



Title	Partitioning of root respiration into growth, maintenance, and ion uptake components in a young larch-dominated forest
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1 Title: Partitioning of root respiration into growth, maintenance, and ion uptake components in a young
2 larch-dominated forest

3

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13

14 **Abstract**

15 *Purpose:* Fine roots play an essential role in global carbon cycles, but phenological variations in root
16 function and metabolism are poorly understood. To illustrate the dynamics of fine root function and
17 metabolism in the field, we partitioned root respiration (R_r) into growth (R_g), maintenance (R_m), and ion
18 uptake (R_{ion}) components using a modified traditional model.

19 *Methods:* A year-round experiment was conducted in a young larch-dominated forest regrowing on bare
20 soil. Soil respiration was measured with a chamber method and partitioned into R_r and heterotrophic
21 respiration by trenching. Fine root biomass and production were measured simultaneously. Using the
22 field data, the model was parameterized, and R_r was further partitioned.

23 *Results:* Annually, R_r (210–253 g C m⁻² yr⁻¹) accounts for 45–47% of the total soil respiration. The
24 contribution of fine root R_g , fine root R_m , coarse root R_m , and fine root R_{ion} were 26–40, 46–51, 10–16,
25 and 12%, respectively. The R_g contribution showed a clear seasonal variation, with a peak in mid-spring
26 and a minimum in early fall, mainly because of different seasonality between fine root production and
27 soil temperature.

28 *Conclusion:* The model parameters were consistent with those from our previous study conducted by
29 the same method in the same site. Thus, we believe that our approach was robust under a relatively
30 simple condition. However, our growth respiration parameter resulting from only field data was much
31 higher than those from laboratory experiments. To further improve our understanding of root respiration,
32 more field data should be accumulated.

33

34 **Keywords:** Chamber, fine root, root biomass, root production, sap flow, soil respiration

35

36 **1. Introduction**

37 Soil respiration (R_s) is composed of autotrophic respiration by plant roots (R_r) and heterotrophic
38 respiration (R_h) by soil microorganisms and fauna. R_r corresponds to mycorrhizosphere respiration
39 consisting of living root, rhizomicrobial, and mycorrhizal respiration. R_h is equivalent to the
40 decomposition of soil organic matter (SOM) and root litter by soil microbes (Kuzyakov 2006; Moyano
41 et al. 2009). The global annual R_r was reported to be approximately 44 Pg C yr⁻¹ (Tang et al. 2019),
42 which is approximately fourfold greater than anthropogenic carbon emissions (Friedlingstein et al. 2020).
43 The contribution of R_r to R_s varies from 10 to 90% in forest ecosystems (Hanson et al. 2000) but is
44 typically 45–50% annually (Subke et al. 2006). Because R_r and R_h respond differently to environmental
45 factors, such as temperature and water content (Boone et al. 1998; Lavigne et al. 2004; Scott-Denton et
46 al. 2006), R_s should be partitioned into two components to understand ecosystem-scale carbon cycling.

47 Plant root systems are composed of fine and coarse roots that serve contrasting functions. Fine roots,
48 commonly defined as roots thinner than 2 mm in diameter (Brunner et al. 2013; Finér et al. 2011b),
49 absorb water and nutrients from the soil. Despite their small biomass, fine roots have a large net primary
50 production (NPP), accounting for 22% of terrestrial NPP (McCormack et al. 2015a) because of their fast
51 turnover rates (Brunner et al. 2013; Finér et al. 2011b). Thus, fine roots play a dominant role in
52 belowground carbon cycling (Finér et al. 2011b; Richter et al. 1999). Although fine root phenology
53 strongly influences belowground carbon dynamics, seasonality and variability in fine root function are
54 poorly understood (Abramoff and Finzi 2015; McCormack et al. 2014; Radville et al. 2016).

55 Autotrophic respiration is further separated into growth (R_g) and maintenance (R_m) components
56 (Amthor 2000; McCree 1974; Penning de Vries 1974; Thornley 1970) and sometimes into an ion uptake
57 component (R_{ion}) for fine root respiration (Chapin et al. 2011; Johnson 1990; Lambers et al. 2008) using
58 a conceptual model. In the model, R_g , R_m , and R_{ion} were linearly correlated with growth (production),
59 biomass, and ion uptake, respectively. However, the model has been criticized for its weak scientific
60 basis in quantitative partitioning into R_g and R_m (Cannell and Thornley 2000; Sweetlove et al. 2013;
61 Thornley 2011), although experimental results indicate that the model is useful for understanding
62 ecological control of autotrophic respiration (Chapin et al. 2011; Lambers et al. 2008). Most terrestrial
63 biosphere models do not explicitly incorporate root respiration because of a lack of mechanistic

64 respiration models (Collalti et al. 2020; Hopkins et al. 2013; Sweetlove et al. 2013; Warren et al. 2015).
65 Respiration is frequently estimated from other processes using correlation (Sweetlove et al. 2013), and
66 important processes contributing to respiration have been oversimplified (Ballantyne et al. 2017). The
67 partitioning model is effective for understanding and quantifying intrinsic processes, such as acclimation
68 to warming.

69 The partitioning model has been applied to R_r measured through laboratory experiments in
70 controlled environments (Lambers et al. 2008; Thongo M'Bou et al. 2010). In the field, (George et al.
71 2003) partitioned R_r into R_g , R_m , and R_{ion} (nitrogen uptake), based on laboratory data and a short-term
72 field experiment. (Sun et al. 2020) conducted a year-round experiment in two mature forests and
73 estimated annual R_g and R_m . Because experimental conditions in the field are complex, especially in
74 mature natural forests, the uncertainty in partitioning should be large. To decrease the uncertainty, (Cui
75 et al. 2021) conducted an experiment in a young forest regenerating on bare soil in relatively simple
76 conditions resulting from homogeneous tree age, little litter accumulation, limited coarse roots, little
77 ground vegetation, and poor SOM. However, their study's spatial replication was small ($n = 10$), and
78 R_{ion} was ignored. More field data are indispensable for the robustly parameterization and verification of
79 the partitioning model. Thus, a field experiment was conducted at the same site as (Cui et al. 2021). We
80 increased the number of replications and added R_{ion} as a respiratory component. The objectives of this
81 study were 1) to modify the partitioning model including R_{ion} , 2) to robustly parameterize the modified
82 model using a large size of field data, 3) to quantitatively partition R_r into R_g , R_m , and R_{ion} , and 4) to
83 show the seasonal variations of the R_r components.

84

85 **2. Material and Methods**

86 **2.1. Study site**

87 An experiment was conducted in a young forest in Hokkaido, Japan (42°44.27'N, 141°31.42'E, 116
88 m above sea level), which was the same site as (Cui et al. 2021). The forest was dominated by Japanese
89 larch (*Larix kaempferi*) and dotted with Japanese white birch (*Betula platyphylla*). The site was used as
90 a mature larch plantation growing on volcanogenous regosol but was severely damaged by a windstorm
91 in 2004 (Sano et al. 2010). All tree stems were removed in 2005. In 2006, a thin layer of organic topsoil

92 (A horizon), coarse woody debris, stumps, accumulated litter, regenerating ground vegetation, and
93 buried seeds were removed. As a result, volcanic pumice stones (C horizon) were exposed because B
94 horizon was originally lacking. Wind-blown larch seeds germinated in 2007. The ground was sparsely
95 covered with understory species. Aboveground biomass of trees taller than 2 m was 27.3 ± 12.9 and 32.8
96 ± 9.8 t ha⁻¹ (mean \pm standard deviation (SD) of three plots of 20 m \times 20 m) in September 2019 and
97 September 2020, respectively, of which larch accounted for 82% and 87%, respectively. Belowground
98 biomass of larch coarse roots was 4.50 ± 2.10 and 5.57 ± 1.75 t ha⁻¹ in the respective years. Tree biomass
99 was estimated from diameter at breast height (DBH) using allometric equations (Yazaki et al. 2016).
100 Soil bulk density, total carbon (C) and nitrogen (N) concentrations were 0.446 ± 0.042 g cm⁻³, $15.2 \pm$
101 13.8 g kg⁻¹, and 0.742 ± 0.794 g kg⁻¹ (mean \pm SD, $n = 32$) for the top 15 cm fine soil layer (< 2 mm) in
102 2016. Soil C concentration decreased with distance from tree stems, mainly because of decreasing litter
103 fall with distance.

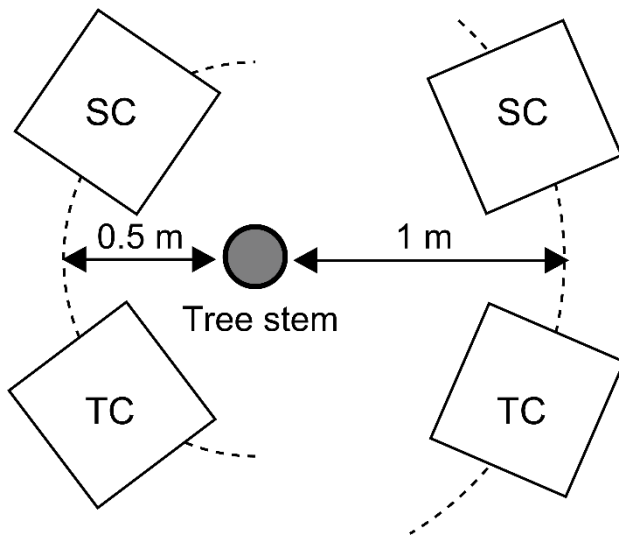
104 Mean annual air temperature and precipitation were $8.1 \pm 0.3^\circ\text{C}$ and 1305 ± 202 mm yr⁻¹, respectively,
105 from 2011 through 2020 at an observatory (Tomakomai) 14 km from the study site. The mean monthly
106 air temperature was highest in August (21.0°C) and lowest in January (-3.9°C). Snow usually covers the
107 ground from early December to early April.

108

109 **2.2. Experimental design**

110 Nine pairs of aluminum collars (0.5 m \times 0.5 m) were concentrically installed 0.5 m and 1.0 m,
111 respectively, from nine isolated larch trees in 50 m \times 50 m in July 2019 (Fig. 1). Because root density
112 and root respiration were expected to depend on distances from tree stems, we installed collars at the
113 two positions to ensure a wide range of data. For each pair, collars were positioned at a 0.3–0.4 m
114 interspace and inserted 3 cm deep into the soil. To exclude root respiration, four PVC boards were
115 inserted 30 cm into the soil around the collar (TC) for each pair in July 2019. The soil profiles showed
116 that almost all roots were distributed in the top 15 cm. Fine roots were sampled from the other collar
117 (SC).

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120 **Fig.1.** Layout of collars for root sampling (SC) and trenching (TC) 0.5 m and 1.0 m from the tree stem.

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122 2.3. Soil CO₂ flux

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Soil CO₂ flux was measured on each collar using a previously described method (Cui et al. 2021; Sun et al. 2017) between 10:00 and 16:00 at intervals of approximately three weeks from August 2019 through November 2020 with a five-month suspension from mid-November 2019 through mid-April 2020. Seedlings were carefully pulled from the collars before flux measurements, although they were rarely found. Flux was measured using a portable system composed of two 0.5-m-tall cubic chambers and a CO₂ analyzer (LI820; Li-Cor Inc., Lincoln, NB, USA). The two chambers were automatically closed for 3 min and opened sequentially. Thus, the flux measurement on the two collars took 6 min. During closing, the CO₂ concentration was measured every 5 s, and its rate of increase was determined using the least-squares method to calculate CO₂ flux. In each collar, soil temperature at a depth of 5 cm and volumetric soil moisture of the top 5 cm were measured immediately after the flux measurement. In addition, soil temperature and soil moisture were recorded half-hourly at depths of 6 cm and 3 cm, respectively, at a station (Hirano et al. 2017) approximately 150 m from the study site.

After trenching, CO₂ flux from the TC (R_{TC}) was equivalent to the sum of the original R_h and additional CO₂ flux resulting from the decomposition of dead roots (R_{DR}) caused by trenching. R_{DR} estimation method is described later. Although the CO₂ flux from the SC (R_{SC}), which was equivalent to the total R_s , was influenced by core sampling, the sampling effect on the CO₂ flux was expected to

139 negligible owing to the limited sampling area (Sun et al. 2020). R_r was estimated for each collar pair as
140 $R_r = R_{SC} - R_{TC} + R_{DR}$ under the assumption that R_h was identical in each pair. Because they were
141 concentrically installed (Fig. 1), SOM and litter fall were assumed to be the same between the two collars
142 in each pair.

143 The following equation was applied to relate the CO₂ flux (R_c , $\mu\text{mol m}^{-2} \text{s}^{-1}$) to soil temperature
144 (T_s , °C) for each collar.

$$145 \quad R_c = a \cdot \exp(b \cdot T_s) \quad (1)$$

146 where a and b are the fitting parameters. Using this equation, R_{SC} and R_{TC} were calculated half-hourly
147 from half-hourly soil temperature, and daily R_r was calculated from daily R_{SC} , R_{TC} and R_{DR} .

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149 **2.4. Decomposition of dead roots**

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

$$152 \quad R_{DR} = C_c \cdot (X_{t-1} - X_t) = C_c \cdot X_0 \cdot \exp(-k \cdot t) \cdot \{\exp(k) - 1\} \quad (2)$$

153 where C_c is the C concentration of roots (g g^{-1}), X_t is the dry weight of the remaining dead roots (g m^{-2})
154 at t , X_0 is the initial dry weight of dead roots (g m^{-2}), and k is the decay constant (d^{-1}). X_0 was set for each
155 TC based on the root biomass measured in its paired SC by soil core sampling in September 2019 for
156 fine roots and soil bulk sampling in April 2021 for coarse roots. The root biomass (X_0) was 134 ± 54 at
157 0.5 m and $111 \pm 75 \text{ g m}^{-2}$ at 1.0 m for fine roots, and 41.6 ± 10.0 at 0.5 m and $18.3 \pm 6.3 \text{ g m}^{-2}$ at 1.0 m
158 for coarse roots (mean \pm SD, $n = 9$). The diameter of the coarse roots was mostly less than 10 mm with
159 a rough average of 5 mm. The C_c was set separately for fine and coarse roots based on the CN analysis
160 of root samples collected in April 2021; C and N concentrations were $0.455 \pm 0.026 \text{ g g}^{-1}$ and $9.22 \pm$
161 0.83 mg g^{-1} , respectively, for fine roots, and $0.489 \pm 0.014 \text{ g g}^{-1}$ and $7.10 \pm 1.25 \text{ mg g}^{-1}$, respectively, for
162 coarse roots (mean \pm SD, $n = 10$). The C and N concentrations differed significantly between fine and
163 coarse roots ($P < 0.01$, two-sided t -test). We used k values determined from litter bag experiments in our
164 previous studies. For fine roots, the k was set at $2.1 \times 10^{-3} \pm 7.4 \times 10^{-4} \text{ d}^{-1}$ (\pm standard error (SE)) before
165 mid-November 2019, 0.0 d^{-1} in winter, and $1.7 \times 10^{-3} \pm 4.5 \times 10^{-6} \text{ d}^{-1}$ after mid-April 2020 (Cui et al.
166 2021), whereas it was set at $6.8 \times 10^{-4} \pm 4.5 \times 10^{-5} \text{ d}^{-1}$ for coarse roots throughout the period (Sun et al.

167 2020).

168

169 **2.5. Biomass and production of fine roots**

170 The same method as in (Cui et al. 2021) was applied to measure fine root biomass and production.
171 Biomass density (B_f , g m^{-2}) was determined by soil coring eight times from September 2019 through
172 November 2020 with a suspension for five months in winter. Soil cores were collected down to 15 cm
173 using a stainless-steel edged tube with an inner diameter of 2.4 cm. Three cores were collected from
174 randomly selected single-use grid positions with an 8 cm spacing in each SC. The area of pits caused by
175 core sampling came to 109 cm^2 in total for each SC ($= 4.52 \text{ cm}^2 \times 3 \text{ positions} \times 8 \text{ times}$), accounting for
176 4.3% of the collar area ($0.5 \text{ m} \times 0.5 \text{ m}$). Core samples were stored in PVC tubes in a freezer. Living fine
177 roots were visually extracted from the soil samples dispersed in tap water, dried at 70°C for 48 h, and
178 weighed to determine biomass.

179 The ingrowth core method was applied to measure production (P_f , $\text{g m}^{-2} \text{ period}^{-1}$). Plastic hair
180 curlers with an outer diameter of 2.3 cm were wrapped in a 2 mm mesh fabric and filled with air-dried
181 root-free soil. The soil was collected from the study site and sieved through 2 mm meshes. In each SC,
182 three ingrowth cores were inserted down to 15 cm into the pit dug through soil core sampling, and the
183 three ingrowth cores installed the previous time were collected. Fine root biomass in the cores,
184 corresponding to root production during the interval, was analyzed using the same method as described
185 above. In addition, annual mortality (M_f , $\text{g m}^{-2} \text{ yr}^{-1}$) were estimated by subtracting the annual difference
186 in root biomass (ΔB_f) from annual production ($M_f = P_f - \Delta B_f$). The dry weight was converted to C by
187 using C_c (0.455 g g^{-1}). In addition, turnover rates were determined by dividing the annual production by
188 the mean biomass (Brunner et al. 2013).

189

190 **2.6. Sap flow**

191 The sap flow was measured to quantify ion uptake respiration (R_{ion}). In laboratory experiments, R_{ion}
192 was usually correlated with N uptake as a major nutrient ion, as determined by destructive sampling
193 (Lambers et al. 2008). However, applying this method to trees is difficult in the field because the N
194 analysis of whole trees is expensive and labor-intensive. It was reported that N uptake depends on root

195 water uptake, causing water mass flow in the soil, especially when root density is low (Henriksson et al.
196 2021; McMurtrie and Nasholm 2018; Oyewole et al. 2014). We adopted the sap flow rate as a proxy for
197 water uptake and incorporate it into the partitioning model described below.

198 Sap flow velocity was measured using the thermal dispersion method (Granier 1987) in three trees
199 from July 2019 through November 2020 with a suspension during the leafless season. Sap flow sensors
200 (CUP-SPF-M; Climatec Inc., Tokyo, Japan) were installed 25 cm below the lowest branch to measure
201 the entire sap flow of each tree. From the destructive sampling, we presumed that the stem area at the
202 sensor height (25–72 cm²) was occupied by sapwood, excluding bark. Thus, sap flow rates were
203 calculated as the product of the sap flow velocity and the stem area. Although sap flow, transpiration,
204 and water uptake were not the same, their daily rates were almost identical. Because DBH of larch trees
205 averaged 54.4 ± 28.3 mm in 2019 ($n = 215$) and 58.2 ± 30.4 mm in 2020 ($n = 225$) in the study site, the
206 three trees with DBH of 37–84 mm in 2019 and 43–91 mm in 2020 were almost within the range of
207 mean \pm SD in size. The total coarse root biomass of each sample tree was estimated from the DBH using
208 an allometric equation, and the total fine root biomass of each tree was estimated from the coarse root
209 biomass using a factor of 0.185, which was determined from boreal trees (Yuan and Chen 2010).
210 Specific sap flow rates normalized by fine root biomass (S_s ; g H₂O g dry matter (DM)⁻¹ d⁻¹) were
211 calculated for each tree and averaged. The water uptake rate in each SC was estimated as a product of
212 the average S_s and fine root biomass.

213

214 2.7. Partitioning of root respiration

215 R_r can be partitioned into R_g , R_m , and R_{ion} using the conceptual model below (Amthor 2000; Lambers
216 et al. 2008; Thornley 1970).

$$217 \quad R_r = R_g + R_m + R_{ion} = g \cdot P_f + m \cdot B_f + u \cdot U_i \quad (3)$$

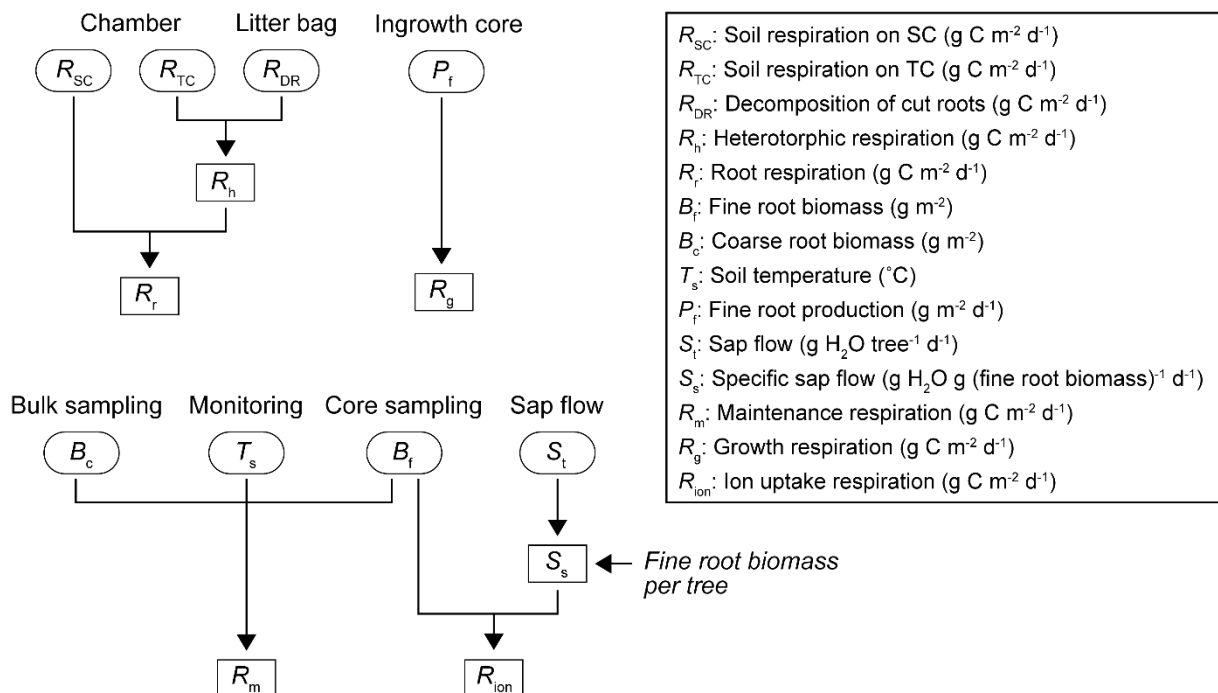
218 where g , m , and u are the coefficients of growth, maintenance, and ion uptake respiration, and U_i is the
219 ion uptake rate. Considering the field conditions, we modified the model, including one without R_{ion} to
220 be consistent with our previous study (Cui et al. 2021), as follows.

$$221 \quad R_r = R_g + R_m + R_{ion} = g \cdot P_f + d \cdot \exp(f \cdot T_s) \cdot (B_f + B_c) + u \cdot S_s \cdot B_f: \text{Model 1 (4)}$$

222 $R_r = R_g + R_m = g \cdot P_f + d \cdot \exp(f \cdot T_s) \cdot (B_f + B_c)$: Model 2 (5)

223 where g is the growth coefficient (g C g DM^{-1}), d is the R_m of the unit biomass at 0°C ($\text{g C g DM}^{-1} \text{ d}^{-1}$),
 224 f is the temperature coefficient ($^\circ\text{C}^{-1}$), B_c is the coarse root biomass (g m^{-2}), and u is the ion uptake
 225 coefficient ($\text{g C g H}_2\text{O}^{-1}$). Although respiration components and root production were originally
 226 expressed per unit root biomass, they are per unit ground area here, because respiration per area is easier
 227 to measure in the field and more useful to quantify ecosystem carbon cycles. In these models,
 228 temperature affects only R_m exponentially (Moyano et al. 2009; Thornley 2011). Although the tree
 229 survey indicated coarse root growth during the study period, the growth was ignored in R_g because of
 230 the lack of data. However, coarse root biomass was incorporated into R_m based on the assumption that
 231 the temperature responses of fine and coarse roots were the same. A nonlinear mixed-effects model was
 232 applied to the time-series (eight times) datasets for 18 pairs ($n = 8 \times 18$) to parameterize the models. The
 233 data preparation for the parametrization is summarized in Fig. 2. Fine root production was measured
 234 eight times and converted into daily values using the day length of the measurement intervals. Fine root
 235 biomass was the average of two consecutive measurements at the beginning and end of each interval.
 236 Soil temperature and specific sap flow are the mean values of the interval. Coarse root biomass was set
 237 to a fixed value measured in April 2021 for each pair.

238



239

240 **Fig. 2.** Workflow of data preparation for model parameterization.

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242 **2.8. Data analysis**

243 Student's *t*-test was applied to compare two means, assuming homoscedasticity. Two-way repeated
244 measures analysis of variance (ANOVA) was used to test the effects of factors. For the mixed-effects
245 model application, we used the package 'nlme' in R (Pinheiro et al. 2022). Uncertainties (SD) in the
246 annual summation of respiration components due to model parameterization (Eqs. 1, 2, 4 and 5) were
247 determined by a bootstrap approach ($n = 1000$), in which model parameters were randomly generated
248 according to a normal distribution with the mean \pm SE of each parameter. The uncertainties were
249 propagated by the law of error propagation. Finally, the uncertainties due to parameterization and spatial
250 variation were combined (combined SD) at 0.5 m and 1.0 m, respectively.

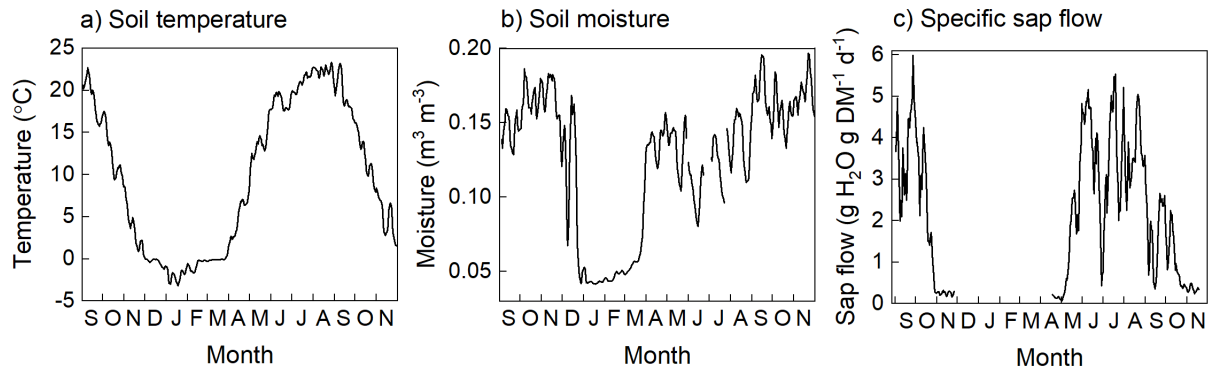
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252 **3. Results**

253 **3.1. Environmental conditions**

254 The field experiment was conducted from September 2019 through November 2020. In the annual
255 period from October 2019 to September 2020, the mean air temperature was 8.6°C, which was higher
256 than its decadal mean + 1 SD, whereas the total precipitation of 1168 mm was within the range. The
257 five-day moving average of soil temperature broadly peaked at 22–23°C from early August to mid-
258 September and was below -1°C from late December to mid-February, with a negative peak at -3°C in
259 mid-January (Fig. 3a). Soil moisture fluctuated between 0.1 and 0.2 m³ m⁻³ in the snowless season
260 mainly according to precipitation but rapidly decreased in December by soil freezing and then gradually
261 increased under snow accumulation because of the thawing of frozen soil (Fig. 3b). Sap flow showed a
262 seasonal pattern like temperature seasonality but with a large fluctuation mainly due to variable solar
263 radiation (Fig. 3c).

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270 3.2. Soil CO₂ flux

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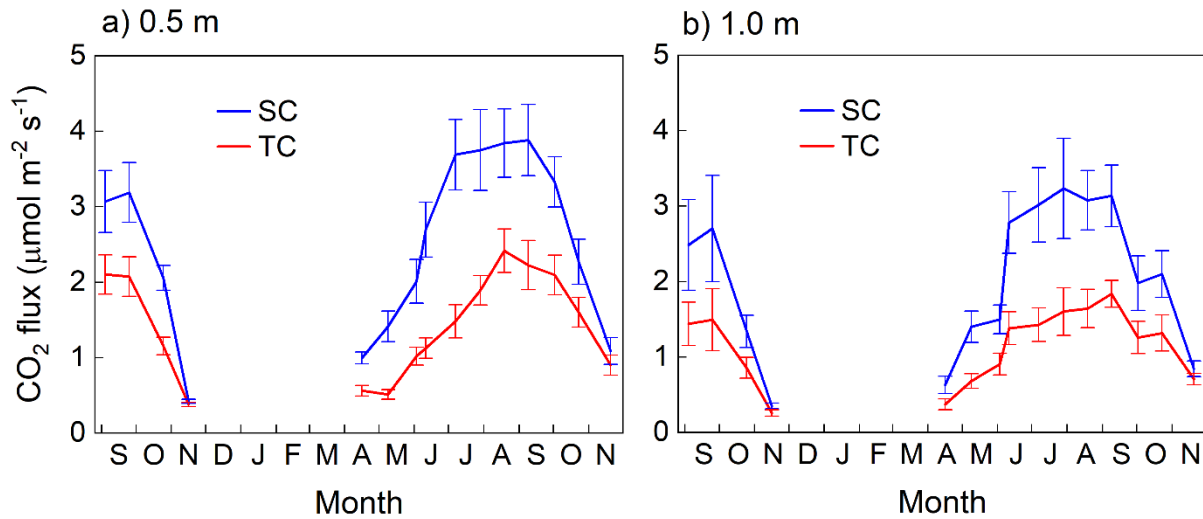
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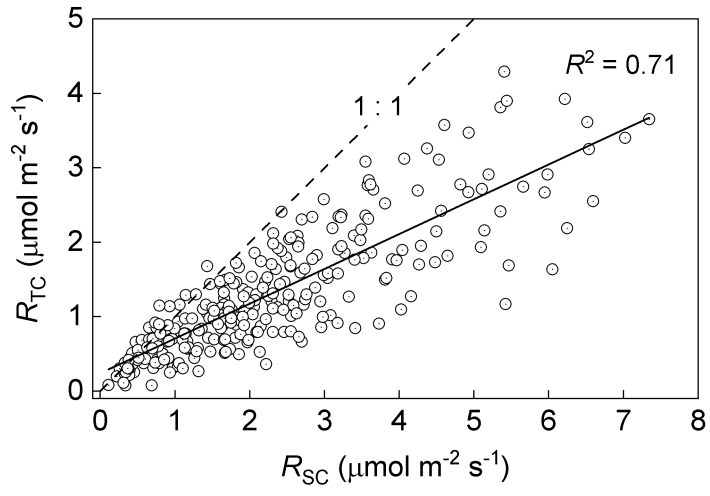
Fig. 3. Seasonal variations in daily means of soil temperature at a depth of 6 cm (a), volumetric soil moisture at a depth of 3 cm (b), and mean specific sap flow ($n = 3$) (c) from September 2019 to November 2020. Five-day moving averages are shown.

Soil CO₂ flux varied seasonally, following temperature variation (Fig. 4a). Fluxes were 2.54 ± 1.53 (R_{SC}) and 1.44 ± 0.89 (R_{TC}) $\mu\text{mol m}^{-2} \text{s}^{-1}$ at 0.5 m and 2.03 ± 1.53 (R_{SC}) and 1.15 ± 0.80 (R_{TC}) $\mu\text{mol m}^{-2} \text{s}^{-1}$ at 1.0 m (mean \pm SD, $n = 135$). According to two-way repeated measures ANOVA by setting the date as a block factor, R_{TC} was significantly smaller than R_{SC} at both positions ($P < 0.0001$, $n = 9$). In addition, R_{TC} was smaller than R_{SC} in each pair, with a few exceptions when R_{SC} was smaller than $1.5 \mu\text{mol m}^{-2} \text{s}^{-1}$, and a significant correlation was found between the fluxes ($P < 0.0001$) (Fig. 5). Meanwhile, a significant exponential relationship was found between soil CO₂ flux and soil temperature (Eq. 1) on each collar ($R^2 = 0.48\text{--}0.77$, $P < 0.01$). However, no significant linear or curvilinear relationship was found between temperature-normalized fluxes and soil moisture, as in our previous studies (Cui et al. 2021; Sun et al. 2020). Thus, half-hourly R_{SC} and R_{TC} were calculated for each collar from monitoring soil temperature (Fig. 3a), using each exponential equation. Both soil temperature and soil moisture measured in collars did not differ significantly between positions (0.5 m vs. 1.0 m) or treatments (SC vs. TC).



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Fig. 4. Seasonal variations in soil CO₂ flux on control collars (SC) and trenched collars (TC) at 0.5 m (a) and 1.0 m (b) from September 2019 to November 2020. Vertical bars denote standard errors ($n = 9$).



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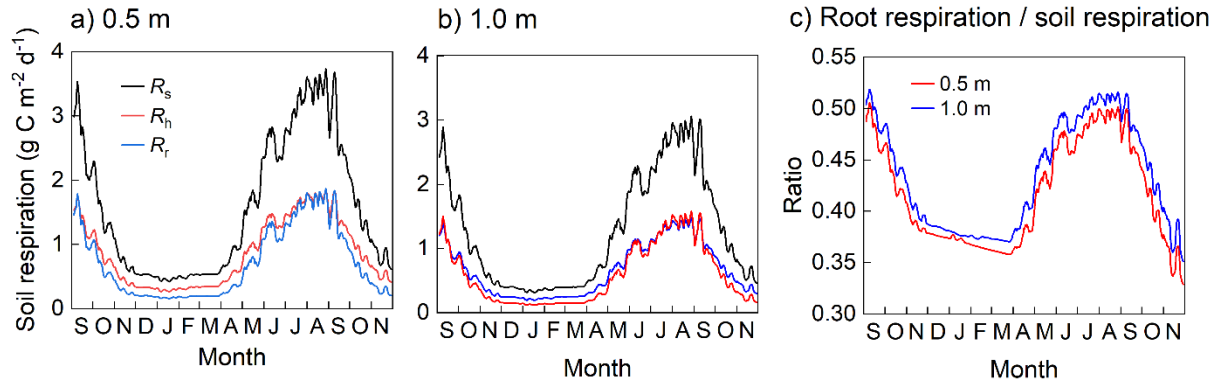
Fig. 5. Relationship between soil CO₂ fluxes measured in trenched collars (R_{TC}) and control collars (R_{SC}) of each pair. The dashed line denotes a 1:1 relationship. The solid line denotes liner regression.

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In each pair of collars, daily soil respiration ($R_s = R_{SC}$) was partitioned into R_h and R_r . R_s , R_r , and R_h varied similarly to the seasonal pattern of soil temperature, because both R_{SC} and R_{TC} were calculated from soil temperature (Figs. 6a and 6b). In addition, the contribution of R_r to R_s (R_r / R_s) showed a clear seasonal variation (Fig. 6c). The R_r / R_s decreased sharply during the fall until late November and continued decreasing to 0.36–0.37 until late March under snow accumulation. After snow disappearance

299 in April, R_r / R_s rapidly increased and reached a broad peak of approximately 0.5 in summer from late
 300 June to early September 2020.

301



302

303 **Fig. 6.** Seasonal variations in mean daily soil respiration (R_s), heterotrophic respiration (R_h) and root
 304 respiration (R_r) at 0.5 m (a) and 1.0 m (b), and the ratio of root respiration and soil respiration
 305 (c) ($n=9$) from September 2019 to November 2020. Five-day moving averages are shown.

306

307 Annually, R_s was partitioned into R_h and R_r by 55% vs. 45% at 0.5 m and 53% vs. 47% at 1.0 m
 308 (Table 1). The CO₂ emissions through dead root decomposition (R_{DR_all}) accounted for 5.9% and 4.5%
 309 of R_s at 0.5 m and 1.0 m, respectively.

310

311 **Table 1.** Annual soil CO₂ fluxes (g C m⁻² yr⁻¹) (mean ± combined standard deviation).

Position	R_{SC} (R_s)	R_{TC}	R_{DR_f}	R_{DR_c}	R_{DR_all}	R_h	R_r
0.5 m	562 ± 123 (100)	341 ± 100 (61)	27 ± 16 (4.8)	6 ± 3 (1.1)	33 ± 16 (5.9)	308 ± 101 (55)	253 ± 159 (45)
1.0 m	447 ± 107 (100)	256 ± 74 (57)	17 ± 21 (3.8)	3 ± 2 (0.7)	20 ± 21 (4.5)	237 ± 77 (53)	210 ± 132 (47)

312 1) R_{SC} (R_s): soil CO₂ flux in the sampling collar (SC) or total soil respiration, R_{TC} : soil CO₂ flux in
 313 trenched collars (TC), R_{DR_f} : CO₂ emissions through the decomposition of dead fine roots, R_{DR_c} : CO₂
 314 emissions through the decomposition of dead coarse roots, R_{DR_all} : the sum of R_{DR_f} and R_{DR_c} ; R_h :
 315 heterotrophic respiration, R_r : root respiration

316 2) The numbers in parentheses denote the percentages of R_{SC} at each position. The annual value was
 317 calculated as the average of the sums for the two annual periods, i.e., October 2019 through September
 318 2020 and November 2019 through October 2020.

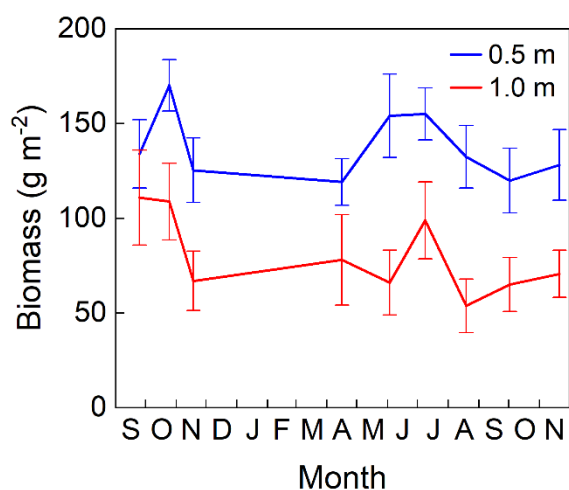
319

320 3.3. Biomass and production of fine roots

321 Seasonal variation in fine root biomass was ambiguous, despite a small peak in early summer (Fig.
322 7). In contrast, fine root production showed a clear seasonal pattern (Fig. 8), with a peak in June to July.
323 In the cold season from mid-November thorough mid-April, root production was small at 0.11 ± 0.005
324 and $0.12 \pm 0.069 \text{ g m}^{-2} \text{ d}^{-1}$ (mean \pm SE) at 0.5 m and 1.0 m, respectively. Annual values were shown in
325 Table 2. Only the turnover rates were significantly different between the two positions ($P < 0.05$).

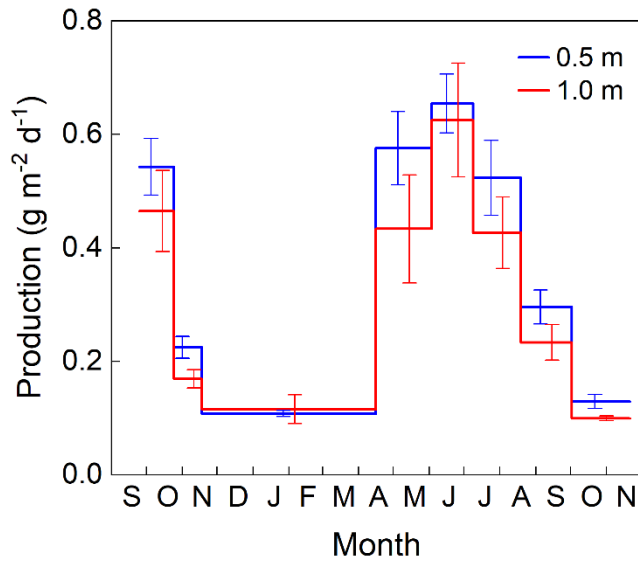
326 To compare the spatial variation of biomass and production between two scales of the collar (0.5
327 m \times 0.5 m) and the study area (50 m \times 50 m), the standard deviations (SDs) of biomass and production
328 measured at three points within each SC were calculated and averaged for nine locations at 0.5 m and
329 1.0 m, respectively, for each sampling date. For all sampling dates ($n = 8$), the mean \pm SD values of the
330 averaged SD (within collar) were 47.2 ± 5.7 (0.5 m) and 37.9 ± 6.2 (1.0 m) g m^{-2} for biomass, and 0.249
331 ± 0.155 (0.5 m) and 0.229 ± 0.130 (1.0 m) $\text{g m}^{-2} \text{ d}^{-1}$ for production. Meanwhile, the SD of the mean
332 biomass and production from nine individual locations (within study area) was calculated and averaged
333 for all sampling dates to be 76.6 ± 14.4 (0.5 m) and 73.6 ± 23.8 (1.0 m) g m^{-2} for biomass, and $0.363 \pm$
334 0.210 (0.5 m) and 0.309 ± 0.190 (1.0 m) $\text{g m}^{-2} \text{ d}^{-1}$ for production. Spatial variation expressed by the
335 mean SD was smaller within the collar than within the study area by 40–50% for biomass and 25–50%
336 for production.

337



338 **Fig. 7.** Seasonal variation in fine root biomass at 0.5 m and 1.0 m ($n = 9$) from September 2019 to
339 November 2020. Means (\pm standard errors) were shown.

341



342

343 **Fig. 8.** Seasonal variation in fine root production at 0.5 m and 1.0 m ($n = 9$) from September 2019 to
 344 November 2020. Means (\pm standard errors) were shown.

345

346 **Table 2.** Annual fine root dynamics (mean \pm standard deviation, $n = 9$).

Position	P_f (g m ⁻² yr ⁻¹)	ΔB_f (g m ⁻² yr ⁻¹)	M_f (g m ⁻² yr ⁻¹)	Mean B_f (g m ⁻²)	Turnover rate (yr ⁻¹)*	Mean B_c (g m ⁻²)
0.5 m	116 \pm 19	3 \pm 48	113 \pm 99	133 \pm 40	0.90 \pm 0.30	44 \pm 42
1.0 m	103 \pm 29	4 \pm 26	98 \pm 39	78 \pm 43	1.68 \pm 0.84	20 \pm 26

347 * $P < 0.05$, between positions by two-sided t test

348 1) P_f : fine root production, ΔB_f : annual difference in fine root biomass, M_f : fine root mortality, B_f : fine
 349 root biomass, B_c : coarse root biomass

350 2) The annual value was calculated as the average of the sums for the two annual periods, i.e., October
 351 2019 through September 2020 and November 2019 through October 2020.

352

353 3.4. Partitioning of root respiration

354 Both models (Eqs. 4 and 5) were significantly parameterized using the dataset ($P < 0.0001$, $R^2 =$
 355 0.57–0.59) (Table 3). All parameters were determined to be statistically significant ($P < 0.012$).

356 Parameter d , the maintenance respiration of the unit biomass at 0°C, was almost identical in the two
 357 models. The Q_{10} values calculated from the parameter f were 2.34 and 2.61 in Models 1 and 2,
 358 respectively. $d \cdot \exp(f \cdot T_s)$ in the models, corresponding to the maintenance respiration coefficient (m) in

359 Eq. 3, was 0.0013 at 5°C, 0.0030 at 15°C, and 0.0070 g C g DM⁻¹ d⁻¹ at 25°C in Model 1 and 0.0013 at

360 5°C, 0.0034 at 15°C, and 0.0089 g C g DM⁻¹ d⁻¹ at 25°C in Model 2. The coefficients were the same at
 361 5°C across the models, but 12% and 21% lower in Model 1 at 15°C and 25°C, respectively, because of
 362 a lower temperature coefficient. In addition, the coefficient of growth respiration (*g*) was 22% lower in
 363 Model 1. The decreases in *f* and *g* in Model 1 were compensated for by the coefficient of ion uptake
 364 respiration (*u*).

365

366 **Table 3.** Model parameters (\pm standard error).

	Model 1		Model 2	
	Parameter	<i>P</i>	Parameter	<i>P</i>
Growth respiration coefficient (<i>g</i>) (g C g DM ⁻¹)	0.57 \pm 0.14	0.0001	0.73 \pm 0.13	< 0.0001
Maintenance respiration coefficient at 0°C (<i>d</i>) (g C g DM ⁻¹ d ⁻¹)	0.00084 \pm 0.00027	0.0019	0.00081 \pm 0.00025	0.0015
Temperature coefficient (<i>f</i>) (°C ⁻¹)	0.085 \pm 0.015	< 0.0001	0.096 \pm 0.014	< 0.0001
Ion uptake respiration coefficient (<i>u</i>) (g C g H ₂ O ⁻¹)	0.00045 \pm 0.00018	0.012		
Adjusted <i>R</i> ²	0.59		0.57	
<i>P</i>	< 0.0001		< 0.0001	

367

368 Annual *R_r* was partitioned into fine root *R_g*, fine root *R_m* (*R_{m_f}*) and coarse root *R_m* (*R_{m_c}*), and *R_{ion}*
 369 using the fitting parameters (Table 4). The results from the models were overestimated by 7% at 0.5 m
 370 and underestimated by 10% at 1.0 m in total (Sum / *R_r*). *R_{m_f}* contributed the most to *R_r* (46–51%),
 371 followed by *R_g* (26–40%). *R_g*, *R_{m_f}*, and *R_{m_c}* were smaller in Model 1 by 19, 8, and 5 g C m⁻² yr⁻¹,
 372 respectively, at 0.5 m and by 16, 5, and 2 g C m⁻² yr⁻¹, respectively, at 1.0 m. *R_g* showed the largest
 373 difference between the two models, suggesting that the majority of *R_{ion}* was lumped together with *R_g* in
 374 Model 2. Fine root *R_r* (Sum – *R_{m_c}*) accounted for 86–90% and 84–89% of the total *R_r* (Sum) in Models
 375 1 and Model 2, respectively.

376

377 **Table 4.** Annual sums of root respiration components (g C m⁻² yr⁻¹) (mean \pm combined standard
 378 deviation).

Model 1						
Position	<i>R_r</i>	<i>R_g</i>	<i>R_{m_f}</i>	<i>R_{m_c}</i>	<i>R_{ion}</i>	Sum
0.5 m	253 \pm 227 (93)	70 \pm 23 (26)	130 \pm 66 (48)	39 \pm 45 (14)	32 \pm 17 (12)	271 \pm 93 (100)

1.0 m	210 ± 151 (112)	60 ± 32 (32)	87 ± 74 (46)	18 ± 44 (10)	23 ± 17 (12)	188 ± 122 (100)
Model 2						
Position	R_r	R_g	R_{m_f}	R_{m_c}	Sum	
0.5 m	253 ± 227 (93)	89 ± 25 (33)	138 ± 76 (51)	44 ± 51 (16)	271 ± 99 (100)	
1.0 m	210 ± 151 (112)	76 ± 39 (40)	92 ± 83 (49)	20 ± 49 (11)	188 ± 124 (100)	

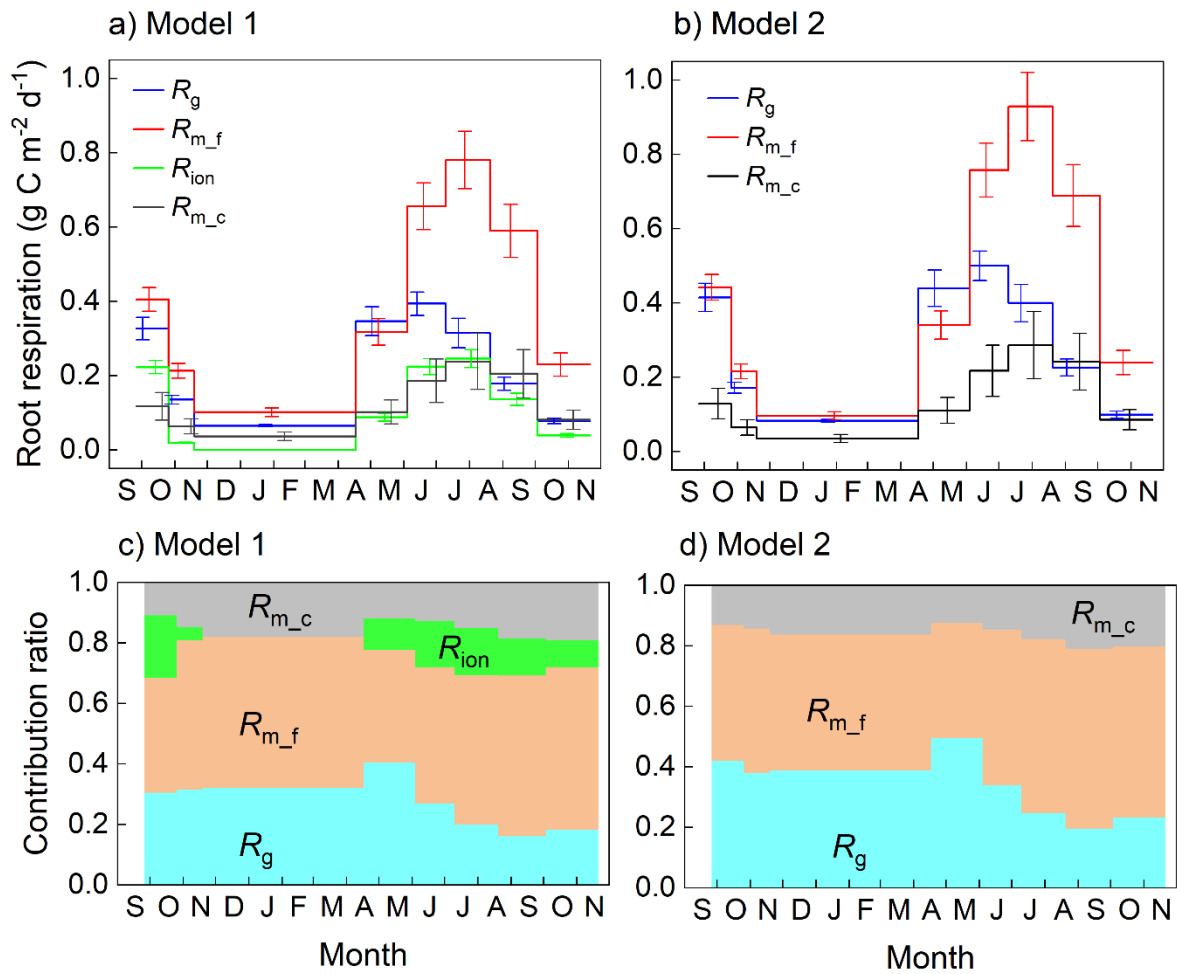
379 1) R_r : root respiration (from Table 2), R_g : growth respiration, R_{m_f} : fine root maintenance respiration,
380 R_{m_c} : coarse root maintenance respiration, R_{ion} : ion uptake respiration, Sum: $R_g + R_{m_f} + R_{m_c} + R_{ion}$
381 (Model 1) or $R_g + R_{m_f} + R_{m_c}$ (Model 2)

382 2) The numbers in parentheses denote percentages of the sum. The annual value was calculated as the
383 average of the sums for the two annual periods, e.g., October 2019 to September 2020 and November
384 2019 to October 2020.

385

386 The respiration components varied seasonally with different peak periods. Even though Fig. 9
387 shows the result at 0.5 m, the seasonal variation was similar at 1.0 m. R_g peaked from June to July in
388 proportion to root production (Fig. 8), whereas R_{m_f} peaked from July to August owing to its positive
389 relationship with soil temperature (Fig. 3a) and fine root biomass (Fig. 7). In addition, R_{m_c} peaked
390 following the temperature variation under the assumption of no seasonality in coarse root biomass. R_{ion}
391 peaked from July to August according to the seasonality of fine root biomass and sap flow (Fig. 3c) and
392 was zero in winter because of defoliation. The relative contribution of each respiration component to R_r
393 also showed seasonality (Figs. 9c and 9d). Seasonal variation in R_g contribution was relatively large,
394 with a peak from April to May at 0.40 (Model 1) and 0.49 (Model 2) and reached a minimum of 0.16
395 (Model 1) and 0.20 (Model 2) from August to September.

396



397

398 **Fig. 9.** Seasonal variations in fine root growth respiration (R_g), fine root maintenance respiration (R_{m_f}),
 399 coarse root maintenance respiration (R_{m_c}), and ion uptake respiration (R_{ion}) at 0.5 m estimated
 400 by Model 1 (a) and Model 2 (b) from September 2019 to November 2020. Means (\pm standard
 401 errors, $n = 9$) were shown. Contribution ratios of the respiration components from Model 1 (c)
 402 and Model 2 (d) are also shown.

403

404 4. Discussion

405 4.1. Partitioning of soil respiration

406 The CO₂ emission (R_{DR}) from the decomposition of dead roots caused by trenching was estimated
 407 using the decay constant from root litterbag experiments, which were reported to underestimate fine root
 408 decomposition by 10–20% because of rhizosphere disturbance (Dornbush et al. 2002). However, the
 409 effect of the underestimation would be limited, because annual fine root decomposition was small,
 410 accounting for 4–5% of total soil respiration (Table 1). Meanwhile, trenching would have decreased R_h

411 because of the lack of litter supply from the living roots. In addition, no priming effect of labile exudate
412 from roots on microbial decomposition was expected (Kuzyakov 2010). Thus, R_h was potentially
413 underestimated, although the underestimation could have been limited because of low root density,
414 which was much lower at 78–133 g m⁻² (Table 2) than the average density (505 g m⁻²) of temperate
415 deciduous forests (Finér et al. 2011a). Although soil moisture was expected to increase in TC because
416 of no water uptake by roots (Subke et al. 2006), there was no difference between SC and TC, probably
417 because of the low root density.

418 Periodically measured CO₂ fluxes were extrapolated to sequential data for each collar using an
419 exponential equation (Eq. 1) from the continuously measured soil temperature. It is common to
420 determine representative R_h and R_r values from the spatial averages of soil CO₂ fluxes in a study area
421 because of their large spatial variations (Sun et al. 2020). However, we determined R_h and R_r in each
422 pair of collars to ensure the spatial variation of R_r based on the assumption that R_h values on the two
423 collars (SC and TC) in each pair were similar. The assumption was because the two collars were closely
424 installed (0.3–0.4 m apart) and equally distant from each isolated larch stem, suggesting that SOM, leaf
425 litter accumulation, and root density were at a similar level in the two neighboring collars. We confirmed
426 that soil CO₂ fluxes in the two collars were similar before trenching, and soil C concentration decreased
427 with increasing distance from tree stems (Cui et al. 2021). The significant linear relationship between
428 R_{TC} and R_{SC} (Fig. 4) supports this assumption. In addition, the result that spatial variation in fine root
429 biomass was considerably smaller on a collar scale than on the scale of the study area suggests a similar
430 soil condition in each collar pair.

431 Compared to our previous study conducted two years ago (Cui et al. 2021), annual R_h slightly
432 decreased by 2% at 0.5 m and 9% at 1.0 m, but annual R_r increased by 40% at 0.5 m and 412% at 1.0 m.
433 The R_r increase was due to tree growth; fine root biomass increased twofold at 0.5 m and sixfold at 1.0
434 m in two years (Table 2). The annual contribution of R_r to R_s was 45–47% (Table 1), which is comparable
435 to the results of meta-analyses (Hanson et al. 2000; Subke et al. 2006).

436

437 **4.2 Partitioning of root respiration**

438 Soil CO₂ flux and fine root dynamics were simultaneously measured within the same collar (SC) to

439 minimize spatial mismatches. Although soil core sampling disturbed soil conditions, the disturbance
440 would be insignificant to CO₂ flux (Sun et al. 2020) because the total pit area caused by eight-time core
441 samplings was only 4.3% in each SC, and sampling intervals were more than a month.

442 We applied the ingrowth core method to measure root production. The method tends to
443 underestimate root production compared to the minirhizotron method which potentially yields more
444 reliable estimates (Addo-Danso et al. 2016; Finér et al. 2011b; Hendricks et al. 2006). The annual fine
445 root production was 103–116 g m⁻² yr⁻¹ in this study (Table 2), which was much smaller than the average
446 (337 g m⁻² yr⁻¹) of temperate forests (Finér et al. 2011b). However, turnover rates (0.90–1.68 yr⁻¹, Table
447 2) were comparable to those of temperate forests (Brunner et al. 2013; Finér et al. 2011b). Thus, our
448 results might not have been underestimated, because ingrowth cores were sampled at relatively short
449 intervals of 5–7 weeks using thinner cores with a diameter of 2.3 cm. Short intervals probably enhanced
450 root production in conditions of low root competition and less decomposition, and thin cores could
451 minimize the delayed root recolonization (Hertel and Leuschner 2002; Li et al. 2013).

452 All parameters were significantly determined in the models, whereas the models explained R_r
453 variations by only 57–59% (Table 3). We excluded coarse root growth from R_g . (Wieser and Bahn 2004)
454 reported that R_m of coarse roots (R_{m_c}) accounted for 73–83% of total coarse root respiration.
455 Accordingly, coarse root growth respiration was roughly estimated from R_{m_c} (Table 4) to be 8–12 g C
456 m⁻² yr⁻¹ at 0.5 m and 4–5 g C m⁻² yr⁻¹ at 1.0 m, which accounted for 3–4% and 2–3% of total R_r ,
457 respectively. In addition, we set coarse root biomass at the measurements in April 2021 after the
458 experiment, ignoring its phenological variation. Coarse root biomass would have increased during the
459 growing season because tree surveys indicated an annual growth in the study site from 2019 to 2020.
460 Thus, the root biomass in April 2021 would be close to the maximum for the experimental period, and
461 consequently, R_{m_c} was probably overestimated to some extent. The parameters related to R_m (d and f)
462 were common for fine and coarse roots in the models to make the model simpler and nonlinear fitting
463 converge. However, the parameters might be smaller for coarse roots, because N concentration was
464 significantly lower in coarse roots than in fine roots (7.10 ± 1.25 vs. 9.22 ± 0.83 mg g⁻¹); R_m is positively
465 related to protein content (Lambers et al. 2008). Because trenching was conducted using PVC boards,
466 calculated R_r consists of respiration by roots alone and rhizomicrobial and mycorrhizal respirations

467 (Moyano et al. 2009). Rhizomicrobial and mycorrhizal respirations were not incorporated in the models.
468 However, these respirations were probably stimulated by the translocation of photosynthate to roots,
469 depending on root-derived compounds. Therefore, rhizomicrobial and mycorrhizal respirations should
470 be included in R_g estimated from root production. In a mature Japanese larch forest, the contribution of
471 respiration by roots plus rhizomicrobial respiration to R_s and mycorrhizal respiration to R_s were 42%
472 and 6%, respectively, during the growing season (Makita et al. 2021).

473 The annual partitioning of R_r to four (Model 1) or three components (Model 2) at 0.5 m and 1.0 m
474 were similar (Table 4), although the absolute values were smaller at 1.0 m. R_{m_f} accounted for the
475 majority (46–51%), followed by R_g (26–40%) and R_{m_c} (10–16%) or R_{ion} (12%). In comparison between
476 the two models, the largest difference was found in R_g , suggesting that the majority of R_{ion} was lumped
477 together with R_g when R_{ion} was not considered, which is supported by the strong correlation between
478 plant growth and ion uptake (Lambers et al. 2008).

479 Fine root growth even in the snow season (Radville et al. 2016) was suggested by ingrowth core
480 sampling in mid-April (Fig. 8). Thus, relatively high contribution of R_g to R_r was possible during winter
481 (Fig. 9). However, the root production measured in mid-April may have resulted from rapid growth after
482 snow disappearance in early April (Fig. 3a) (McCormack et al. 2015b). The contribution of R_g showed
483 a clear seasonal variation, with a small peak in mid-spring and a minimum in early fall, because of the
484 time lag of seasonal variation between fine root production (Fig. 8) and soil temperature (Fig. 3a). R_g
485 exceeded R_{m_f} only in mid-spring. Although R_g and R_{m_f} were larger in this study compared to our
486 previous study (Cui et al. 2021) because of large increase in fine root production and biomass in two
487 years, the annual contribution ratios of R_g , R_{m_f} , and R_{m_c} to R_r was unchanged at 0.5 m. However, the
488 results of this study (Table 4) were much different from those of a field study in evergreen and deciduous
489 plantations (George et al. 2003), in which fine root R_m accounted for 86–92% of R_r and the contribution
490 of R_{ion} was only 4%. The difference is mainly attributable to different methods as described below.

491 The coefficients of Models 1 and 2 are compared with those from other studies (Table 5). To convert
492 the unit of O_2 to C of CO_2 , the respiration quotient was assumed to be one. Compared with (Cui et al.
493 2021), the g for growth respiration of the same model (Model 2) rose by 26% in this study, whereas the
494 m for maintenance respiration was almost the same. Although R^2 was almost the same, the standard

495 errors of the parameters (g , d , and f) were smaller in this study (Table 3) mainly because of more
 496 replications. This and our previous studies (Cui et al. 2021; Sun et al. 2020) showed a larger g than those
 497 of the other tree species (*Quercus suber*, *Eucalyptus* sp., *Pinus Taeda*, and *Liquidambar styraciflua*) The
 498 difference is mainly due to different methods and different experimental conditions. For *Quercus suber*
 499 and *Eucalyptus* sp., the g for all roots, including coarse roots, was determined from relative growth rates
 500 of hydroponically cultured seedlings or cuttings in a controlled environment (Lambers et al. 2008;
 501 Thongo M'Bou et al. 2010). In addition, the fine root g for *Pinus taeda* and *Liquidambar styraciflua*
 502 was determined from a laboratory calorimetric experiment (George et al. 2003). The carbon cost of
 503 producing new root biomass was reported to be 0.536 g C g DM⁻¹ on average (Chapin et al. 2011; Poorter
 504 1994). From the carbon cost, carbon consumed through growth respiration was roughly estimated to be
 505 0.11 g C g DM⁻¹ under the assumption that respiration cost accounts for 20% of the total cost (Chapin
 506 et al. 2011). Our g derived from field experiments were consistently higher than the respiration cost
 507 from laboratory experiments. The large difference in g suggests that more energy is necessary for fine
 508 root production in the field. In contrast, the m was relatively stable among tree species, except for smaller
 509 m for mature spruce.

510

511 **Table 5.** Comparison of model parameters.

Plant species	Experiment	Growth respiration coefficient (g) (g C g DM ⁻¹)	Maintenance respiration coefficient (m) (mg C g DM ⁻¹ d ⁻¹)	Temperature (°C)	Ion Uptake respiration (R_{ion})	Reference
<i>Dactylis glomerta</i>	Laboratory	0.13	27	No data	No	Lambers <i>et al.</i> , 2008
<i>Festuca ovina</i>		0.23	22			
<i>Quercus suber</i>		0.14	6.2			
<i>Triticum aestivum</i>		0.22	23			
<i>Eucalyptus</i> sp.	Greenhouse	0.06	10	22	No	Thongo M'Bou <i>et al.</i> , 2010
<i>Pinus taeda</i>	Forest	0.061	9.2	25	Yes	George <i>et al.</i> , 2003
<i>Liquidambar styraciflua</i>		0.070	11			
Mature larch	Forest	0.32	5.7	22	No	Sun <i>et al.</i> , 2020
			8.2	25		
Mature spruce			0.24	2.8		
			3.7	25		

Young larch	Forest	0.58	$\frac{6.8}{8.1}$	$\frac{22}{25}$	No	Cui <i>et al.</i> , 2021
Young larch	Forest	0.57	$\frac{5.5}{7.0}$	$\frac{22}{25}$	Yes	This study (Model 1)
Young larch	Forest	0.73	$\frac{6.7}{8.9}$	$\frac{22}{25}$	No	This study (Model 2)

512

513 We conducted a year-round experiment by increasing spatial replication and incorporating R_{ion} in a
514 young larch-dominated forest regrowing on bare ground. The experimental conditions were
515 considerably simplified because of an almost pure stand, the same tree age, low tree density, little ground
516 vegetation, little litter accumulation, and a small amount of SOM. From the experiments in this study
517 and (Cui *et al.* 2021), we derived similar parameters (g , d , and f) for partitioning. The Q_{10} of maintenance
518 respiration (2.33–2.61) was reasonable. Therefore, we believe that root respiration was partitioned with
519 a certain level of reliability and the approach was robust under relatively simple conditions. However,
520 we should note that our results were yielded in an unnaturally simple field condition, because the soil
521 without the organic layer was not typical among forest soils. Moreover, our growth respiration parameter
522 (g) resulting from only field data was much higher than those from laboratory experiments. To further
523 improve our understanding of root respiration in the field, more experimental data should be
524 accumulated.

525

526

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530

531

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532

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Statements and Declarations

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