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Separating rhizosphere respiration from total soil respiration in two larch plantations in northeastern China

LIFEN JIANG,[1,2] FUCHEN SHI,[3,4] BO LI,[1] YIQI LUO,[1,5] JIQUAN CHEN[1,6] and JIAKUAN CHEN[1]

[1] *Ministry of Education Key Laboratory for Biodiversity Science and Ecological Engineering, Institute of Biodiversity Science, Fudan University, Shanghai 200433, P.R. China*

[2] *Key Laboratory of Forest Plant Ecology, Ministry of Education, Northeast Forestry University, Harbin 150040, P.R. China*

[3] *College of Life Science, Nankai University, Tianjin 300071, P.R. China*

[4] *Corresponding author (fcshi@nankai.edu.cn)*

[5] *Department of Botany and Microbiology, University of Oklahoma, Norman, OK 73019, USA*

[6] *Department of Earth, Ecological and Environmental Sciences, University of Toledo, Toledo, OH 43560, USA*

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Summary The potential capacity of soil to sequester carbon in response to global warming is strongly regulated by the ratio of rhizosphere respiration to respiration by soil microbial decomposers, because of their different temperature sensitivities. To quantify relative contributions of rhizosphere respiration to total soil respiration as influenced by forest stand development, we conducted a trenching study in two larch (*Larix gmelini* (Rupr.) Rupr.) plantations, aged 17 and 31 years, in northeastern China. Four plots in each plantation were randomly selected and trenched in early May 2001. Soil surface CO_2 effluxes both inside and outside the plots were measured from May 2001 to August 2002. Soil respiration (i.e., the CO_2 effluxes outside the trenched plots) varied similarly in the two plantations from 0.8 μmol m^{-2} s^{-1} in winter to 6.0 μmol m^{-2} s^{-1} in summer. Rhizosphere respiration (i.e., CO_2 efflux outside the trenched plots minus that inside the plots) varied from 0.2 to 2.0 μmol m^{-2} s^{-1} in the old forest and from 0.3 to 4.0 μmol m^{-2} s^{-1} in the young forest over the seasons. Rhizosphere respiration, on average, accounted for 25% of soil respiration in the old forest and 65% in the young forest. Rhizosphere and soil respiration were significantly correlated with soil temperature but not with soil water content. We conclude that the role forests play in regulating climate change may depend on their age.

Keywords: carbon dioxide, forest age, Q_{10}, soil respiration, soil temperature, soil water, trenching method.

Introduction

Soil contains the largest active terrestrial carbon (C) pool, and, through soil respiration, contributes an annual flux of carbon dioxide (CO_2) to the atmosphere 10 times greater than that from fossil fuel combustion (Schlesinger 1997). Soil respiration is the process of CO_2 release by soil microorganisms and plant roots (Keutgen and Huysamer 1998). Annual transfer of CO_2 to the atmosphere by soil respiration is estimated to be 60–80 Pg C $year^{-1}$ (Raich and Potter 1995), accounting for a major portion of the global carbon cycle (Raich and Schlesinger 1992). Thus, even a small change in soil respiration rate (SRR) could have profound effects on atmospheric CO_2 concentration (Andrews et al. 1999). Many studies have shown that SRR is highly sensitive to environmental factors, such as soil temperature and soil water content (Schleser 1982, Jenkinson et al. 1991, Schlesinger 1991, Luo et al. 1996, Trumbore et al. 1996, Keith et al. 1997, Rustad et al. 2000, Euskirchen et al. 2003). Accordingly, enhanced decomposition associated with climate warming of 1 °C would release 11–30 Pg C annually to the atmosphere (Schimel et al. 1994).

Root respiration is an important component of soil respiration. The estimated contribution of root respiration to total soil respiration varies from 10 to 90% (Hanson et al. 2000), depending on ecosystem type. Responses of microbial and root respiration to temperature differ (Davidson et al. 1998), suggesting that the potential change in soil carbon fluxes associated with increased temperature will largely depend on the relative contributions of root (including rhizosphere) and microbial respiration (Buchmann 2000). If we are to predict feedbacks between global climate change and soil processes, we must first understand the relative contributions of root respiration and respiration by soil microbial decomposers to total soil respiration (Andrews et al. 1999).

Increasing attention has been given to methods for measuring root respiration, particularly techniques for separating root respiration from total soil respiration. However, measuring root respiration under field conditions remains challenging (Andrews et al. 1999, Bouma and Bryla 2000, Buchmann 2000). In previous studies, several methods (other than regression) have been used to separate root respiration from total soil respiration (Kučera and Kirkham 1971, Behera et al. 1990, Xu et al. 2001). For example, the excised-root method (Burton et

al. 1998) and subtraction method (Gansert 1994) have been employed to measure soil respiration before and after root removal. However, both methods introduce significant disturbances to both roots and soil. The root cuvette method involves measuring respiration of intact roots (Bouma and Bryla 2000), but the method is more suitable for use in greenhouses than in the field. A more elegant method, isotopic tracing based on Keeling plots, has recently been applied by labeling with ^{13}C (Andrews et al. 1999) or ^{14}C (Horwath et al. 1994). Although the isotopic method can be applied in the field, it is relatively complicated and costly. An alternative method is to exclude roots from plots through trenching (Boone et al. 1998), which allows the measurement of rhizosphere respiration rate (RRR) versus bulk soil decomposer respiration rate (BSRR). Although the results can be complicated by starvation of the rhizosphere and the potential shifts from symbionts to detritovores, the method is simple, cost effective, and can provide realistic estimates of root respiration (Rochette et al. 1999, Lee et al. 2003). The method is widely used to partition components of soil respiration in forest ecosystems (Hanson et al. 2000).

In China, larch-dominated forests are a major forest type with high carbon storage (Liu et al. 2000). Larch forests account for more than 83% of the stocking volume of the forests in northeastern China (Dong 2001). Although Xingan larch (*Larix gmelini* (Rupr.) Rupr.) forest is the most abundant among all larch ecosystems in China (Zhou et al. 1997), there is limited quantitative information about the extent to which these forests might act as a carbon sink (Shi et al. 2001, Jiang and Zhou 2002). Because of the relative dominance of this forest type in the Chinese landscape, it is important to understand rhizosphere and soil respiration of these ecosystems.

To investigate the contribution of rhizosphere respiration to total soil respiration and the influence of stand age and relevant environmental factors (soil temperature and soil water content) on rhizosphere and soil respiration of Xingan larch plantations, we carried out a study in two Xingan larch plantations of different ages (17 and 31 years old) in northeastern China. We used the root-exclusion approach with trenching to estimate the contribution of rhizosphere respiration to total soil respiration. Our objectives were to determine: (1) how much rhizosphere respiration contributes to total soil respiration; (2) how plantations of different ages differ in their rhizosphere and soil respiration rates; (3) seasonal patterns of rhizosphere and soil respiration; and (4) how rhizosphere and soil respiration are regulated by soil temperature and soil water content.

Materials and methods

Study site

This field study was conducted at Lao Shan Experimental Station in Mao'er Shan Forest of Northeast Forestry University, China. The station is located in the northwest part of Mt. Zhangguangchai in the Changbai range (45°20′ N, 127°34′ E, about 340 m a.s.l.). Lao Shan Experimental Station has a continental monsoon climate, with long, cold, dry winters and short, warm, humid summers. Mean annual air temperature is 2.8 °C and the growing season varies from 120 to 140 days. Rain falls mainly in July and August. Mean annual precipitation and mean potential annual evaporation are 724 and 1094 mm, respectively.

To examine the effect of stand age on the contribution of rhizosphere respiration to total soil respiration, we selected a 17- and a 31-year-old Xingan larch plantation. Both plantations were 0.1 ha in size and the sites had been reforested with larches following abandonment as agricultural fields. The distance between the plantations was about 100 m. Both stands are on typical dark brown forest soil (Table 1). Total soil nitrogen (N) and C contents differed significantly between the stands ($F_{1, 18} = 144.39$, $P < 0.001$ for total N and $F_{1, 18} = 74.55$, $P < 0.001$ for total C). Specifically, the total N and C contents in the top 30 cm of soil were significantly higher in the old forest than in the young forest (for both soil N and C contents at 0–5 cm, $P < 0.01$, $n = 2$; for both soil N and C contents at 0–10 cm, $P < 0.01$, $n = 3$; for both soil N and C contents at 10–20 and 20–30 cm, $P < 0.05$, $n = 3$), but there were no significant differences between the stands in soil N and C contents below 30 cm (Table 2) or in forest floor litter biomass (Table 3).

Measurements

In early May 2001, we trenched four randomly selected plots (each 40 × 40 cm). A trench around the boundaries of each plot was dug to bedrock (about 35 cm below the surface) and plastic boards inserted to isolate the plots. The aboveground parts of all plants were clipped to eliminate aboveground respiration. Kelting et al. (1998) suggested that root death occurs rapidly after severing and that decomposition begins within the first month. Because of a possible increase in BSRR caused by root decomposition and soil disturbance immediately following trenching (Lee et al. 2003), we did not measure respiration rates until more than a month after trenching (i.e., from the

Table 1. Stand characteristics of the young (17-year-old) and old (31-year-old) larch plantations. Abbreviation: DBH = diameter at breast height.

Characteristic	Young	Old
Tree		
Age (year)	17	31
Mean DBH (cm)	10.2 ± 4.6	16.4 ± 4.8
Mean tree height (m)	10.1 ± 2.3	14.2 ± 3.6
Density (stems ha^{-1})	1533	1420
Soil		
pH [1]	4.46	4.97
Organic matter (%) [1]	1.06	1.92
Thickness of A_0 horizon (cm)	4.3	5.0
Thickness of A horizon (cm)	9.8	15.0
Thickness of B horizon (cm)	15.2	20.3

[1] Data from Chen (2003) and values are for the soil of 0–20 cm depth.

Table 2. Mean (± SE) soil nitrogen (N) and carbon (C) contents (%) in the young (17-year-old) and old (31-year-old) larch plantations measured in 2002 and 2004.

Year	Soil depth (cm)	Soil N		Soil C	
		Old	Young	Old	Young
2002	0–5	0.66 ± 0.01	0.21 ± 0.01	7.53 ± 0.05	2.22 ± 0.11
	30–35	0.04 ± 0.002	0.05 ± 0.02	0.39 ± 0.02	0.40 ± 0.04
	60–65	0.05 ± 0.01	0.04 ± 0.001	0.38 ± 0.09	0.35 ± 0.005
2004	0–10	0.69 ± 0.03	0.26 ± 0.02	7.98 ± 0.80	3.17 ± 0.31
	10–20	0.43 ± 0.06	0.14 ± 0.01	4.44 ± 0.79	1.39 ± 0.11
	20–30	0.27 ± 0.04	0.09 ± 0.01	2.99 ± 0.71	0.89 ± 0.11

middle of June onward). We measured SRR both inside and outside the plots on a monthly basis. Trenching disrupts input to roots and affects the microbial communities dependent on current autotrophic input, suggesting that the respiration rate inside the plots represented bulk soil decomposer respiration. Rhizosphere respiration was obtained by subtracting the trenched plot or bulk soil decomposer respiration from total soil respiration.

We measured SRR with a soil respiration chamber (LI-6400-09; Li-Cor, Lincoln, NE) connected to a Li-Cor LI-6400 portable photosynthesis system. The soil chamber was placed on a PVC collar inserted into the soil to a depth of about 4 cm at least 12 h before measurement. For each trenched plot, a collar was inserted both inside and outside the plot. The collar inside the plot was inserted randomly and left installed throughout the study. The collar outside the plot was inserted randomly at 0.5–1 m from the plot each time a measurement was made, the soil inside the collar being sampled following a measurement. Measurements were repeated three times. The time taken for each measurement varied from 2 to 20 min, depending on the rate of CO_2 release. To minimize errors caused by differences in measuring time, we measured SRR of both stands on the same day.

We also measured total SRR at different soil depths in August 2002. Because of the difficulty of digging in rocky soil, we were able to make only two repeated measurements for each stand. We measured SRR on the ground surface first, then dug to a depth of 30 cm and measured SRR at the horizontal soil surface at that depth. The process was repeated at a depth of 60 cm.

Table 3. Monthly means (± SE) of litter biomass (kg m^{-2}) in the young (17-year-old) and old (31-year-old) larch plantations.

Month (year)	Old	Young
June (2001)	3.1 ± 0.7	2.6 ± 0.3
July (2001)	4.5 ± 1.4	2.8 ± 0.4
August (2001)	2.9 ± 0.1	2.0 ± 0.4
September (2001)	3.1 ± 0.1	2.1 ± 0.2
October (2001)	3.3 ± 0.6	2.7 ± 0.7
May (2002)	3.2 ± 0.4	3.0 ± 0.6
June (2002)	2.5 ± 0.5	2.0 ± 0.3
August (2002)	2.0 ± 0.1	1.7 ± 0.3
Overall	3.1 ± 0.2	2.4 ± 0.2

After measuring soil respiration, soil in the top 5 cm inside the collars was sampled with a soil sampler (5 cm long, 5 cm in diameter) to determine soil water content and root biomass. Litter inside the collars was collected to determine the litter biomass on the forest floor. Because of the relatively small area inside the trenched plots, soil water was not measured there to avoid disturbance to the soil. Fresh soil samples were weighed (M_t) and roots were extracted and weighed (M_r). The soil, excluding roots, was then dried to constant mass at 105 °C to calculate soil water as: $100(M_{fresh} - M_{dry})/M_{fresh}$ (where $M_{fresh} = M_t - M_r$). To remove soil residues from the roots, the fresh roots were soaked in tap water overnight and then gently washed with a low-pressure jet of water over a 0.15-mm mesh sieve. The roots sampled in 2001 and 2002 were not divided into size classes. To obtain more information on the distribution of coarse and fine roots with soil depth, N and C contents of coarse and fine roots, and N and C contents at different depths, we sampled the soil again in August 2004. We dug three soil profiles to a depth of 30 cm in each stand, and sampled soil (including roots) every 5 cm with the soil sampler described above, for a total of three replicates per depth in each stand. The coarse roots (≥ 1 mm in diameter) and fine roots (< 1 mm in diameter) were separated, soaked and washed as described, and dried at 50 °C to constant mass. After weighing, coarse and fine roots for every two consecutive 5-cm layers were combined for measurement of N and C contents. Roots and soils were then ground, sieved and measured with a Flash EA1112 series NC Soil Analyzer (Thermo Electron).

Soil temperature at a depth of 5 cm was measured with a hand-held thermometer RT-21S (ESPEC MIC, Aichi, Japan). Precipitation data were recorded at a microclimate station at the Experiment Station, located 200 m from the young forest and 300 m from the old forest.

Data analysis

We used analysis of variance (ANOVA) to test differences in repeated measures of soil, rhizosphere and bulk soil decomposer respiration rates, percentage of rhizosphere respiration to the total soil respiration, air and soil temperature, and litter biomass on the soil surface between the two stands. Plots were nested within a stand in the ANOVA; a *t* test was used to test

the difference in SRR, root biomass and total N and C contents of roots and soils of the same depths between the two stands. The significance of the difference in soil and rhizosphere respiration rates over seasons was analyzed with a one-way ANOVA. Regression analyses were applied to explore the relationship between respiration rate and soil temperature and soil water. The effects of soil water were assessed with a simple linear model. To analyze soil temperature effects, we used an exponential function in the form: $y = \beta_0 e^{\beta_1 x}$, where y is the measured rhizosphere or soil respiration, β_0 and β_1 are estimated coefficients, and x is measured soil temperature. Values of Q_{10}, an indicator of temperature sensitivity, were calculated as: $Q_{10} = e^{10\beta_1}$. Differences in regression lines between the two stands, and also between rhizosphere and soil respiration rates of the same stand were tested by ANOVA after log transformation of the data.

Results

Seasonal change of soil and rhizosphere respiration

There was no significant difference in air temperature ($F_{1, 48}$ = 0.02, $P > 0.05$) or soil temperature ($F_{1, 48} = 1.44$, $P > 0.05$) between the stands when SRR was measured. There was considerable seasonal variation in precipitation, with precipitation greatest in summer and least in autumn (Figure 1).

We detected a significant seasonal difference in SRR for both the old forest ($F_{8, 27} = 22.64$, $P < 0.001$) and the young forest ($F_{8, 27} = 8.20$, $P < 0.001$) (Figure 2a). In both forests, SRR was higher in spring and summer than in other seasons, and peaked in August. In the old forest, SSR varied from 0.83 to 6.22 μmol m^{-2} s^{-1}, whereas SRR ranged from 0.73 to 5.90 μmol m^{-2} s^{-1} in the young forest. However, there was no statistical difference in SRR between stands ($F_{1, 48} = 0.54$, $P >$ 0.05).

There were also significant seasonal changes in RRR in both the old forest ($F_{7, 24} = 7.71$, $P < 0.001$) and the young forest ($F_{7, 24} = 11.18$, $P < 0.001$) (Figure 2b). Unlike SRR, RRR of the young forest was consistently and significantly higher than that of the old forest ($F_{1, 42} = 21.19$, $P < 0.01$). In particular, RRR of the young forest was 4.41 times that of the old forest in June 2002. In contrast, BSRR was significantly lower in the young forest than in the old forest ($F_{1, 42} = 32.04$, $P < 0.01$) (Figure 2c).

Rhizosphere respiration accounted for 18–90% of total soil respiration, depending on forest age and season (Figure 3). Rhizosphere respiration contributed a significantly greater

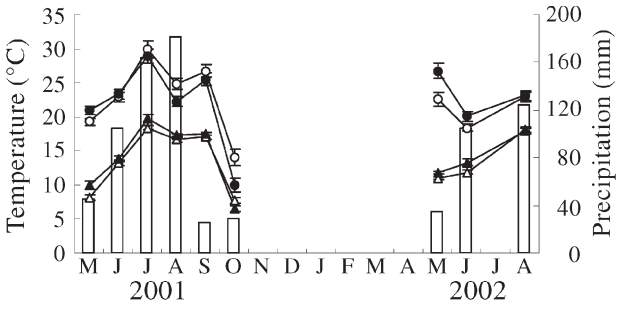

Figure 1. Monthly precipitation and seasonal variations in microclimate in the young (17-year-old) and old (31-year-old) larch plantations. Symbols: ○ = air temperature of the old forest; ● = air temperature of the young forest; △ = soil temperature of the old forest; and ▲ = soil temperature of the young forest. The histogram bars represent precipitation. The vertical bars on the data points represent standard errors.

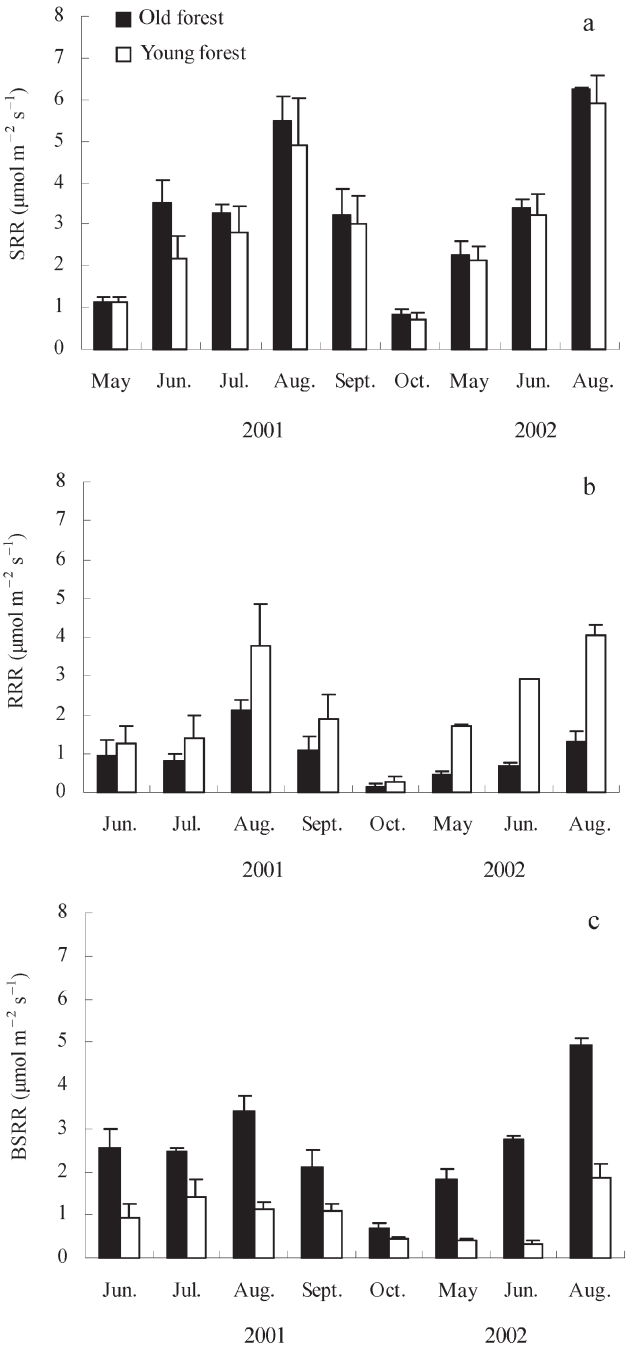

Figure 2. Seasonal changes in (a) total soil respiration rate (SSR), (b) rhizosphere respiration rate (RRR) and (c) bulk soil respiration rate (BSRR) in the young (17-year-old) and old (31-year-old) larch plantations. The vertical bars represent standard errors.

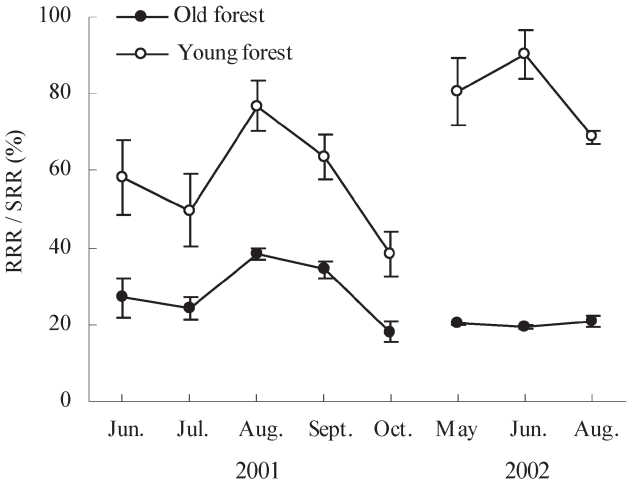

Figure 3. Contribution (%) of rhizosphere respiration (RRR) to total soil respiration (SRR) in the young (17-year-old) and old (31-year-old) larch plantations. The vertical bars represent standard errors.

proportion of total soil respiration in the young forest than in the old forest ($F_{1, 42} = 36.26$, $P < 0.01$).

The SRR at different soil depths differed significantly between the stands ($F_{1, 6} = 15.54$, $P < 0.01$). Specifically, there was a significant difference in SRR between stands at the ground surface ($P < 0.05$, $n = 2$), but not at depths of 30 ($P > 0.05$, $n = 2$) and 60 cm ($P > 0.05$, $n = 2$) (Figure 4). This pattern was consistent with that of soil C and N contents in the two stands (Table 2).

Biomass of coarse and fine roots differed significantly between the stands ($F_{1, 24} = 8.98$, $P < 0.01$ for the coarse roots and $F_{1, 24} = 101.21$, $P < 0.001$ for the fine roots) (Table 4). The vertical patterns of coarse root and fine root biomass also differed between the stands. Fine root biomass of the young forest was significantly greater than that of the old forest in the first three layers between 0 and 15 cm ($P < 0.01$, $n = 3$ for each layer), but significantly lower at the deeper layers ($P < 0.05$, $n = 3$ for each layer). Similarly, coarse root biomass of the young forest was significantly greater than that of the old forest in the 10–15 cm layer ($P < 0.05$, $n = 3$), but significantly lower in the two deeper layers between 20 and 30 cm ($P < 0.01$, $n = 3$ for each layer). There were no significant differences in the other layers. Total root biomass (both fine and coarse roots) had a similar pattern to that of the fine root biomass. The total root biomass of the young forest was less than that of the old forest at depths of 15–30 cm, but much greater in the first 15 cm. Overall, root biomass of the young forest was much greater than that of the old forest (Table 4). The total N and C contents of both the coarse and fine roots showed no statistical differences between stands (Table 5).

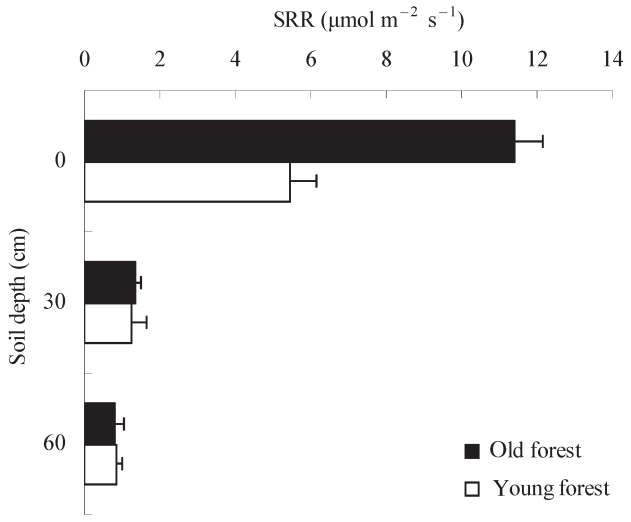

Figure 4. Soil respiration rate (SRR) at different depths in the young (17-year-old) and old (31-year-old) larch plantations. The vertical bars represent standard errors.

Relations to soil temperature and water availability

Rhizosphere respiration rate and SRR increased exponentially with soil temperature at 5-cm depth (Figure 5). However, RRR and SRR showed delayed responses to soil temperature, i.e., RRR and SRR reached their maxima in August, whereas the highest soil temperature occurred in July (Figures 1 and 2).

The Q_{10} values for soil respiration of the old and young forests were 3.94 and 3.70, respectively, whereas the corresponding values for rhizosphere respiration were 5.56 and 4.17. However, analysis of covariance showed no significant difference in Q_{10} between the stands or between rhizosphere and soil respiration of the same stand (for soil respiration: $P > 0.05$, $n = 9$; and for rhizosphere respiration: $P > 0.05$, $n = 8$). Although soil water content is a factor controlling rhizosphere and soil respiration, no significant relationships were observed in either stand (Table 6, Figure 6).

Discussion

By trenching to exclude roots, we were able to estimate rhizosphere respiration and calculate its contribution to total soil CO_2 efflux of larch plantations of different ages. The plantations were similar in soil type, site history, and soil C and N contents below 30 cm. However, other properties of soil such as C and N contents of the top 30 cm soil, organic matter and thickness of the humus horizon may have differed, because net primary production (Shi et al. 2001, Jiang and Zhou 2002), litterfall (Chen et al. 1998), root biomass (Table 4), microbial communities (Chen 2003) and decomposition rate (Liu and Li 1993) may change with development of larch forests.

Because the plantations are adjacent to one another and similar in several ways (e.g., soils), we can reasonably assume that the differences in respiration rate were a result of stand age, not of location; however, our experiment lacked stand-level replication, thus precluding an unequivocal conclusion. To minimize disturbance of roots and soil by trenching, we measured only four trenched plots in each plantation and, therefore, may have missed some spatial variability in SRR.

Rhizosphere respiration accounted, on average, for 25 and

Table 4. Means (± SE) of coarse root and fine root biomass at different soil depths in the young (17-year-old) and old (31-year-old) larch plantations.

Depth (cm)	Old			Young		
	Coarse roots (g m^{-2})	Fine roots (g m^{-2})	Total roots (g m^{-2})	Coarse roots (g m^{-2})	Fine roots (g m^{-2})	Total roots (g m^{-2})
0–5	40.27 ± 5.33	67.60 ± 8.00	107.87 ± 13.33	52.31 ± 7.00	161.44 ± 12.38	213.76 ± 19.38
5–10	42.97 ± 6.14	40.76 ± 5.13	83.74 ± 11.27	61.66 ± 8.08	140.47 ± 14.62	202.12 ± 22.70
10–15	25.14 ± 3.49	40.59 ± 4.90	65.73 ± 8.39	52.48 ± 6.03	84.50 ± 5.36	136.99 ± 11.39
15–20	20.98 ± 2.92	32.95 ± 3.99	53.93 ± 6.91	15.63 ± 2.10	18.00 ± 2.69	33.63 ± 4.79
20–25	5.40 ± 0.75	24.48 ± 1.85	29.87 ± 2.60	1.53 ± 0.35	11.89 ± 2.27	13.42 ± 2.62
25–30	3.04 ± 0.36	12.74 ± 1.89	15.78 ± 2.25	0.00	6.45 ± 1.28	6.45 ± 1.28
Total	137.80 ± 18.99	219.13 ± 25.76	356.93 ± 44.75	183.61 ± 23.56	422.76 ± 38.60	606.37 ± 62.16

65% of soil respiration in the old and the young forest, respectively; however, the range was greater than that (27–71%) in a secondary, deciduous, broad-leaved forest composed mainly of *Quercus crispula* Blume and *Betula ermanii* Cham in central Japan (Lee et al. 2003). Both RRR and its relative contribution to soil respiration were significantly higher in the young forest than in the old forest (Figures 2b and 3). A possible explanation for this difference is that more fine roots were produced in the young forest than in the old forest (Table 4). Also, on a mass basis, the respiration rate of fine roots is much higher than that of coarse roots (Pregitzer et al. 1998). Vogt et al. (1987) reported that fine root biomass of a 13-year-old *Pseudotsuga menziesii* (Mirb.) Franco stand is significantly higher than that of older stands. Smith and Resh (1999) found that the total root carbon allocation is significantly lower in older than in younger lodgepole pine (*Pinus contorta* Dougl. ex Loud.) forests, which might have resulted in higher RRR in the young forest because of increased substrate for respiration. Additional information (e.g., root turnover Grier et al. 1981) is needed to fully understand the mechanisms controlling rhizosphere respiration in relation to stand age.

Ewel et al. (1987) reported that soil respiration increased with tree age in slash pine (*Pinus elliottii* Engelm.) plantations, with higher belowground CO_2 efflux in the older plantation attributable to greater root activity. Pypker and Fredeen (2003) found the greatest cumulative seasonal belowground CO_2 efflux in 2- and 5-year-old cut blocks and the lowest cumulative seasonal belowground CO_2 efflux in new cut blocks (all cut blocks were replanted to hybrid spruce) and these differences paralleled the differences in aboveground biomass. However, Aikio et al. (2000) reported that soil respiration decreases when calculated on an area basis (as in our study), but increases on a per unit organic matter basis with succession of Scots pine (*Pinus sylvestris* L.) forests. We found no significant difference in SRR between the 17- and 31-year-old larch plantations, although BSRR increased with stand age, which might be associated with higher C and N contents in the top 30 cm of soil and well-developed microbial communities in the old forest (Chen 2003). As a stand ages, the contribution of bulk soil respiration to total soil respiration increases, whereas the contribution of rhizosphere respiration to total soil respiration decreases. Consequently, total soil respiration should be relatively unaffected by stand age.

Sensitivity of root and soil respiration to temperature is commonly expressed by the coefficient Q_{10}, which varies among ecosystems and across temperature ranges. Values of Q_{10} for rhizosphere respiration in our study were much higher than those reported for a variety of forests in North America (from 2.4 to 3.1; Burton et al. 2002), which were measured with a respiration cuvette attached to an infrared gas analyzer, as for O_2 consumption. Our Q_{10} values for soil respiration were within the range of 2.0–3.9 generally given for bulk soil respi-

Table 5. Means (± SE) of coarse root and fine root nitrogen and carbon contents (%) at different soil depths in the young (17-year-old) and old (31-year-old) larch plantations.

Element	Depth (cm)	Old		Young	
		Coarse root (%)	Fine root (%)	Coarse root (%)	Fine root (%)
Nitrogen	0–10	1.14 ± 0.23	1.77 ± 0.07	1.08 ± 0.13	1.68 ± 0.05
	10–20	0.94 ± 0.28	1.72 ± 0.02	1.02 ± 0.07	1.74 ± 0.09
	20–30	1.12 ± 0.15	1.52 ± 0.11	1.03 ± 0.11	1.58 ± 0.09
	All	1.07 ± 0.12	1.67 ± 0.05	1.04 ± 0.05	1.67 ± 0.05
Carbon	0–10	43.89 ± 1.79	40.94 ± 0.36	44.68 ± 0.48	39.40 ± 0.93
	10–20	44.19 ± 0.55	39.61 ± 2.21	43.87 ± 0.19	39.72 ± 0.21
	20–30	41.79 ± 0.45	39.66 ± 1.27	41.58 ± 0.34	37.37 ± 0.14
	All	43.29 ± 0.67	40.07 ± 0.77	43.38 ± 0.50	38.83 ± 0.46

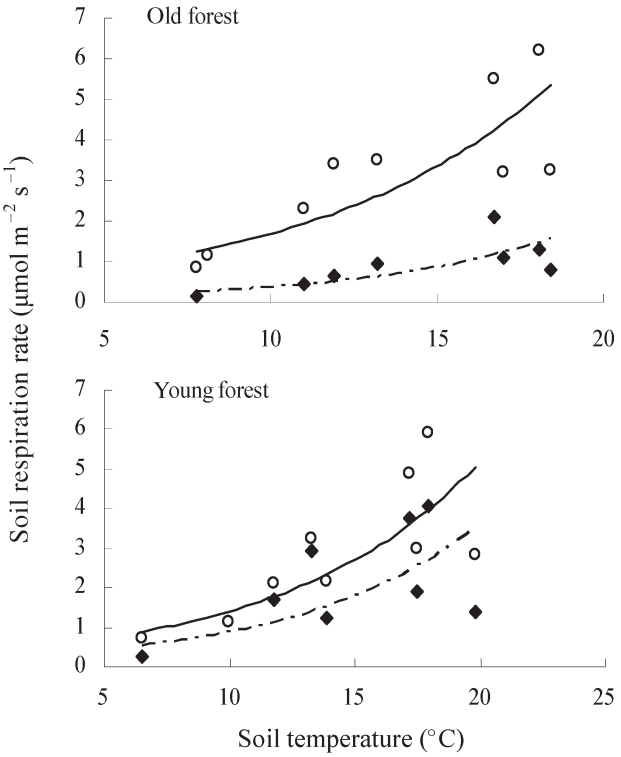

Figure 5. Temperature response curves of soil respiration and rhizosphere respiration in the young (17-year-old) and old (31-year-old) larch plantations. Temperature was measured at a depth of 5 cm. In the old forest, the fitted equation for soil respiration (○ and ——) is: $y = 0.43e^{0.14x}$, $r^2 = 0.74$, $n = 9$, $P < 0.005$; and the fitted equation for rhizosphere respiration (◆ and – —) is: $y = 0.07e^{0.17x}$, $r^2 = 0.70$, $n = 8$, $P < 0.01$. In the young forest, the fitted equation for soil respiration (○ and —) is: $y = 0.38e^{0.13x}$, $r^2 = 0.73$, $n = 9$, $P < 0.005$; and the fitted equation for rhizosphere respiration (◆ and – —) is: $y = 0.21e^{0.14x}$, $r^2 = 0.52$, $n = 8$, $P < 0.05$.

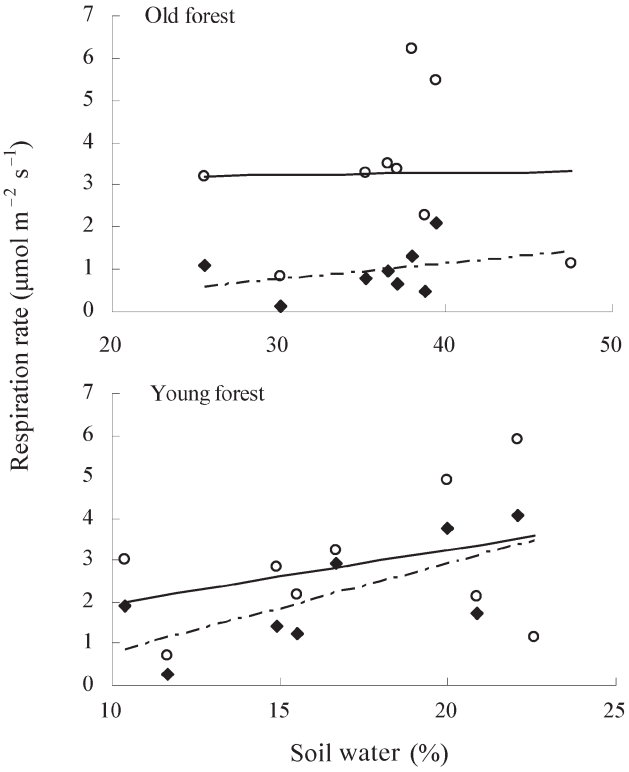

Figure 6. Relationships between soil water (%) and rhizosphere respiration rate and soil respiration in the young (17-year-old) and old (31-year-old) larch plantations. There was no significant correlation between soil water and rhizosphere respiration or soil respiration for either stand. Abbreviations and symbols: ○ and —— = soil respiration; ◆ and – –– = rhizosphere respiration.

ration, but they were high compared with the mid-point of this range (Buchmann 2000). However, previously reported Q_{10} values are based on the soda lime method, which may have underestimated CO_2 flux (and hence the Q_{10} values) when respiration rates were high (Davidson et al. 1998). Moreover, our slightly higher Q_{10} values for rhizosphere and soil respiration might be attributable to the cold climate in northeastern China (cf. Raich and Schlesinger 1992). Schlesinger and Andrews (2000) reported that the greatest response to elevated temperature (expressed by Q_{10}) was in samples of surface detritus and in soils in cold climates. Soil respiration has been found to change seasonally (e.g., Keith et al. 1997, Boone et al. 1998, Raich 1998, Koizumi et al. 1999, Luo et al. 2001). We found that total soil respiration also showed significant seasonal variation, and the seasonal patterns and soil respiration rates were similar to those in Japanese larch (*Larix kaempferi* (Lamb.) Carr.) (Wang et al. 2001).

Table 6. Changes in monthly means (± SE) of soil water (%) in the young (17-year-old) and old (31-year-old) larch plantations.

Month (year)	Old	Young
May (2001)	47.6 ± 1.6	22.6 ± 1.1
Jun (2001)	36.6 ± 1.3	15.5 ± 0.9
July (2001)	35.2 ± 1.2	14.9 ± 1.7
August (2001)	39.4 ± 2.5	20.0 ± 0.7
September (2001)	25.6 ± 2.6	10.4 ± 0.4
October (2001)	30.2 ± 2.3	11.7 ± 1.2
May (2002)	38.8 ± 1.3	20.9 ± 1.3
June (2002)	37.1 ± 4.2	16.7 ± 0.8
August (2002)	38.0 ± 3.6	22.1 ± 0.5

An exponential model has been widely used to describe the relationship between respiration rate and temperature (Ryan et al. 1995, Carey et al. 1996, Edwards and Hanson 1996, Lavigne and Ryan 1997, Luo et al. 2001, Euskirchen et al. 2003). Davidson et al. (1998) argued that soil temperature often accounts for a large fraction of seasonal variation in soil CO_2 efflux. We also observed exponential relationships between CO_2 efflux and soil temperature that explained most of the seasonal variation in rhizosphere and soil respiration. Another possible explanation for seasonal changes in soil respiration, especially rhizosphere respiration, is seasonal variation in substrate supply, for example, seasonal differences in the amount

of photosynthate transported belowground (Högberg and Ekblad 1996, Näsholm et al. 1998).

In contrast to soil temperature, soil water availability has varying effects on soil respiration (Edwards 1975, Orchard and Cook 1983, Euskirchen et al. 2003, Ma et al. 2004). Boone et al. (1998) found that soil respiration closely tracked seasonal soil temperature, but was unaffected by soil water availability. We obtained similar results. However, effects of soil water availability on rhizosphere and soil respiration were observed when respiration was measured at the same temperature but at varying soil water availabilities, which would explain the hysteresis we observed in rhizosphere and soil respiration responses to soil temperature. Hysteresis may have been associated with relatively low soil water in July compared with August, suggesting that increases in soil water promote rhizosphere and soil respiration at high soil temperatures. However, when soil temperature was low, an increase in soil water availability did not necessarily promote metabolic activities, and hence there was no effect on rhizosphere and soil respiration (e.g., in May 2001). This result supports the conclusions of Keith et al. (1997) and Ma et al. (2004) that a change in soil water content has a large effect on soil respiration only at high temperatures. Moreover, a burst of CO_2 in response to wetting of dry soil has also been reported in field experiments (e.g., Rochette et al. 1991, Bloem et al. 1992). The reason an increase in soil water availability promoted rhizosphere respiration in August may be attributable to intense root activity (e.g., root growth) in response to soil wetting, as suggested by Prokushkin et al. (2002).

Global concern over climate change has focused increasing attention on belowground CO_2 efflux, especially the partitioning of different respiration components. For this purpose, the traditional in situ trenching method has merits: it is simple, easy to control and measurements can be made over a long time. However, the trenching method causes disturbance to soil and roots and is limited by effects of trenching on root mortality, soil water and nutrient content and a shift of microbial energy source from exudates to detritus with consequent alterations in trophic interactions. Therefore, the disturbance caused by trenching should be carefully considered, and the components of the measured respiration should be carefully identified. By using a trenching method with these precautions, our study revealed that rhizosphere contribution to soil respiration was greater in a young forest than in an old forest (Figure 2b), suggesting that the interaction between climate change and forests may vary with forest age.

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