *Quercus acutidentata* dominated all stands

measured. We measured mass-based soil carbon content (%) and bulk density (g m^{-3}) for each soil sample at three layers across the chronosequence. Capillary porosity (CP), non-capillary porosity (NCP) and total porosity (TP) for each soil sample at 0–5 cm was determined as described by Liu et al. (2009). Soil light fraction organic matter was obtained by density fractionation based on Six et al. (1998), but with a modification using CaCl_2 solution (density of 1.5 g ml^{-1} ; Garten et al. 1999). Bulk soil and light fraction organic carbon contents were determined using the wet oxidation method with $133 \text{ mM K}_2\text{Cr}_2\text{O}_7$ at $170\text{--}180^\circ\text{C}$ (Lu 2000). Soil nitrogen concentrations in bulk soil (TN) were determined by the micro-Kjeldahl method. Soil carbon stocks (SOC; g m^{-2}) at the depth of 0–10, 10–30, and 30–50 cm and light fraction organic carbon stocks (LFOC; g m^{-2}) at the depth of 0–5 cm were calculated using carbon content and bulk density. Tree diameter at breast height (DBH) was measured for each tree in each stand. Leaf area index (LAI) was measured in August 2009 along a 25 m transect in each stand with WinSCANOPY (Regent Instruments Inc., Quebec, Canada).

Data analysis

We used an exponential equation (Eq. 1) to describe the relationship between R_S and soil temperature at 5 cm depth:

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

where R_S is the soil respiration, T is the soil temperature at 5 cm depth, and α , β are fitted parameters. The temperature sensitivity parameter, Q_{10} , was then derived using the following equation:

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

R_{10} was defined as the basal respiration rate at reference temperature of 10°C . The number of samplings required to estimate the mean soil respiration of each stand at the 10 or 20% of its actual value at the 95% probability level was obtained using Eq. 3 described by Snedecor GW and Cochran WG (1967):

$$n = \left(\frac{t_{\alpha s}}{D} \right)^2 \quad (3)$$

where t_{α} is Student's t with degrees of freedom at 0.05 significance level, s is standard deviation derived from

data obtained for this study, and D is allowable error of field sampling process.

Repeated measures GLMs were employed with LSD for comparisons of the means of T_5 , SWC, and R_S among forests across the measurement period. One way analysis of variance (ANOVA) was performed to assess the age effect on SD and CV of R_S , R_{10} , Q_{10} , FR, SOC, TN, LFOC, TP, CP and NCP. Regression analyses were used to examine the relationships between mean R_S , soil, and stand properties as well as the relationship between R_{10} and SOC, LFOC. Statistical analyses were performed using the SPSS 13.0 software package for Windows.

Results

Soil CO_2 flux and seasonal patterns

The means of R_S in the four forests were divided into two significant ($P < 0.05$) groups (Table 2). The mean R_S in the 143-year-old forest was the highest ($3.32 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), and 40% higher than that in the 40-year-old forest ($2.37 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). R_S varied greatly among the forests compared to the mean T_5 and SWC. The 80-year-old and 143-year-old forests had significantly lower T_5 compared to 40-year-old and 48-year-old forests ($P < 0.05$). The mean SWC in the 143-year-old forest was the highest ($0.3236 \text{ cm}^3/\text{cm}^3$ soil), whereas that in the 40-year-old forest was the lowest ($0.2734 \text{ cm}^3/\text{cm}^3$ soil) among the forests (Table 2).

The R_S for the four forest ecosystems all corresponded to seasonal changes of T_5 (Fig. 1a and c). Hence, temporal variation of R_S was well described by T_5 using an exponential equation, with R^2 ranging from 0.74 to 0.83 ($p < 0.001$; Fig. 2a). We only found a weak negative relationship between R_S and SWC in the 48-year-old forest (Fig. 2b). We found a significant higher Q_{10} in the 80-year-old forest compared to other forests ($p < 0.05$; Table 2). Basal respiration (R_{10}) increased significantly with forest age ($p < 0.05$; Table 2).

Spatial variability of soil respiration

The spatial variability of soil respiration, soil temperature and soil water content was described by the coefficient of variation (CV). We did not find clear seasonal trends in CV of SWC (Fig. 3a), while we

Table 2 Means of soil respiration rate (R_S), soil temperature (T_S) and soil water content (SWC) at 5 cm depth for four forests

Forest types	T (°C)	SWC (cm ³ /cm ³)	R_S (μ mol CO ₂ m ⁻² s ⁻¹)	R_{10} (μ mol CO ₂ m ⁻² s ⁻¹)	Q_{10}
40-year-old	12.42(0.0454)a*	0.2734(0.0054)a	2.37(0.0830)a	1.58(0.06)a	3.38(0.15)a
48-year-old	12.44(0.0505)a	0.3004(0.0067)b	2.59(0.1086)a	1.67(0.03)a	3.55(0.18)a
80-year-old	11.36(0.0524)b	0.3045(0.0032)b	2.99(0.1068)b	2.05(0.05)b	4.14(0.05)b
143-year-old	11.99(0.0521)c	0.3236(0.0092)c	3.32(0.2125)b	2.24(0.07)c	3.50(0.22)a

* Means with the different lowercase letters in a column represent significant difference at $P=0.05$ level

Values in parentheses are standard errors (SE)

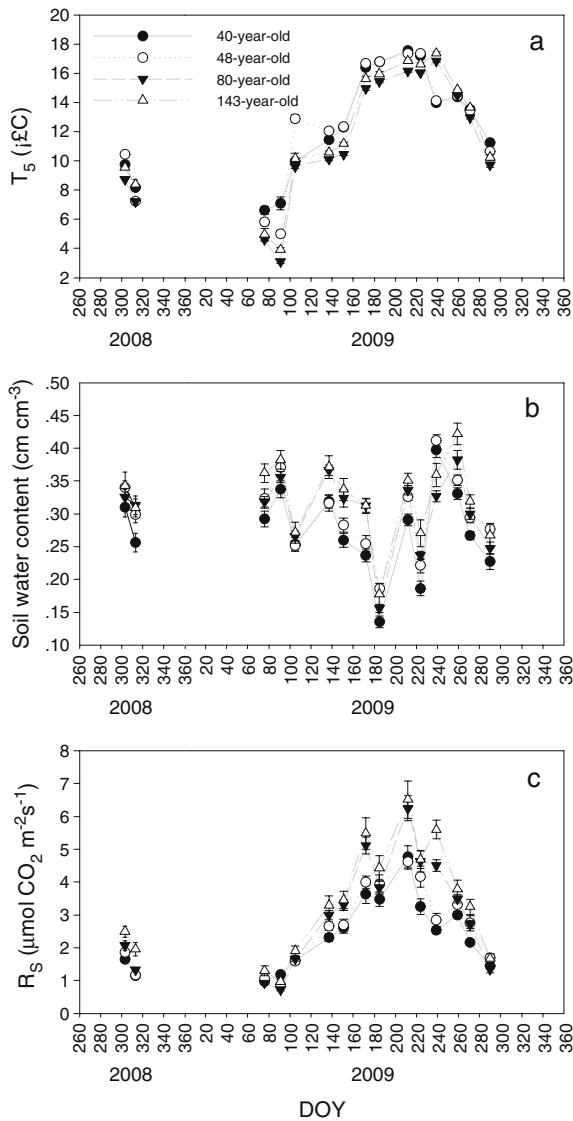


Fig. 1 Seasonal changes in soil temperature (T_S) **a**, soil water content (SWC) **b** at 5 cm depth, and **c** soil respiration rate (R_S) for four forests. The error bars represent standard errors ($n=3$)

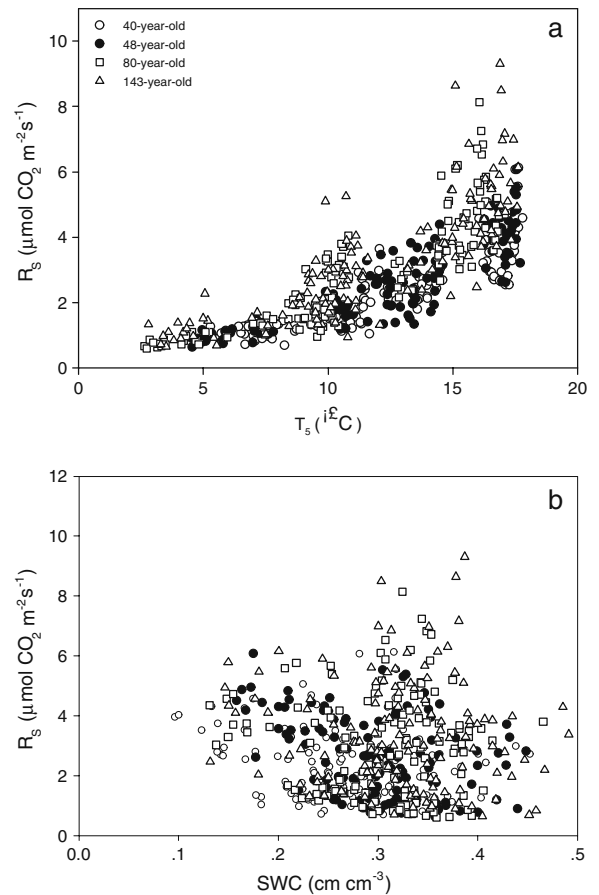


Fig. 2 **a** Relationships between soil respiration rates (R_S) and soil temperature (T_S) for four forests, Open circle: 40-year-old ($y = 0.465 \exp(0.122 x)$, $R^2 = 0.79$, $P < 0.001$); Closed circle: 48-year-old ($y = 0.482 \exp(0.125 x)$, $R^2 = 0.81$, $P < 0.001$); Open square: 80-year-old ($y = 0.498 \exp(0.143 x)$, $R^2 = 0.83$, $P < 0.001$); Open triangle: 143-year-old ($y = 0.644 \exp(0.125 x)$, $R^2 = 0.74$, $P < 0.001$). **b** Relationships between soil respiration rates (R_S) and soil water content (SWC) at 5 cm depth for four forests. Significant correlation was only found in 48-year-old forest ($y = -6.09 x + 4.37$, $R^2 = 0.09$, $P < 0.001$)

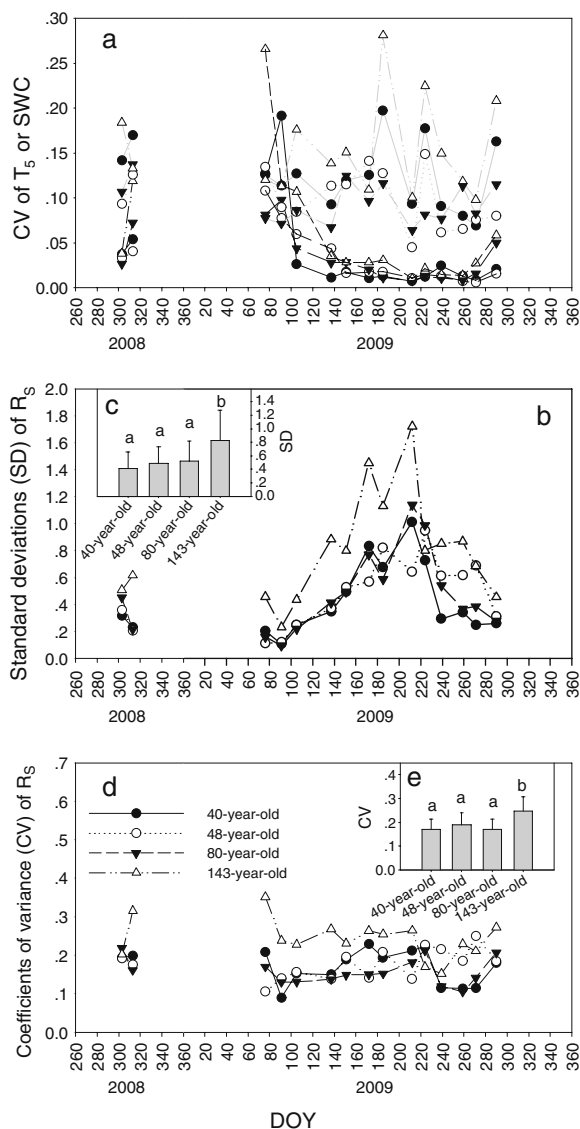


Fig. 3 a Seasonal patterns of coefficients of variation (CVs) of soil temperature (T₅) (black line) and soil water content (SWC) (grey line) at soil depth of 5 cm for four forests; b Seasonal pattern of the standard deviation (SD) of soil respiration; c Mean SD of different forests; d Seasonal pattern of the coefficients of variation (CVs) of soil respiration; e Mean CV of different forests. The error bars represent standard deviation and different lowercase letters represent significant difference at P=0.05 level

found a higher CV of soil temperature in late autumn and early spring (Fig. 3a).

The standard deviation (SD) of R_S showed the similar seasonal pattern with soil temperature (Fig. 3b). The mean SDs of R_S for the four forests were 0.41, 0.49, 0.52 and 0.83 μmol CO₂ m⁻² s⁻¹, respectively

(Fig. 3c). There was no clear seasonal trend in the spatial variability of soil respiration (Fig. 3d). The CVs ranged from a minimum value of 9% for the 40-year-old stand to a maximum value of 35% for the 143-year-old stand (Fig. 3d). The number of measurements required to estimate soil respiration per stand within 10% or 20% of allowable error at 0.05 significance level in the 143-year-old forest was significantly higher compared to other forests (p<0.05; Fig. 4). Our sampling strategy of 9 sampling points per stand was adequate to obtain an average rate of soil respiration within 20% of its actual value at the 95% confidence level.

Stand characteristics and their relationships with R_S

Bulk soil carbon and nitrogen stocks of 0–10 cm increased with forest age, while no significant difference was found among forests (Table 3). However, we found a significantly higher LFOC stock in the 143-year-old forest compared to other forests (p<0.05; Table 3). CP and TP at 0–5 cm depth of soil showed a significant decline with forest age, while no significant different NCP existed among the forests (Fig. 6a).

SOC of 0–10 cm showed a significant relationship with mean R_S, while we did not find significant relationships between mean R_S and SOC at 10–30, 30–50 cm depth of soil, TN at 0–10 cm, 10–30 cm and 30–50 cm of soil depth (Fig. 5a, b). On the other hand, mean CO₂ flux variation among stands largely

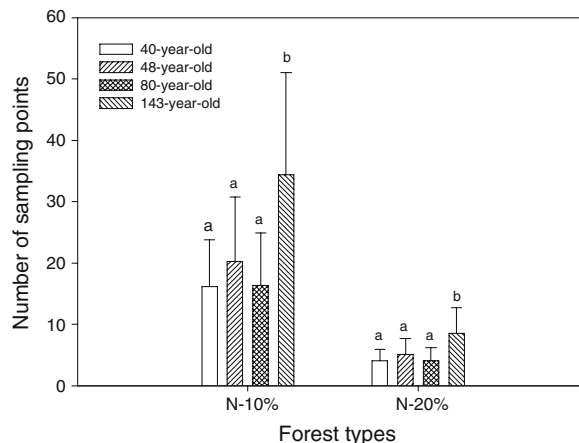


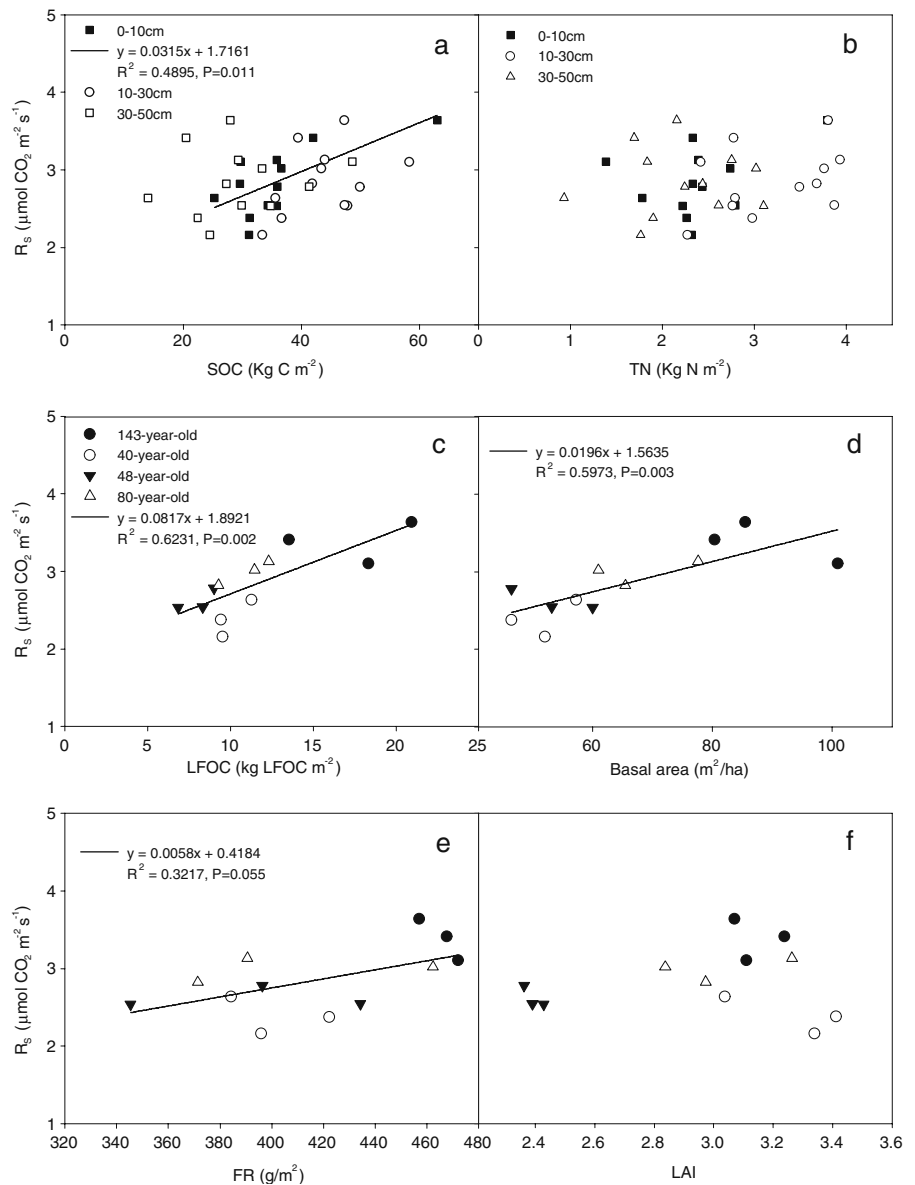
Fig. 4 Mean number of sampling points required to estimate mean soil respiration within 10 or 20% of its actual value at 95% probability level for each forest. The error bars represent standard deviation and different lowercase letters represent significant difference at P=0.05 level

Table 3 Mean soil chemical and physical characters, fine root biomass in four forests

Depth	SOC (kg C/m ²)			TN (kg N/m ²)			kg LFOC m ⁻²	FR (g/m ²)
	0-10 cm	10-30 cm	30-50 cm	0-10 cm	10-30 cm	30-50 cm	0-5 cm	0-30 cm
40-year-old	29.2a(1.9)*	35.2a(0.97)	20.3a(3.21)	2.12a(0.17)	2.68a(0.21)	1.53a(0.30)	10.1a(0.60)	400.7a(11.2)
48-year-old	35.3a(0.5)	48.3b(0.79)	35.3a(3.28)	2.48a(0.17)	3.37ab(0.32)	2.65b(0.25)	8.1a(0.64)	391.9a(25.8)
80-year-old	34.0a(2.2)	43.1ab(0.63)	30.0a(1.77)	2.49a(0.13)	3.79b(0.07)	2.74b(0.17)	11.0a(0.90)	408.1ab(27.7)
143-year-old	44.9a(9.7)	48.3b(5.46)	32.4a(8.42)	2.50a(0.7)	3.00ab(0.42)	1.89a(0.14)	17.6b(2.16)	465.5b(4.5)

* SOC: Soil organic carbon; TN: Total nitrogen; LFOC: Light fraction organic carbon; FR: Fine root biomass. Means with the different lowercase letters in a column represent significant difference at $P=0.05$ level. Values in parentheses are standard errors (SE)

Fig. 5 **a** Relationships between mean soil respiration (R_s) of 12 stands and soil organic carbon (SOC) at 0-10, 10-30 and 30-50 cm of soil depth separately, significant linear regression was only found between R_s and SOC at 0-10 cm of soil depth; **b** Relationships between mean R_s of 12 stands and total nitrogen (TN) at 0-10, 10-30 and 30-50 cm of soil depth separately; Relationships between mean R_s of 12 stands and light fraction organic carbon (LFOC) for 0-5 cm soil depth **c**, basal area **d**, fine root biomass (FR) **e**, and leaf area index (LAI) **f**



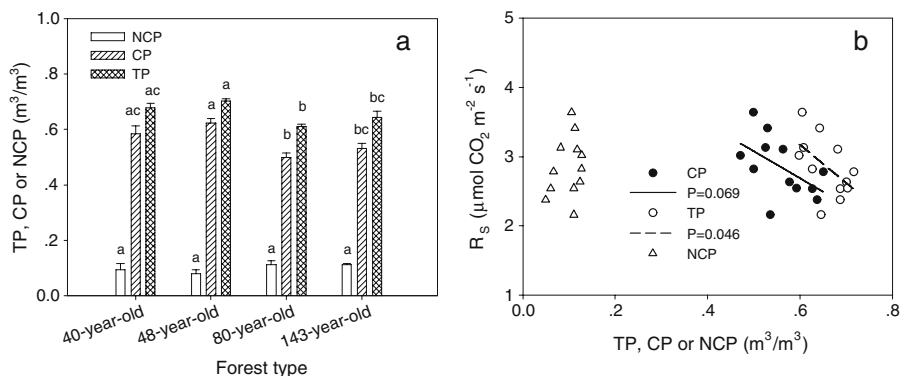


Fig. 6 **a** Total porosity (TP), capillary porosity (CP) and non-capillary porosity (NCP) for 0–5 cm soil depth for four forests, different lowercase letters of the same item represent significant

difference at $P=0.05$ level; **b** Relationships between mean R_s of 12 stands and total porosity (TP), capillary porosity (CP) and non-capillary porosity (NCP) for 0–5 cm soil depth

depended on LFOC (Fig. 5c) and basal area (Fig. 5d). A marginal significant relationship between mean R_s and fine root biomass was found in our study ($p=0.055$; Fig. 5e). The mean R_s and LAI were not significantly correlated to each other (Fig. 5f). Additionally, negative relationships were found between TP, CP and mean R_s (Fig. 6b). Basal respiration (R_{10}) variation among forests largely depended on SOC and LFOC (Fig. 7).

Discussions

Soil CO_2 flux among forests and its seasonality

The measured soil respiration rates in this study were comparable with previous studies in temperate forests

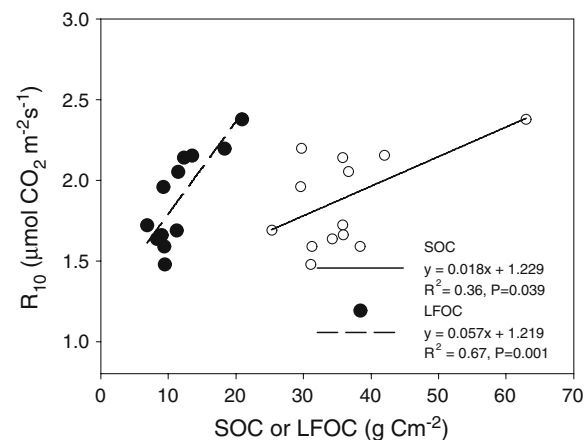


Fig. 7 Relationships between basal respiration (R_{10}) of 12 stands and soil organic carbon (SOC), light fraction organic carbon (LFOC) stocks

(Boone et al. 1998; Subke et al. 2006; Wang and Yang 2007; Wang et al. 2006). As previously reported in other temperate forests (Davidson et al. 1998; Raich and Schlesinger 1992; Wang et al. 2006), we also observed a high correlation between soil temperature and soil respiration (Fig. 2a). Although the temperature dependence varied across forests (Table 2), soil temperature explained 73.8–82.5% of temporal variation of R_s among forests. However, we did not find significant relationships between R_s and SWC for most forests, only a weak relationship was found in the 48-year-old forest (Fig. 2b). This may primarily be caused by the decoupling of SWC and R_s in our study area.

Vegetation structure, species composition, as well as forest succession status strongly influence C allocation patterns (Tang et al. 2009; Wang et al. 2006), soil microclimate (Raich and Tufekciogul 2000), and R_s . In this study, the mean R_s of 80-year-old and 143-year-old forests were significantly higher than that of 40-year-old and 48-year-old forests (Table 2); which is in agreement with Litton et al's (2003) result reporting higher soil respiration rates in older (110 years) versus younger forests (13 years). Wiseman and Seiler (2004) also found an increase of soil respiration rate with forest age in loblolly pine plantations. In contrast, Wang et al. (2002) reported that a black spruce fire chronosequence showed a decrease of annual soil surface CO_2 flux from 11 to 130 years old forests. We speculate that these contrasting results may be partly explained by different chronosequence origins. For example, the experiment by Wang et al. (2002) was conducted in a fire chronosequence, the abrupt increase of substrate supply, such as easily decomposed organic carbon input after fire (Ilstedt et al. 2003), caused the

higher soil CO₂ efflux at the early regeneration stage of the forest. However, our experiment was conducted in a chronosequence regenerated naturally from harvested sites, which presented a rapid loss of soil labile carbon at the early stage of forest regeneration (Luan et al. 2010). On the other hand, both autotrophic and heterotrophic components of respiration contributed to soil surface CO₂ efflux through respiration (Boone et al. 1998; Hanson et al. 2000), hence, the uncertainties of stand age effects on soil respiration were likely attributed to the lack of understanding of respiration components partition.

Seasonal pattern of spatial variability in soil respiration

In our study, we found that both SD and CV of R_S within plots varied with forest age (Fig. 3b, d). The 143-year-old forest showed significantly higher SD and CV compared to other forests (Fig. 3c, e). This may be because of the heterogeneity caused by plant root distributions, substrate supply variation, or modified microhabitats (Tang et al. 2005; Wang et al. 2006; Buchmann 2000). We found a clear seasonal variation pattern of SD (Fig. 3b), which was consistent with the seasonal pattern of soil temperature. We did not find any clear seasonal trends of CV for the four forests (Fig. 3d) which was in consistent with the result reported by Wang et al. (2006). In contrast, Saiz et al. (2006) found a seasonal trend in the spatial variability of soil respiration for the Sitka spruce stands. They found that the sharp increase of spatial variability of SWC during autumn drought explained the increased CV of R_S . No seasonal trend of spatial variability of SWC was found in our study and this may explain the contrasting results. In this study, even though we found an abrupt increase of CV of SWC on 4 July, however, the SWC values (0.1357–0.186 cm³/cm³) were sufficient to support microbial activity hence no drought stress occurred. The seasonal pattern of spatial variability in soil respiration can also be expressed by the number of measurements required to estimate soil respiration within a given percentage of its actual value (Saiz et al. 2006). In our study, the total 9 sampling points per stand were made and this number was adequate to yield an average rate of soil respiration within 20% of its actual value at the 95% probability level. Furthermore, the number of measurements needed is also determined by the area covered by the

chamber (Davidson et al. 2002). Hence, higher inner diameter of collar used in the study may yield the lower sampling points. Corresponding to the higher CV in the 143-year-old forest, the number of measurements needed is also higher than in other forests.

Soil CO₂ flux and stand properties

The factors contributing among-ecosystem R_S variability are complex because soil CO₂ flux is composed of several different components (Hanson et al. 2000). The R_S is significantly influenced by SOC concentration, especially more recently produced labile SOC in the litter (Laik et al. 2009; Wang et al. 2006). This was also illustrated in our study (Fig. 5a, c). We found a significant relationship between R_S and SOC at 0–10 cm depth of soil, while no relationship between R_S and SOC was found at 10–30 cm and 30–50 cm depth of soil. This indicated that SOC cumulated at top soil mainly contributed to the spatial variation of R_S among forests. Soil carbon decomposes much slower in deeper soil probably due to lower oxygen availability, and higher soil aggregation (Six et al. 2002). Therefore, we did not find significant relationships between R_S and SOC stock at soil depth of 10–30, 30–50 cm, although a significant difference in SOC stock existed at soil depth of 10–30 cm (Table 3). On the other hand, a strong relationship between R_S and soil LFOC was found at 0–5 cm of soil depth (Fig. 5c). We also found significantly higher LFOC stock in the 143-year-old forest compared to other forests (Table 3). This indicated that older forests cumulated more readily decomposable organic carbon than younger forests (Table 3), which accounted for the variation of R_S among forests. Furthermore, a higher slope of LFOC vs. R_S than SOC vs. R_S may imply that higher proportion of soil labile organic carbon will lead to higher soil respiration rate (Fig. 5a, c). Therefore, the variation of R_S across the chronosequence was mainly attributed to different substrate (i.e. labile carbon) availability (Wang et al. 2010) and organic matter quality (Cisneros-Dozal et al. 2006; Wang and Yang 2007). In addition, the extrapolation of the results from Fig. 7 for both SOC and LFOC indicated that the absence of organic matter equates to a basal respiration rate of ca. 1.2 μ mol m⁻² s⁻¹. This may roughly represent the basal respiration of autotrophic respiration.

There was a positive relationship between R_S and basal area (BA), which was consistent with the result

reported by Nsabimana et al. (2009). Katayama et al. (2009) also found a significant correlation between soil respiration and basal area in a tropical forest. They argued that basal area was positively correlated to root density, which explained the high respiration rate. However, we did not find a significant linear relationship between R_S and LAI as Tang et al. (2009) reported. Root biomass may have more effects on R_S than LAI does (Tang et al. 2009). Belowground metabolism also contributed to the R_S variation. We found that the R_S was correlated to fine root biomass (Fig. 5f), while low R^2 existed partly because the contribution of root respiration to total soil respiration may be lower in our study. This hypothesis was confirmed in a separate study (Luan et al. 2011). As reported, R_S is also strongly coupled to aboveground metabolism (Högberg et al. 2001; Tang et al. 2005). The confounding influence of autotrophic respiration which varies seasonally and in synchronisation with temperature may have contributed to relatively high Q_{10} values in our study (3.50–4.14; Table 5), as Q_{10} values in our study is apparent temperature sensitivity other than inherent temperature sensitivity (Davidson and Janssens 2006). Therefore, further measurement of photosynthesis may help elucidate these issues.

Additionally, forest types also affect R_S by modifying microhabitats (Wang et al. 2006). As a result we found both soil total porosity (TP) and capillary porosity (CP) declined significantly with forest age, while no significant difference in no-capillary porosity (NCP) among forests was found (Fig. 6a). We also found a significant negative relationship between R_S and TP. We speculate that this negative effect of TP on R_S was mainly contributed to restriction of soil CO_2 efflux by capillary hanging water. We found a negative relationship between R_S and CP while no relationship between NCP was found (Fig. 6b). As reported, CP also influences the soil surface CO_2 efflux through limiting oxygen availability for both microbial decomposition and autotrophic activities (Davidson et al. 1998; Xu and Qi 2001). No significant relationship between SOC with CP and NCP were found in our study further elucidated our speculation.

Conclusions

Soil temperature at 5 cm depth well explained the seasonal variation of R_S for the four forests. Top soil

organic carbon, especially top soil labile organic carbon accumulation, could partially explain the variation of R_S among forests. Forest growth and yield in terms of basal area and fine root biomass could be also contributed to R_S variation among stands, which was reflected by a strong correlation between R_S and basal area. Forest succession also influenced CO_2 emission through altering soil physical properties such as capillary porosity. However, partitioning of respiration components still needs to be further studied to elucidate age effect on R_S variation.

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