Variations in biomass, production and respiration of fine roots in a young larch forest

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Abstract

Root respiration (R_r) plays a crucial role in the global carbon balance, because R_r accounts for about a half of soil respiration in typical forest ecosystems. Plant roots are different in metabolism and functions according to size. Fine roots, which are typically defined as roots < 2 mm in diameter, perform important ecosystem functions and consequently govern belowground carbon cycles mainly because of their high turnover rates. However, the phenological variation of fine root functions is not well understood yet. To quantitatively examine the fine root functions, we adopted an approach to partition R_r into growth respiration (R_g) and maintenance respiration (R_m) using a modified traditional model, in which R_g was proportional to root production, and R_m was proportional to root biomass and exponentially related to soil temperature. We conducted a field experiment on soil respiration and fine root biomass and production over a year in a larch-dominated young forest developing on the bare ground after removing surface organic soil to parameterize the model. The model was significantly parameterized using the field data measured in such simplified field conditions, because we could control spatial variation in heterotrophic respiration and contamination from roots other than fine roots. The annual R_r of all roots was $94 \text{ g C m}^{-2} \text{ yr}^{-1}$ and accounted for 25% of total soil respiration on average. The annual R_r was partitioned into fine root R_g , fine root R_m and coarse root R_m by 30, 44 and 26%, respectively; coarse root R_g was presumed to be negligible. Fine root R_g and R_m varied according to the seasonal variations of fine root production and soil temperature, respectively; the contribution of fine root biomass was minor because of its small seasonality. The contribution of R_g to total fine root respiration was lower in the cold season with low production.

Key words: Fine root, Growth respiration, Maintenance respiration, Root respiration, Soil respiration

1. Introduction

Net ecosystem production (NEP) is the tiny balance of two huge CO_2 fluxes of gross primary production (GPP) and ecosystem respiration (RE). Soil respiration (R_s) accounts for 30–80% of RE on an annual basis in forest ecosystems (Davidson *et al.*, 2006) but typically 70% in temperate forests (Ryan and Law, 2005). On a global scale, R_s (98 Pg C yr^{-1} ; Bond-Lamberty and Thomson, 2010) accounts for about 80% of GPP (123 Pg C yr^{-1} ; Beer *et al.*, 2010). These facts indicate that R_s plays a crucial role in terrestrial carbon cycles.

The R_s is composed of autotrophic respiration (R_a) and heterotrophic respiration (R_h). The R_a is equivalent to respiration from roots (root respiration: R_r) using photosynthate and non-structural carbohydrates as substrate (NSC), whereas R_h is the microbial decomposition of soil organic matter (SOM) and carbohydrates derived from roots (Moyano *et al.*, 2009). The R_a

and R_h respond to temperature and moisture in a different manner (Scott-Denton *et al.*, 2005; Boone *et al.*, 1998). Thus, to examine the environmental response of R_s , R_s has been partitioned into R_r and R_h by root-exclusion methods, such as trenching (Sha *et al.*, 2021). In forest ecosystems, the ratio of R_r to R_s (R_r / R_s) ranged between 10 and 90% depending on vegetation types and seasons (Hanson *et al.*, 2000) but typically 45–50% (Subke *et al.*, 2006).

Roots are classified into non-woody fine roots and woody coarse roots by anatomical traits and physiological functions. Fine roots are physiologically active apexes of root branches and conventionally defined as thinner roots < 2 mm in diameter (e.g. Brunner *et al.*, 2013; Finér *et al.*, 2011). Fine roots absorb and transport water and nutrients, whereas coarse roots, which are $\geq 2 \text{ mm}$ in diameter, transport them and anchor and support their aboveground part. The net primary production (NPP) of fine roots is large and consequently accounted for 22% of global terrestrial NPP (McCormack *et al.*, 2015). In boreal forests, although fine root biomass accounted for only 16% of root biomass, 73% of all belowground NPP arose from fine root NPP (Yuan and Chen, 2010); fine root NPP can be an index of belowground NPP (Yuan and Chen, 2013). Because root turnover rates become faster as root diameter becomes thinner (Yuan and Chen, 2010), fine roots supply a large amount of litter to the soil together with labile exudate, which stimulate soil microbial activities and change soil carbon stock. Majority of soil carbon

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in forest ecosystems certainly results from fine root turnover (Richter *et al.*, 1999). The respiration rate normalized by dry matter was much higher from fine roots than from coarse roots (Makita *et al.* 2012; Rewald *et al.*, 2014). When the respiration rate was scaled up based on biomass data, stand-level respiration of fine roots accounted for 50–70% of R_s in plantations of acacia and eucalyptus (Chen *et al.*, 2009; Marsden *et al.*, 2008). Thus, fine roots are the most important component contributing to belowground carbon dynamics in forest ecosystems (Finér *et al.*, 2011). However, the function of fine roots in carbon cycles is not well understood yet (McCormack *et al.*, 2015), because the production and turnover of fine roots substantially depend on plant functional types and climates (Lambers *et al.*, 2008; Yuan and Chen, 2012). In addition, information is still lacking on belowground phenology (Abramoff and Finzi, 2015).

Fine root respiration has been frequently partitioned into growth (R_g) and maintenance (R_m) components (Amthor, 2000; McCree, 1974; Thornley, 1970; Penning de Vries, 1974), plus occasionally into ion uptake (R_i) (Chapin *et al.*, 2011; Johnson, 1990; Lambers *et al.*, 2008) to examine belowground phenology and predict root respiration using a simple model, in which R_g , R_m and R_i are proportioned to growth (production), biomass and nutrient uptake of fine roots, respectively. Terrestrial biosphere models, such as Biome-BGC, are adopting the partitioning model (Sun Q *et al.*, 2017). Although there is a criticism that the scientific basis is lacking in the quantitative division between R_g and R_m (Cannell and Thornley, 2000; Sweetlove *et al.*, 2013), experimental data indicate that the model is a valuable tool in understanding the carbon balance of plants and the ecological controls on plant respiration (Lambers *et al.*, 2008; Chapin *et al.*, 2011). The model has been parameterized and verified mostly based on laboratory experiment data taken in the controlled environment (e.g. Lambers *et al.*, 2008; M'Bou *et al.*, 2010). Only two studies from field experiments reported the partitioning of fine root respiration using the model (George *et al.*, 2003; Sun *et al.*, 2020). George *et al.* (2003) estimated annual values of R_g , R_m and R_i (due to nitrogen uptake) from a short-term chamber experiment and literature information. Sun *et al.* (2020) (our previous study) conducted a field experiment for more than a year in adjacent two mature forests: an evergreen spruce plantation and a larch-dominated deciduous forest. We quantified annual R_g and R_m and discussed their difference between the two forests. However, the results can have large uncertainty arising from field conditions, such as a high ratio of coarse roots, rich understory species in the deciduous forest and a high spatial variation in litter accumulation, root density and SOM especially in the deciduous forest, because the forests were mature at the age over 35 years and the deciduous forest was damaged by windthrow. These site conditions probably increased the spatial variation of R_h and the contamination from other roots than fine roots, which resulted in uncertainty in R_i separation from R_g and model parameterization. Although it is a challenge to substantially decrease uncertainty in field experiments, the following site conditions can improve data reliability: 1) homogeneity in tree age, 2) young forest with less litter accumulation and coarse roots, 3) no or little understory species, and 4) a small amount of SOM.

We measured soil CO₂ efflux and fine root dynamics from 2017 to 2018 in a young larch forest regenerating on the topsoil-removed bare ground to meet the above conditions. Using carefully measured field data, the objectives of this study are 1) to continuously separate fine root R_f from total R_s , 2) to robustly parameterize the partitioning model, 3) to partition the R_f into R_g and R_m using the model, and 4) to show the phenological variations of fine root respiration along with fine root production and biomass.

2. Material and Methods

2.1 Study site

A field experiment was conducted in a regenerating young forest dominated by Japanese larch (*Larix kaempferi*) with sparse Japanese white birch (*Betula platyphylla*) in Tomakomai national forest, southern Hokkaido, Japan (42°44.27'N, 141°31.42'E, 116 m above sea level by Google Earth). The study site was used to be a larch plantation established on volcanogenous regosol with a high water permeability but was severely destroyed by a windstorm due to a typhoon in 2004 (Sano *et al.*, 2010); all stems of both fallen and standing trees were removed, and then organic surface soil (A horizon) was scraped out together with stumps, coarse woody debris, litter accumulation, regenerating understory species and buried seeds in 2006. Because the B horizon is lacking, unweathered pumice stones (C horizon) have been exposed. Wind-blown seeds of larch and birch first germinated on the C horizon in a horizontal flat place in 2007 and have been growing despite poor nutrients. The site was located between two forests used for field experiments by Sun *et al.* (2020). The ground surface was sparsely covered with stunted ground vegetation dominated by red raspberry (*Rubus idaeus*). Aboveground biomass (AGB) of trees taller than 2 m was 16.7 and 20.9 t ha⁻¹, respectively, in 2017 and 2018, of which larch trees accounted for 65–67%. Tree density, tree height and diameter at 1.3 m height in 2018 were 3380 trees ha⁻¹, 4.27 ± 1.21 m and 3.9 ± 2.2 cm (mean ± 1 standard deviation (SD)), respectively. In 2016, bulk density, total carbon (C) concentration, total nitrogen (N) concentration and C/N ratio were 0.446 ± 0.042 g cm⁻³, 15.2 ± 13.8 g kg⁻¹, 0.742 ± 0.794 g kg⁻¹ and 24.5 ± 5.8 (mean ± 1 SD), respectively, for top 15-cm-thick fine soil (< 2 mm). The C concentration showed a decreasing tendency with a distance from tree stems according to the amount of leaf litter fall; the C concentration accounted for about 30% of that of a nearby mature larch-dominated forest studied by Sun *et al.* (2020).

Decadal mean annual air temperature and precipitation were 8.1 ± 0.3°C and 1346 ± 159 mm yr⁻¹, respectively, from 2010 to 2019 at a meteorological station (Tomakomai) 14 km apart from the study site. The highest and lowest monthly mean air temperatures in the same decade were 21.0°C in August and -3.9°C in January, respectively. Snow usually covers the ground for about four months between early December and early April.

2.2 Experimental design

Ten pairs of aluminum collars were installed in May 2017 around isolated larch trees. Six pairs of collars were set at 0.5 m (Near), and the others were set at 1.0 m (Far) from the target

larch stems. The other trees were more than 1.5 m away from collars. In each pair, two collars were set at a 0.4 m space on the bare ground without ground vegetation. Collars were 0.5 m × 0.5 m in size and inserted 3 cm deep into the soil. We trenched a collar (TC) of each pair in early July 2017 by inserting four PVC boards 20 cm deep into the soil around the collar to exclude root respiration. We found by eye from soil profiles that almost all roots appeared in the top 15 cm layer. The other collar (SC) was used for fine root sampling without trenching.

2.3 Soil CO₂ efflux

A field experiment was conducted at intervals of about three weeks between May 2017 and August 2018 with a six-month suspension from mid-November 2017 to mid-May 2018 mainly because of snow. Soil CO₂ efflux was manually measured on each collar with the same method as in Sun *et al.* (2017; 2020). Young plants germinating in collars were carefully pulled out before measurement, though it was rare. The measurement was conducted between 10:00 and 16:00 on each date with a portable closed-chamber system equipped with two 0.5-m-tall cubic chambers, an air pump, a datalogger (CR1000; Campbell Scientific Inc., Logan, UT, USA), a CO₂ analyzer (LI820; Li-Cor Inc., Lincoln, NB, USA), thermometers (MHP; Omega Engineering, Stanford, CA, USA) and a soil moisture sensor (SM150; Delta-T Device Ltd., Cambridge, UK). The datalogger was used to control the system and record data. CO₂ concentration in the chamber was measured every 5 s during chamber closing for 3 min. The CO₂ increasing rate was determined from the continuous data by the least squares method, and then soil CO₂ efflux was calculated from the increasing rate, chamber air temperature, air pressure and chamber height. Soil temperature (T_s) at a depth of 5 cm and volumetric soil water content (SWC) of the top 5-cm soil were measured immediately after the efflux measurement in each collar. Also, T_s at a depth of 6 cm and SWC at a depth of 3 cm were monitored at four points at a nearby station 150 m from the study site (Hirano *et al.*, 2017); we used the data measured at an open place where the C horizon was exposed like the study site.

After trenching in early July 2017, CO₂ efflux from TC (R_{TC}) corresponded to the sum of original R_b and CO₂ emissions through the decomposition of dead roots (R_{DR}) by trenching (Sha *et al.*, 2021). The method to estimate R_{DR} is described later. Meanwhile, CO₂ efflux from SC (R_{SC}) corresponded to total R_s . Although SC was disturbed by soil sampling, its effect on CO₂ efflux was insignificant because sampling area was negligible (Sun *et al.*, 2020). Thus, the sum of fine and coarse root respirations (R_r) was determined for each pair of collars, as $R_r = R_{SC} - (R_{TC} - R_{DR})$. Since the distance from a target larch tree was the same, two collars in a pair were expected to have similar root density and litter fall.

We applied the following simple exponential model to analyze the effect of T_s (°C) on soil CO₂ efflux (R_c , $\mu\text{mol m}^{-2} \text{s}^{-1}$) on each collar.

$$R_c = a \cdot \exp(b \cdot T_s) \quad (1)$$

where a and b are fitting parameters. From the temperature response parameter (b), we calculated Q_{10} , which is the factor by

which R_c increases with a 10°C temperature rise. In addition, the effect of SWC was analyzed using the temperature-normalized R_c at a base temperature (T_b).

$$R_b = R_c \cdot \exp(b \cdot (T_b - T_s)) \quad (2)$$

In this study T_b was set at 15°C, mean T_s for the snow-free season. Using the relationship of R_c with T_s and/or SWC, R_{SC} and R_{TC} were calculated half hourly on every collar from the monitoring data of T_s and/or SWC. Daily R_r was calculated for each pair from daily R_{SC} , R_{TC} and R_{DR} .

2.4 Decomposition of dead roots

We conducted a root litter bag experiment to determine the decay constant (k) (Gholz *et al.*, 2000; Silver and Miya, 2001; Sun *et al.* 2020). In June 2017, we collected topsoil to a depth of 15 cm from the total area of 1 m² and extracted fine roots from mixed soil samples with the same method as described later. The root samples were air-dried and weighed, and then some were oven dried. We determined the water content of air-dried samples from the dry weight and calculated the dry weight of air-dried samples. Air-dried samples corresponding to 0.48 g of dry weight were put into each 2-mm mesh bag of 10 cm × 10 cm in size. The sample amount was equivalent to measured root density. A total of 60 bags were buried at a depth of 10 cm at about 1 m from a larch stem in July 2017. Ten bags were collected six times until October 2018, and remaining samples were oven-dried and weighed. The k was determined by fitting the following equation (Wieder and Lang, 1982) to the data.

$$Y = Y_0 \cdot \exp(-k \cdot t) \quad (3)$$

where Y is the dry weight of remaining root samples in bags (g bag^{-1}) at elapsed time t (days), Y_0 the initial dry weight of root samples (0.48 g bag^{-1}) and k the decay constant (d^{-1}). As for the k of coarse roots, we used a reported value of $0.44 \times 10^{-3} \text{ d}^{-1}$ ($= 0.16 \text{ yr}^{-1}$) from a nearby larch-dominated forest (Sun *et al.*, 2020).

The R_{DR} ($\text{g C m}^{-2} \text{ d}^{-1}$) at elapsed time t (days) was calculated daily, separately for fine and coarse roots using the following equation.

$$R_{DR} = C_c \cdot (X_{t-1} - X_t) = C_c \cdot X_0 \cdot \exp(-k \cdot t) \cdot \{ \exp(k) - 1 \} \quad (4)$$

where C_c is the carbon concentration of roots (g g^{-1}), X_t the dry weight of remaining dead roots (g m^{-2}) at t and X_0 the initial dry weight of dead roots (g m^{-2}). For both fine and coarse roots, we used C_c of 0.484 g g^{-1} (Neumann *et al.*, 2020), which was the average value of fine roots in European forests. The X_0 of fine roots were set at 66 (Near) and 29 (Far) g m^{-2} , which were based on fine root biomass measured by soil core sampling from SC in July 2017. As for coarse roots, X_0 were determined to be 55 (Near) and 49 (Far) g m^{-2} from soil sampling down to 15 cm in May and September 2019.

2.5 Biomass and production of fine roots

The biomass and production of fine roots were measured by the same method as in Sun *et al.* (2020). Fine root biomass density (B_f , g m^{-2}) was measured by soil coring five times from July 2017 to August 2018 for about 14 months with a six-month suspension from mid-November 2017 to mid-May 2018. Soil

cores were extracted down to 15 cm with a stainless-steel edged tube with an inner diameter of 2.4 cm. We sampled three cores from each SC every time, using a perforated board for positioning. Sampling positions were randomly selected from a grid with 8 cm spacing and not reused. In total, the pit area by sampling amounted to 68 cm² for each SC, which accounted for only 2.7% of each collar area. Soil samples were put into PVC tubes and stored in a freezer, and then dispersed in a vat filled with tap water. Only living fine roots with a diameter < 2 mm were visually extracted, dried at 70°C for 48 hours and weighed. The fine roots should have originated from larch trees, because the other plants did not exist in the vicinity.

Fine root production rates (P_f , g m⁻² period⁻¹) were measured by the ingrowth core method (e.g. Vogt *et al.*, 1998) with plastic hair curlers wrapped in a 2 mm mesh sheet. The cores were 20 cm long and had a diameter of 2.3 cm. Air-dried fine soil, which was collected from the study site and sieved through 2 mm meshes, was put into the cores up to 15 cm. For each SC, three cores were inserted down to 15 cm into the pits made by soil core sampling, and three cores inserted previously were collected simultaneously with the core sampling. Collected ingrowth cores were put into PVC tubes and stored in a freezer, and then dry weight of fine roots was determined with the same method as described above. Fine roots penetrate root-free soil in ingrowth cores through meshes during a period between two sampling dates. Thus, the dry weight of fine roots in ingrowth cores corresponds to P_f . Also, annual fine root mortality (M_f , g m⁻² yr⁻¹) was calculated as a difference between annual P_f and an annual difference in B_f (ΔB_f) ($M_f = P_f - \Delta B_f$). We converted dry weight to carbon using a factor of 0.484. In addition, turnover rates were calculated as the ratio of annual P_f and mean B_f (Brunner *et al.*, 2013).

2.6 Partitioning root respiration

Originally, R_r was partitioned into R_g and R_m by the following equation (Amthor, 2000; Thornley, 1970).

$$R_r = R_g + R_m = g_R \cdot P_f + m_R \cdot B_f \quad (5)$$

where g_R is the growth respiration coefficient and m_R the maintenance respiration coefficient. We modified the equation as follows, considering field conditions.

$$\text{Model 1: } R_r = R_g + R_m = c \cdot P_f + d \cdot \exp(f \cdot T_s) \cdot (B_f + B_c) \quad (6)$$

$$\text{Model 2: } R_r = R_g + R_m = c \cdot P_f + \exp(f \cdot T_s) \cdot (d_f \cdot B_f + d_c \cdot B_c) \quad (7)$$

where c corresponds to g_R (g C g dry matter (DM)⁻¹), d the R_m of unit biomass at 0°C (g C g DM⁻¹ d⁻¹), f a temperature coefficient (°C⁻¹), B_c coarse root biomass (g m⁻²). In Model 2, d is separated into d_f for fine roots and d_c for coarse roots, considering the difference in respiration efficiency (Makita *et al.*, 2012; Rewald *et al.*, 2014). We added temperature effect on R_m in an exponential form, because temperature directly affects R_m (Moyano *et al.*, 2009; Thornley, 2011). Although tree survey suggested that coarse roots had grown during the study period, we assumed that the contribution of coarse roots to R_g was negligible because of no available data. However, we incorporated B_c into the second term on the assumption that coarse roots showed the same temperature response as fine roots.

We determined the parameters of c , d and f by curve fitting to measured data of R_r , P_f , T_s , B_f and B_c . For the fitting, mean daily R_r (g C m⁻² d⁻¹) for each period of core sampling intervals was used. The P_f was converted to daily value (g m⁻² d⁻¹). The B_f (g m⁻²) was a mean of two consecutive data measured at the beginning and the end of the period. The T_s (°C) was mean soil temperature for the period. The B_c was set at 55 and 49 g m⁻², respectively, at Near and Far positions, neglecting its seasonal variation. All the data were prepared from each pair of collars ($n = 10$) for each period ($n = 5$). In comparison with our previous study (Sun *et al.*, 2020), the data size for curve fitting increased considerably from five to 50 to obtain a robust result. In addition, we incorporated B_c in the second term, considering the temperature response of R_m of coarse roots and deleted a constant term (h), which represented the respiration of coarse roots and herbaceous roots.

2.7 Statistical analysis

We applied Student's t -test to compare two means, assuming homoscedasticity. Also, we applied two-way repeated measures ANOVA to test the effects of factors. The significance of curve fitting and parameters were tested using F -test and t -test, respectively. Uncertainties (± 1 SD) of annual R_g and R_m were estimated from those of the parameters and measurements using the law of error propagation. All the statistical analyses were conducted with a software package (Origin Pro 2015 J; Origin Lab Corporation, Northampton, MA, USA).

3. Results

3.1 Environmental conditions

We conducted a field experiment on fine root dynamics from July 2017 to August 2018. During the annual period between August 2017 and July 2018, mean air temperature and total precipitation were 7.7°C and 1425 mm at the Tomakomai meteorological station. The annual mean air temperature was low beyond the range of its decadal mean ± 1 SD ($8.1 \pm 0.3^\circ\text{C}$) between 2010 and 2019, whereas annual precipitation was within the decadal range (1346 ± 159 mm yr⁻¹). The T_s at a depth of 6 cm showed an obvious seasonal variation with the maximum of 27.4°C in mid-July 2017 and the minimum of -0.64°C in early December 2017 on a daily basis (Fig. 1a). Under snow cover, T_s was stable at $-0.26 \pm 0.14^\circ\text{C}$ between December and February. The SWC at 3 cm increased to 0.21 m³ m⁻³ in late November and rapidly decreased by soil freezing in December (Fig. 1b). In January and February, SWC was stable at 0.067 ± 0.005 m³ m⁻³, and then gradually increased in March with the thaw of frozen soil.

Soil temperature measured simultaneously with flux measurement was not significantly different between positions nor between treatments (Table 1). Meanwhile, SWC was significantly lower at Far positions ($p < 0.05$).

3.2 Soil CO₂ efflux

Soil CO₂ efflux (R_c) was measured three and 15 times, respectively, before and after trenching in early July 2017 (Fig. 2). Overall, R_c varied according to a seasonal variation in T_s (Fig. 1a). Before trenching, no significant difference was found between SC and TC in all pairs ($p > 0.05$), which suggested

Fig. 1. Temporal variations in daily means of soil temperature (T_s) at a depth of 6 cm (a) and volumetric soil water content (SWC) at a depth of 3 cm (b) measured at a nearby station 150 m from the study site from May 2017 to August 2018.

Fig. 2. Temporal variations in soil CO_2 efflux (R_c) in collars for root sampling (SC) and trenched collars (TC) at Near ($n = 6$) (a) and Far ($n = 4$) (b) from May 2017 to August 2018. Vertical bars denote 1 standard deviation. The dashed vertical lines denote the time of trenching.

Table 1. Soil temperature (T_s) at a depth of 5 cm and volumetric soil water content (SWC) of the top 5-cm soil measured in each collar immediately after CO_2 efflux measurement. Means (± 1 standard deviation) were shown in each cell. Two-way repeated measure ANOVA was applied.

Position	Treatment	T_s (°C)	SWC ($\text{m}^3 \text{m}^{-3}$)
Near	Control	20.4 ± 7.1	0.097 ± 0.024
	Trenched	19.5 ± 6.9	0.088 ± 0.018
Far	Control	20.7 ± 7.4	0.079 ± 0.022
	Trenched	19.8 ± 7.2	0.080 ± 0.016
ANOVA (p -value)	Position	0.89	0.018
	Treatment	0.65	0.44
	Interaction	0.99	0.36

that initial R_c was almost the same in each pair. Meanwhile, significant difference was found between the two collars in all pairs ($p < 0.05$) after trenching. Mean R_c after trenching was 2.41 ± 1.50 (SC) and 1.54 ± 1.11 (TC) $\mu\text{mol m}^{-2} \text{s}^{-1}$ at Near and 1.69 ± 0.90 (SC) and 1.30 ± 0.70 (TC) $\mu\text{mol m}^{-2} \text{s}^{-1}$ at Far. The R_c showed a significant positive exponential relationship

with T_s (Eq. 1) on each collar ($p < 0.05$). Figure 3 resulted from mean R_c on each measuring date after trenching. The Q_{10} values were 2.01 (SC) and 2.39 (TC) at Near and 1.58 (SC) and 1.62 (TC) at Far for T_s at a depth of 5 cm. In contrast, no significant linear nor curvilinear relationship was found between temperature-normalized R_c (R_b , Eq. 2) and SWC (data not shown). Thus, we estimate R_{SC} and R_{TC} half hourly for every pair of collars from T_s monitoring data using Eq. 1.

The result of the root litter bag experiment is shown in Fig. 4. A negative exponential equation (Eq. 3) was fitted to the data in 2017 and 2018 separately, because no change was measured in the winter between mid-November and mid-May. The k values before mid-November and after mid-May were 2.1×10^{-3} ($r^2 = 0.88$) and $1.7 \times 10^{-3} \text{d}^{-1}$ ($r^2 = 0.97$), respectively. We set k at 0 in the winter. If the equation is fitted to all data, k is calculated to be $0.44 \times 10^{-3} \text{d}^{-1}$ ($r^2 = 0.74$), which is equivalent to 0.36yr^{-1} .

Daily R_{DR} was calculated from the k values using Eq. 4, and then daily R_s (R_{SC}) was partitioned into R_h and R_r of all roots (Fig. 5). Since R_{SC} and R_{TC} were estimated from T_s , all respiration components varied according to the seasonal variation of T_s (Fig. 1). Under snow, R_s , R_h and R_r were stable at 0.61, 0.37 and 0.24 $\text{g C m}^{-2} \text{d}^{-1}$, respectively, at Near and 0.42, 0.33 and

Fig. 3. Relationship of soil CO₂ efflux (R_s) with soil temperature (T_s) in collars for root sampling (SC) and trenched collars (TC) at Near ($n = 6$) (a) and Far ($n = 4$) (b) from May 2017 to August 2018. An exponential curve (Eq. 1) was significantly fitted; r^2 values were shown.

Fig. 4. Temporal variation in fine root litter left in root litter bags (remainder ratio) from July 2017 to October 2018. Means (± 1 standard deviation) were plotted ($n = 10$). A negative exponential equation (Eq. 3) was separately fitted to data in 2017 and 2018. No change was found in fine root litter between mid-November 2017 and mid-May 2018 (dashed line).

0.08 g C m⁻² d⁻¹, respectively, at Far, which indicates that the ratios of R_r to R_s were 0.39 and 0.19, respectively, at Near and Far under snow. The R_m of coarse roots (R_{m_coarse}) was calculated using Eq. 6. Thus, the difference between R_r and R_{m_coarse} correspond to R_r of fine roots, which were 0.20 and 0.04 g C m⁻² d⁻¹, respectively, at Near and Far under snow. Annual CO₂ efflux was calculated between August 2017 and July 2018 (Table 2). All the CO₂ effluxes were larger at Near than at Far, though only R_{SC} was significantly different ($p < 0.05$). The ratios (Far / Near) of R_{SC} (R_s), R_h and R_r were 0.63, 0.83 and 0.28, respectively. The R_{DR} accounted for 3% of R_s at both positions. The R_r accounted for 37 and 16% of R_s , respectively, at Near and Far.

Similarly, measured R_{CS} was partitioned into R_h and R_r for each collar pair. The R_h and R_r significantly responded to T_s ($p < 0.05$) according to Eq. 1. The Q_{10} values of R_h and R_r were 2.02 ± 1.28 and 2.01 ± 1.21 (mean ± 1 SD), respectively, at Near ($n = 6$) and 2.15 ± 1.20 and 2.14 ± 1.29 , respectively, at Far ($n = 4$). No significant difference was found between R_h and R_r at both positions.

Fig. 5. Temporal variations in mean daily soil respiration (R_s), heterotrophic respiration (R_h), root respiration (R_r) and coarse root maintenance respiration (R_{m_coarse}) at Near ($n = 6$) (a) and Far ($n = 4$) (b) calculated from the monitoring data of soil temperature (T_s) between August 2017 and July 2018.

3.3 Biomass and production of fine roots

Fine root biomass (B_f) at Near showed a small peak in early September 2017, and then tended to increase from November until late August 2018 (Fig. 6a). Similarly, B_f at Far showed an increasing tendency in the warm season. In contrast, fine root production (P_f) showed a clear seasonal variation both at Near and Far (Fig. 6b); it decreased during the fall and increased during the late spring and summer. In the cold season between mid-November and mid-May, including the snowy season for about four months, P_f was small at 0.035 ± 0.018 and $0.043 \pm 0.041 \text{ g m}^{-2} \text{ d}^{-1}$, respectively, at Near and Far. The P_f showed a significant exponential relationship ($p < 0.05$) with T_s at a depth

of 5 cm in the same form as Eq. 1 (Fig. 7a), which resulted in Q_{10} values of 4.48 and 2.51, respectively, at Near and Far. The high Q_{10} of 4.48 reflects a large seasonal variation in P_f at Near (Fig. 6b). Also, B_f showed a significant exponential relationship ($p < 0.05$), though Q_{10} values were lower with 1.08 and 1.49, respectively, at Near and Far. A significant linear relationship with a slope of 1.20 ($r^2 = 0.43$, $p < 0.001$) was found between R_f and P_f , regardless of positions (Fig. 8a). The relationship between R_f and B_f was also significant ($r^2 = 0.33$, $p < 0.01$) (Fig. 8b), whereas P_f was not significantly correlated with B_f ($p > 0.10$). Annually, P_f ($p < 0.05$) and mean B_f ($p < 0.01$) were significantly larger at Near than Far, whereas the turnover rate

Table 2. Annual soil respiration (R_{SC} or R_s), soil CO_2 efflux in trenched collars (R_{TC}), CO_2 emissions through dead root decomposition in trenched collars (R_{DR}), heterotrophic respiration (R_h) and root respiration (R_r) ($\text{g C m}^{-2} \text{ yr}^{-1}$) at Near ($n = 6$) and Far ($n = 4$). Means (± 1 standard deviation) were shown. Numbers in parentheses denote percentages against R_{SC} .

Position	R_{SC} (R_s)	R_{TC}	R_{DR}	R_h	R_r
Near	493 ± 111 (100)	326 ± 75 (66)	13 (3)	313 ± 75 (63)	181 ± 123 (37)
Far	311 ± 68 (100)	269 ± 79 (86)	8 (3)	261 ± 79 (84)	51 ± 34 (16)

Fig. 6. Temporal variations in fine root biomass (B_f) (a) and fine root production (P_f) (b) at Near ($n = 6$) and Far ($n = 4$) from July 2017 to August 2018. Means (± 1 standard deviation) were shown.

Fig. 7. Relationships of fine root production (P_f) with soil temperature (T_s) (a) and fine root biomass (B_f) with soil temperature (T_s) (b) at Near ($n = 6$) and Far ($n = 4$). Soil temperature was averaged for each interval of root sampling. Means (± 1 standard deviation) were plotted. An exponential curve (Eq. 1) was significantly fitted.

Fig. 8. Relationship of root respiration (R_r) with fine root production (P_r) (a) or fine root biomass (B_r) (b) at Near and Far. Root respiration was averaged for each interval of root sampling. A significant regression line was drawn for each scatter plot.

Table 3. Annual values of fine root production (P_r), annual increase in fine root biomass (ΔB_r), fine root mortality (M_r), mean fine root biomass (B_r) and fine root turnover rates at Near ($n = 6$) and Far ($n = 4$). Means (± 1 standard deviation) were shown.

Position	P_r ($\text{g m}^{-2} \text{y}^{-1}$)	ΔB_r ($\text{g m}^{-2} \text{y}^{-1}$)	M_r ($\text{g m}^{-2} \text{y}^{-1}$)	Mean B_r (g m^{-2})	Turnover rate (y^{-1})
Near	81 ± 22	12 ± 33	93 ± 47	70 ± 21	1.27 ± 0.57
Far	41 ± 10	4 ± 5	46 ± 10	13 ± 5	3.26 ± 1.45

Table 4. Fitting parameters of Eqs. 6 and 7 (± 1 standard error) with significance (p value).

	Model 1 (Eq. 6)		Model 2 (Eq. 7)	
	Parameter	p value	Parameter	p value
c (g C g DM^{-1})	0.57 ± 0.22	0.012	0.58 ± 0.24	0.020
d ($\text{g C g DM}^{-1} \text{d}^{-1}$)	0.0021 ± 0.00087	0.022		
d_f ($\text{g C g DM}^{-1} \text{d}^{-1}$)			0.0021 ± 0.00097	0.040
d_c ($\text{g C g DM}^{-1} \text{d}^{-1}$)			0.0020 ± 0.0018	0.28
f ($^{\circ}\text{C}^{-1}$)	0.054 ± 0.021	0.016	0.054 ± 0.022	0.018
Adjusted r^2	0.59		0.58	
p value	< 0.001		< 0.001	

($p < 0.01$) was significantly lower at Near (Table 3).

3.4 Partitioning of root respiration

Model 1 and 2 (Eqs. 6 and 7) were significantly fitted to the data set ($p < 0.001$) with an adjusted r^2 of 0.59 and 0.58, respectively (Table 4). In Model 2, d_f and d_c were almost the same, probably because fixed values were assigned as B_c to Near and Far, respectively, neglecting the spatial variation of B_c . In addition, d_c was not significant ($p = 0.28$). Thus, although the performances of the two models were almost the same, we adopted Model 1 (Eq. 6) to partition R_r .

The Q_{10} calculated from the parameter f was 1.7. Annual R_r was partitioned into R_g and R_m using the fitting parameters (Table 5). At Near, R_g of fine roots, R_m of fine roots and R_m of coarse roots accounted for 26, 57 and 17% of their sum (estimated R_r), respectively. The bias between R_r from Table 2 and the estimated R_r was zero. Meanwhile, R_g , fine root R_m and coarse root R_m accounted for 34, 27 and 39% of their sum at Far;

Table 5. Annual sums ($\text{g C m}^{-2} \text{yr}^{-1}$) of root respiration (R_r) from Table 2, fine root growth respiration (R_g), fine root maintenance respiration (R_{m_fine}), coarse root maintenance respiration (R_{m_coarse}) and the sum of R_g , R_{m_fine} and R_{m_coarse} (Sum) at Near ($n = 6$) and Far ($n = 4$), which corresponds to R_r . Values at Near and Far were spatially averaged with a weight of circumference: 3.14 and 6.28 m for Near and Far, respectively (weighted average). Means (± 1 standard deviation) were shown. Numbers in parentheses denote percentages against Sum.

	Near	Far	Weighted average
R_r	181 ± 123	51 ± 34	94
R_g	47 ± 12 (26)	24 ± 3 (34)	32 (30)
R_{m_fine}	104 ± 31 (57)	19 ± 4 (27)	47 (44)
R_{m_coarse}	30 (17)	27 (39)	28 (26)
Sum	181 ± 32 (100)	70 ± 4 (100)	107 (100)

the bias was $19 \text{ g C m}^{-2} \text{ yr}^{-1}$ (37%). The larger bias at Far was partly due to a smaller number of replications at Far ($n = 4$) than at Near ($n = 6$). The R_g and fine root R_m were significantly larger at Near ($p < 0.05$). In addition, the respirations were spatially averaged with a weight of circumference: 3.14 and 6.28 m for Near and Far, respectively. As a result, R_g , fine root R_m and coarse root R_m accounted for 30, 44 and 26% of the total R_t on average in a circumferential area between 0.5 and 1.0 m in radius.

The R_g varied seasonally in parallel with P_f (Figs. 6b and 9), whereas R_m varied mainly according to a seasonal variation in T_s (Figs. 1 and 9). The contribution of R_g to fine root R_t ($= R_g / (R_g + \text{fine root } R_m)$) was larger at Far with 0.39 in the cold season and 0.59 on average in the warm season than at Near with 0.10 and 0.35, respectively (Fig. 9c).

4. Discussion

We had measured fine root dynamics and soil CO_2 efflux simultaneously within the same collar over a year in adjacent larch-dominated deciduous (DF) and evergreen conifer (EF) forests and quantified annual R_g and R_m of tree fine roots on an annual basis using a multiple regression model (Sun *et al.*, 2020). However, the results would include considerable uncertainty because of relatively complex experimental conditions in the field, which arose from forest maturity and rich understory species. The mature forests were relatively rich in SOM, litter

accumulation and roots. Thus, the forests had a large spatial variation in R_h originating from SOM and litter accumulation. The large spatial variation made it difficult to separate R_s into R_h and R_t in each pair of collars, because R_h was not presumed to be identical even in two neighboring collars. Consequently, representative R_t was determined from the averages of R_s and R_h in each forest, resulting in a small number of available data for curve fitting ($n = 5$). In addition, the DF had canopy gaps caused by a windstorm, and consequently was rich in herbaceous plants. Thus, in the mature forests, a good portion of R_t originated from coarse roots and herbaceous roots, not fine roots targeted for the study.

In this study, we conducted a similar field experiment over a year in a larch-dominated young forest developing on the bare ground after removing surface organic soil along with coarse woody debris to obtain robust results by simplifying experimental conditions and improving the model. The study site was poor in SOM and litter accumulation. Soil C concentration was about 30% of that in DF and showed a decreasing tendency with a distance from tree stems, which was probably caused by the gradient of litter fall. Thus, we believe that R_h was almost equal in each pair by setting two collars on a concentric fashion from an isolated larch tree, which was supported by the fact that R_s was not significantly different in each pair before trenching (Fig. 2). Coefficients of variance (CV) in annual

Fig. 9. Temporal variations in fine root growth respiration (R_g) and maintenance respiration ($R_{m_{\text{fine}}}$) at Near (a, $n = 6$) and Far (b, $n = 4$), and the ratio of R_g to the sum of R_g and R_m (c) from July 2017 to August 2018. Means (± 1 standard deviation) were shown.

R_h were 24 and 30%, respectively, at Near and Far (Table 2), which were smaller than those of DF (59%) and EF (39%). The small CV also supported the smaller spatial variation in R_h . As a result, we were able to calculate R_t in each pair and prepare 50 data sets in total for curve fitting. By separating positions into Near (0.5 m) and Far (1.0 m), we were able to use a wide range of data and make significant fitting (Table 4). In addition, understory vegetation was very scarce, and the density of coarse roots (≥ 2 mm) was low with 55 and 49 g m⁻², respectively, at Near and Far. The contribution of fine roots to total R_t was large at 83% at Near (Table 5), whereas it was 45% and 68%, respectively, at DF and EF. In our previous study (Sun *et al.*, 2020), the large R_t of coarse roots and herbaceous roots (55 and 32%) were treated as a residual without seasonality. In this study, we related coarse root biomass (B_c) with T_s to estimate R_m (Eq. 6). Since root density was low (Table 3), CO₂ emissions through dead root decomposition (R_{DR}) was also small at 13 and 8 g C m⁻² yr⁻¹, respectively, at Near and Far (Table 2), which accounted only 3% of R_s . The small R_{DR} contributed to decrease uncertainty in estimating R_h ($= R_{TC} - R_{DR}$) and consequently R_t . Moreover, although trenching decreases SWC owing to lack of water uptake by roots (Subke *et al.*, 2006; Sun *et al.* 2020), no significant SWC decrease was found in trenched collars (Table 1). Thus, the effect of SWC change was negligible.

We improved the reliability of partitioning fine root respiration, as described above. However, there is still uncertainty. Although the temperature response of coarse root R_m was incorporated into the model (Eq. 6) on the assumption that the temperature coefficient (f) was the same as that of fine root R_m , inter-collar difference in B_c was not considered using a fixed B_c for all collars at each position. The R_g of coarse roots was also ignored, whereas an annual tree survey using allometric equations suggested an annual coarse root growth of 76 g m⁻² yr⁻¹. The B_c was calculated to be 276 g m⁻² in 2017 and 352 g m⁻² in 2018 for larch trees, accounting for 79% of all coarse root biomass. In this study, B_c was 55 and 49 g m⁻², respectively, at Near and Far, which were only 14–20% of the tree survey result. The reasons for the small B_c are that biomass within 0.5 m from trees was not included, and that soil samples were taken round isolated larch trees. Wieser and Bahn (2004) continuously measured the coarse root R_t of *Pinus cembra* and reported that R_m accounted for 73–80% of the sum of R_m and R_g . Using the percentage, the R_g of coarse roots was roughly estimated from coarse root R_m to be 6–8 and 5–7 g m⁻² yr⁻¹, respectively, at Near and Far, which accounted for about 15% (Near) and 25% (Far) of fine root R_g (Table 5). In addition, we did not consider the respiration for ion uptake (R_i). However, R_i is expected to correlate with photosynthesis (Lambers *et al.*, 2008), and fine roots are mainly produced using recent photosynthate (Lynch *et al.*, 2013). Also, the seasonal pattern of P_f (Fig. 6b) is similar to that of GPP of the larch plantation that existed in the study site before a windstorm (Hirano *et al.*, 2003; Hirata *et al.*, 2007). Thus, R_i would be included in R_g , because R_g was proportionate to P_f .

Since the study site was a young forest with a small amount of soil carbon, litter accumulation and roots, soil CO₂ efflux was considerably smaller than those of adjacent forests. For example,

annual values of P_f , mortality (M_f) and mean B_f at Near were 22, 26 and 30% of those in DF, respectively (Table 3). As a result, annual R_s and R_t at Near was 39 and 29% of those in DF (Table 2). In contrast, annual R_h at Near accounted for 74% of that in DF, even though soil carbon concentration was only 30% of that in DF. The larger R_h than expected from carbon concentration was probably due to a difference in the decomposability of SOM. Older SOM in DF could have more recalcitrant fractions (Ryan and Law, 2005). The ratio of R_t to R_s was 37% at Near (Table 2) and 48% in DF, which is consistent with the fact that the contribution of R_t decreases as R_s increases (Subke *et al.*, 2006). The growth respiration coefficient (g_R) of 0.57 g C g DM⁻¹ is equivalent to 48 mmol CO₂ g DM⁻¹ and almost doubles those in DF and EF (Table 4). Meanwhile, the maintenance respiration coefficients (g_m), which is equivalent to $d \cdot \exp(f \cdot T_s)$, were 2.6, 4.6 and 7.8 nmol CO₂ g DM⁻¹ s⁻¹ at 5, 15 and 25°C, respectively. Although the g_m at 25°C was equal to that in DF, g_m was 2–3 times higher at 5 and 15°C, because the base coefficient (d) was much higher but the temperature coefficient (f) was lower than those in DF. In comparison with previous studies conducted in the field for *Pinus taeda* and *Liquidambar styraciflua* (George *et al.*, 2003) and in a greenhouse for eucalyptus cuttings (M'Bou *et al.*, 2010), the g_R and g_m of this study were about ten times higher and slightly lower, respectively. The variation in the coefficients is mainly due to differences in species, environmental conditions and methods (Lambers *et al.*, 2008).

The Q_{10} values calculated from a seasonal variation in soil CO₂ efflux was reported to be higher in R_t than in R_h (Boone *et al.*, 1998; Wang *et al.*, 2010), because it is confounded with root phenology like in Figs. 6 and 7. Wang *et al.* (2010) also reported that the mean Q_{10} values from 13 forest sites were 3.40 and 2.42, respectively, for R_t and R_h . In this study, the Q_{10} of R_t was about 2.0 and was equivalent to that of R_h . We think that the lower Q_{10} of 2.0 was quite possible, because it was a combined result of the apparent Q_{10} values of P_f (4.48 and 2.51), B_f (1.08 and 1.49) (Fig. 7) and R_m (1.7) (Eq. 6). However, uncertainty might be large in Q_{10} calculation, because CO₂ efflux data at low temperatures were insufficient; Q_{10} is sensitive to data at low temperatures.

Soil CO₂ efflux was continuously estimated from the monitoring data of T_s (Fig. 1) using an exponential equation (Eq. 1). Although constant R_s of 0.61 and 0.42 g C m⁻² d⁻¹ were shown during the snowy season in Fig. 5, the R_s might be a little overestimated in comparison with winter R_s (0.5 g C m⁻² d⁻¹) measured under snow in an undisturbed deciduous forest about 5 km apart from the study site (Hirano, 2005). The overestimation was probable caused by uncertainty of the parameters of Eq. 1 (Fig. 3), because data were lacking at low temperatures (< 10°C). In the dormant season, roots respire using NSC accumulated during the previous growing season (Furze *et al.*, 2019; Collalti *et al.*, 2020). Small P_f of about 0.04 g m⁻² d⁻¹ was measured both at Near and Far in the cold season from mid-November to mid-May (Fig. 6b). Although some studies reported fine root growth in winter (Radville *et al.*, 2016), the P_f might include spring P_f after snowmelt in early April. The R_g and R_m of fine roots showed obvious seasonal variations (Fig. 9), reflecting the seasonality of P_f and T_s , respectively. At Near, R_g was smaller than R_m throughout a year, whereas R_g was

slightly larger in the warm season at Far (Fig. 9c). The difference between Near and Far was caused by different turnover rate of fine roots ($= P_f / \text{Mean } B_f$) (Table 3), though the turnover rate at Far had a large SD. The contribution of R_g to R_t increases with increasing turnover rate.

5. Conclusions

In comparison with our previous study, we decreased the number of parameters and incorporated the maintenance respiration of coarse roots in the model for partitioning. Moreover, we simplified the experimental conditions in the field and controlled spatial variation in heterotrophic respiration and contamination from roots other than fine roots. The improvement decreased uncertainty in experiments and considerably increased data size available for model parametrization. As a result, we succeeded in significant partitioning of root respiration into growth and maintenance respirations of fine roots. Also, we quantified the seasonal variation of the growth and maintenance respirations. To improve the partitioning further, spatial variation in coarse root density should be considered, and more frequent measurement of fine root dynamics is given priority.

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