



Title	Fine root dynamics and partitioning of root respiration into growth and maintenance components in cool temperate deciduous and evergreen forests
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1 Title: Fine root dynamics and partitioning of root respiration into growth and maintenance components in cool
2 temperate deciduous and evergreen forests

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16 Running head: Growth and maintenance respirations of tree fine roots

17

18 **Abstract**

19 *Aims:* We aim to show the seasonality of fine root dynamics and examine the relationship between root respiration
20 (R_r) and fine root dynamics. In addition, we try partitioning R_r into growth (R_g) and maintenance (R_m) components.

21 *Methods:* Soil respiration (R_s), fine root biomass (B), and fine root production (P) were measured simultaneously
22 over a growing season in adjoining deciduous (DF) and evergreen (EF) forests. The R_r was separated from R_s by
23 the trenching method, and R_r was partitioned into R_g and R_m using an empirical model.

24 *Results:* The seasonality of P was almost the same in both forests, though that of B was different. The R_r showed
25 a positive correlation with P in both sites. Annual R_r was estimated to be 610 (DF) and 393 (EF) g C m⁻² year⁻¹.
26 Annual R_g and R_m were 121 and 166 (DF), and 86 and 182 (EF) g C m⁻² year⁻¹, respectively.

27 *Conclusions:* We found a clear seasonal pattern in P and a positive linearity between R_r and P . Despite considerable
28 uncertainty due to the small sample size, presence of larger roots, and measurement uncertainty, the results suggest
29 that our approach is capable of partitioning R_r .

30

31 Key words: biomass, chamber, ingrowth core, production, soil respiration, trenching.

32

33 **Introduction**

34 Terrestrial ecosystems have sequestered carbon dioxide (CO₂) at a rate of 3.2 ± 0.8 Pg C year⁻¹ during the last
35 decade until 2016, accounting for 30% of total CO₂ emissions from fossil fuels, industry, and land-use change (Le
36 Quéré et al. 2018). Forests, one of the carbon-richest ecosystems, covers about 30% of the land surface (Bonan
37 2008; Keenan et al. 2015) and was estimated to be a large CO₂ sink of 2.4 ± 0.4 Pg C year⁻¹ from 1990 to 2007
38 (Pan et al. 2011). Therefore, forests are crucial ecosystems for mitigating climate change mostly owing to capturing
39 atmospheric CO₂ during growth.

40 Belowground biological processes, such as root respiration and microbial decomposition of soil organic matter,
41 greatly contribute to the carbon balance of forest ecosystems (Davidson et al. 2006; Janssens et al. 2001). In
42 particular, fine roots, which are commonly defined as thin roots less than 2 mm in diameter, are known for their
43 vital role in global biogeochemical cycles (McCormack et al. 2015). Fine roots function to absorb nutrients and
44 water from the soil and have a shorter life cycle through production, mortality, and littering with average turnover
45 rates of about one year in temperate forests (Brunner et al. 2013; Finér et al. 2011b). In addition, despite their small
46 biomass the contribution of fine roots to the net primary production (NPP) of forests is relatively high at 32% for
47 boreal forest (Yuan and Chen 2010), and 22% globally (McCormack et al. 2015). Also, fine root litter is a major
48 carbon source in forest soils (Richter et al. 1999). Therefore, fine root dynamics are key processes that govern
49 forest productivity and biogeochemical cycles.

50 Fine root phenology strongly influences belowground carbon dynamics and allocation, whereas seasonality and
51 variability in the production and respiration of fine roots are not well understood among forest types (Abramoff
52 and Finzi 2015; McCormack et al. 2014; Radville et al. 2016). Moreover, the underlying mechanisms controlling
53 fine root dynamics remain limited because of the lack of experimental evidence (Liu et al. 2018; Radville et al.
54 2016). In particular, the dynamic functions of fine roots, such as respiration, are not quantitatively understood,
55 which has restrained the improvement of terrestrial biosphere models to predict the responses of forest ecosystems
56 to environmental changes (McCormack et al. 2015; Warren et al. 2015). Therefore, field experiments which
57 simultaneously measure the production and respiration of fine roots in different forest types over a growing season
58 will help improve our qualitative understanding of the role of fine roots in forest carbon cycles.

59 Empirical models exist that partition plant respiration into growth and maintenance requirements (Amthor 2000;
60 McCree 1974; Penning de Vries 1974; Thornley 1970), plus the respiratory cost of ion uptake by fine roots (Chapin
61 III et al. 2011; Johnson 1990; Lambers et al. 2008). In these models, growth and maintenance respirations correlate
62 linearly with production (growth) and biomass, respectively. Problems with plant respiration models occur in the
63 quantification of respiration partitioning (Gifford 2003), which lack a mechanistic basis (Sweetlove et al. 2013).
64 Nevertheless, laboratory experiments suggested that the models were useful for understanding the carbon balance
65 of plants, though the partitioning would differ by plant species and environmental conditions (Lambers et al. 2008).
66 Also, the partitioning of respiration into these functional components will help in the understanding of the
67 ecological controls over plant respiration (Chapin III et al. 2011). These models have been adopted by terrestrial
68 biosphere models, such as Biome-BGC (Thornton and Rosenbloom 2005), to explicitly represent autotrophic
69 respiration as the sum of growth and maintenance respirations. However, the responses of the models' rate
70 coefficients to abiotic and biotic factors have not been well understood (Hopkins et al. 2013) owing to the lack of
71 field experiments (Amthor 2000). So far, there have been no comparisons of model predictions to field conditions,
72 except for (George et al. 2003) partitioning fine root respiration in field conditions. They separately estimated fine
73 root respiration for growth, maintenance, and ion uptake (only nitrogen) in evergreen and deciduous forests using
74 short-term chamber measurements and literature information.

75 In this study, root respiration and fine root dynamics (production and biomass) were measured simultaneously
76 in adjoining deciduous and evergreen forests in a cool temperate climate over a growing season in order to: 1)
77 quantify root respiration with reliability, 2) compare fine root phenology between the different forest types, and 3)
78 examine the relationship between root respiration and fine root dynamics. In addition, we try partitioning the root
79 respiration into growth and maintenance components on an annual basis using an empirical model. After the
80 growth and maintenance respirations of fine roots are quantified in the two forests, the model's rate coefficients
81 are compared between the forests and to coefficients reported from laboratory and greenhouse experiments.

82

83 **Materials and method**

84 *Study site*

85 The study was conducted in two adjacent sites (deciduous and evergreen forests) in southern Hokkaido, northern
86 Japan (42° 44' N, 141° 31' E, 125 m above sea level). The soil type was volcanogenous regosol with a high water
87 permeability. In both sites, below the leaf litter and a 4 cm thick root mat, there is a 10 cm thick surface soil layer
88 (A horizon) and an unweathered pumice layer (C horizon); a B horizon is lacking (Hirano et al. 2003a).

89 The deciduous forest (DF) was established in 1957 as a Japanese larch (*Larix kaempferi*) plantation. However,
90 it was severely devastated by typhoon Songda in 2004. The typhoon blew down about 90% of the trees (Sano et
91 al. 2010). In 2005 the fallen tree stems were removed; afterwards the plantation has not been managed (Hirano et
92 al. 2017). In 2015 the dominant tree species was still Japanese larch, followed by *Ulmus davidiana* var. *japonica*
93 (Japanese elm), *Acer pictum* subsp. *dissectum* (maple), and *Quercus crispula* (oak), with a density of 2360 stems
94 ha⁻¹ for trees taller than 2 m. The forest floor is covered with *Dryopteridaceae* sp. (fern) and shrub species,
95 including *Rubus idaeus* (raspberry) (Yazaki et al. 2016).

96 The evergreen forest (EF) was a Japanese spruce (*Picea glehnii*) plantation established next to the deciduous
97 forest in 1979. Spruce saplings were planted in a double row 1.3 m wide at intervals approximately 6 m between
98 rows. Almost no trees fell during typhoon Songda. Tree density was 2250 stems ha⁻¹ in 2015. Understory vegetation
99 was sparse.

100 Decadal mean annual air temperature and precipitation from 2008 to 2017 were $8.3 \pm 0.3^{\circ}\text{C}$ and 1312 ± 172
101 mm (mean \pm 1 standard deviation (SD)), respectively, at a meteorological station (Tomakomai) 14 km from the
102 study site. The lowest and highest monthly mean air temperatures were -3.9°C in January and 20.8°C in August,
103 respectively. About 85% of the annual precipitation falls in the snow-free period from April to November. Snow
104 usually covers the ground from early December through early April.

105

106 *Experimental design*

107 Field experiments were conducted from September 2014 to November 2015. In September 2014, to measure soil
108 CO₂ efflux, a set of four 0.5 m \times 0.5 m aluminum collars were installed, where one collar was used for a control,
109 another for root sampling, the third for litter removal, and the fourth for trenching. Five replications were
110 established in each site for partitioning total soil respiration (R_s) into leaf litter decomposition (R_l), belowground

111 heterotrophic respiration (R_h), and root respiration (R_r). To keep root density similar, four collars in each set were
112 placed on a circle with a 2 m radius around larch trees in the DF site, or were aligned 2 m away from a tree row in
113 the EF site (Fig. 1). Collar spacing was 20 cm, except for the trenching collars where it was 40 cm to ease the
114 trenching effect on the next collar. Collars were inserted only 1 to 2 cm into the soil to minimize damaging surface
115 roots (Wang et al. 2005). To avoid lateral air leak under the collars, each collar was surrounded with a bank of soil.
116 For control collars (CC), no treatment was applied. In sampling collars (SC), the fine root experiments (described
117 later) were conducted. In litter removal collars (LC), 1 mm meshed screens were set between the litter layer and
118 soil surface in early November 2014. The mesh was temporarily removed with the overlying litter, and then soil
119 CO_2 efflux was measured without leaf litter. After the measurement, the mesh and litter were immediately put back
120 on the collar. The trenching method was applied to remove R_r from R_s . For trenching collars (TC), four PVC boards
121 4 mm thick were vertically inserted to a depth of 0.3 m along a square collar in November 2014 to prevent roots
122 from intruding. The decomposition of dead roots (R_d) left in TC was estimated by the root litter bag method
123 (described later). R_1 and R_r were calculated using the following equations:

$$124 \quad R_1 = R_s - R_{LC} \quad (1)$$

$$125 \quad R_r = R_s - R_1 - R_h = R_s - (R_{TC} - R_d) \quad (2)$$

126 where R_s is soil CO_2 efflux measured in CC or SC, and R_{LC} and R_{TC} are CO_2 effluxes from LC and TC, respectively.
127

128 *Soil CO_2 efflux*

129 Soil CO_2 efflux was measured once or twice a month from September 2014 to November 2015, except during the
130 snow season. Before the treatments, CO_2 efflux was also measured in September and October 2014 to check for
131 initial spatial variations among the CC, SC, LC, and TC collars. The measurements were conducted manually on
132 each collar between 10:00 and 16:00 using a closed chamber system with two 50 cm tall cubic chambers made of
133 transparent acrylic plastic (Sun et al. 2017). CO_2 concentration and air temperature inside the chamber were
134 measured every 5 s with an infrared gas analyzer (LI820; Li-Cor Inc., Lincoln, NB, USA) and a thermocouple
135 probe (MHP; Omega Engineering, Stamford, CA, USA). Outputs were recorded using a data logger (CR1000;
136 Campbell Scientific Inc., Logan, UT, USA). Each chamber was closed for 180 s. Despite the short closing, soil

137 CO₂ efflux might have been underestimated by about 5% because of lateral diffusion in relatively porous root mats
138 (Hutchinson and Livingston 2001). Immediately after measurement, soil temperature (T_s) at a depth of 5 cm and
139 volumetric soil water content (SWC) of the top 5 cm layer were measured, respectively, in each collar with a
140 thermocouple probe (MHP; Omega Engineering) and a soil moisture sensor (SM150; Delta-T Devices Ltd.,
141 Cambridge, UK). Sprouts in each collar were picked carefully before each measurement. In addition, T_s at a depth
142 of 5 cm were monitored hourly in two CC at each site using button-type temperature loggers (Thermochron SL
143 type, KN laboratories, Osaka, Japan). SWC at a depth of 3 cm were also monitored every half-hour in four
144 replications at a nearby re-growing forest site using TDR sensors (CS615; Campbell Scientific, Inc.) along with
145 air temperature and precipitation (Hirano et al. 2017).

146 The relationship between soil CO₂ efflux (R , $\mu\text{mol m}^{-2} \text{s}^{-1}$) and T_s ($^{\circ}\text{C}$) was analyzed for each collar using the
147 following exponential equation:

$$148 \quad R = a \cdot \exp(b \cdot T_s) \quad (3)$$

149 where a and b are fitting parameters. To analyze the relationship with SWC, temperature-normalized soil CO₂
150 efflux (R_b , $\mu\text{mol m}^{-2} \text{s}^{-1}$) was calculated using the following equation (Hirano et al. 2003b):

$$151 \quad R_b = R \cdot \exp\{b \cdot (T_b - T_s)\} \quad (4)$$

152 where T_b is base temperature set as the mean T_s at each site. Also, bivariate models combining Eq. 3 for T_s with
153 various equations for SWC (Reichstein and Janssens 2009) were applied to estimate soil CO₂ efflux. CO₂ efflux
154 was calculated hourly from the monitoring data of T_s and SWC using a best-fit model and converted into annual
155 CO₂ emission between November 2014 and November 2015.

156

157 *Dead root decomposition in trenched collars*

158 The root litter bag method was applied to assess CO₂ emissions (R_d) through the decomposition of dead roots left
159 in TC (Epron et al. 1999; Gholz et al. 2000; Silver and Miya 2001). To determine the initial dry weight of dead
160 roots (X_0 , g DM m⁻²), live roots were extracted in the same manner as in the fine root experiment (described later)
161 from 30 cm thick surface soil samples in a 0.3 m × 0.3 m area near each TC ($n = 5$) at each site in early November
162 2014. The roots were separated into three classes by diameter: fine (< 2 mm), medium (2–10 mm), and coarse

163 roots (> 10 mm). The root samples were air-dried, and parts of the samples were oven-dried at 70°C for 48 hours
164 to determine the water content of each root class. From the water content, the dry weights of the remaining air-
165 dried samples were determined. Air-dried samples were put into 2 mm meshed bags that were 10 cm × 10 cm;
166 samples were 1, 3, and 5 g in dry weight, respectively, for fine, medium, and coarse roots. In each site, 25 bags for
167 each class were buried in the A horizon near TC in late November 2014. Five bags were collected from each class
168 five times until May 2017, and the dead roots remaining in the bags were oven-dried. The decomposition constant
169 k (year⁻¹) was determined using the following equation (Wieder and Lang 1982):

$$170 \quad Y = Y_0 \cdot \exp(-k \cdot t) \quad (5)$$

171 where Y is the dry weight of remaining dead roots (g DM bag⁻¹) at time t (year), and Y_0 is the initial dry weight of
172 root samples (g DM bag⁻¹). From k and X_0 , annual R_d (g C m⁻² year⁻¹) from November 2014 was calculated for
173 each root class using a conventional conversion factor of 0.5 from root dry matter to carbon (Chapin III et al. 2011;
174 Ravindranath and Ostwald 2008).

$$175 \quad R_d = 0.5 \cdot X_0 \{1 - \exp(-k)\} \quad (6)$$

176

177 *Fine root experiment*

178 The sequential soil core method was applied to measure fine root biomass (B ; g DM m⁻²) and its temporal variation
179 (ΔB ; g DM m⁻² period⁻¹). Three soil cores were sampled from each SC in mid-November 2014, early May, mid-
180 June, early August, late September, and mid-November 2015. To confirm the trenching effect on fine root existence,
181 soil cores were also sampled similarly from TC in early May and mid-June 2015. Using a perforated board for
182 positioning, core sampling was made in each SC at three points, which were randomly selected from a grid with 8
183 cm spacing. Soil cores down to 14 cm were taken using a stainless-steel edged tube with an inner diameter of 2.4
184 cm. The total sampling area was 13.6 cm² for each collar each time, which accounted for 0.5% of the collar area
185 (0.25 m²). The collected core samples were first divided into the root mat (top 4 cm) and A horizon (lower 10 cm),
186 and then washed several times with tap water to remove soil particles and fragmented litter. Next, living fine roots
187 were extracted and were visually separated into tree and herbaceous roots in the DF site, where herbaceous plant
188 roots were not negligible. The fine roots were dried for 48 hours at 70°C and weighed. Tree fine roots originated

189 mainly from larch trees and shrub species in the DF site, but were almost entirely from spruce trees in the EF site.

190 The ingrowth core method (e.g. (Vogt et al. 1998)) was applied to measure fine root production (P ; g DM m⁻²
191 period⁻¹). Ingrowth cores were made of plastic cylindrical frames wrapped in a 2 mm meshed sheet. The cores
192 were 14 cm long and had a diameter of 2.3 cm. Soils were taken from the A horizon in September 2014, and roots
193 were removed using a 2 mm mesh after air drying. The cores were filled with root-free, air-dried soil and inserted
194 vertically into three pits after the soil core sampling at each SC. The ingrowth cores were replaced simultaneously
195 with the sequential core sampling. Soil samples in the collected ingrowth cores were first divided into the top 4
196 cm layer (root mat) and below 10 cm (A horizon), and washed to extract living fine roots. The fine roots were
197 weighed after drying for 48 hours at 70°C. The dry matter is equivalent to P through each sampling interval, and
198 annual P was calculated as the sum of periodic P over a year. Using a conventional factor of 0.5, dry matter was
199 converted to carbon. Annual mortality (M ; g DM m⁻² year⁻¹) was calculated as a difference between annual P and
200 annual ΔB . In addition, fine-root turnover rates were calculated as the ratio of annual P and mean B (Brunner et al.
201 2013).

202

203 *Growth and maintenance respirations*

204 The simple equation of growth (R_g) and maintenance respiration (R_m) partitioning follows (Amthor 2000) and
205 (Thornley 1970):

$$206 \quad R_r = R_g + R_m = g_R \cdot P + m_R \cdot B \quad (7)$$

207 where g_R is the growth respiration coefficient, and m_R is the maintenance respiration coefficient. To adopt the
208 equation for field data, it was modified into:

$$209 \quad R_r = R_g + R_m + h = c \cdot P + d \cdot \exp(f \cdot T_s) \cdot B + h \quad (8)$$

210 where c is g_R (g C g DM⁻¹), d is base respiration rate per unit biomass at 0°C (g C g DM⁻¹ day⁻¹), f is a temperature
211 coefficient (°C⁻¹), T_s is soil temperature at a depth of 5 cm (°C), and h is residual (g C m⁻² day⁻¹), which includes
212 the respiration of ion uptake, herbaceous roots, and thicker roots. $d \cdot \exp(f \cdot T_s)$ is equivalent to m_R (g C g DM⁻¹ day⁻¹)
213 at T_s . The parameters of c , d , f , and h were determined by curve fitting to the data set of R_r (g C m⁻² day⁻¹), P (g
214 DM m⁻² day⁻¹), B (g DM m⁻²), and T_s , which were calculated at the same intervals. The R_r and T_s were averaged

215 over each interval of P measurement, and B was the mean of two measurements at the beginning and end of an
216 interval. Next, R_r , P , and B were spatially averaged for each site ($n = 5$). Thus, the number of the data set for the
217 four variables (R_r , T_s , P , and B) was equivalent to the frequency of P measurement ($n = 5$).

218

219 *Statistical analysis*

220 ANOVA and post hoc Tukey's HSD were applied to compare environmental factors, fine root biomass, fine root
221 production, and soil CO₂ effluxes among treatments. t -test was applied to compare mean values between the sites.
222 Parameters in the equations were determined by curve fitting to the data set ($n = 5$) for each forest. In addition,
223 uncertainties (± 1 SD) of annual R_g and R_m were estimated from those of the parameters and measurements using
224 the law of error propagation. Data analyses were conducted with a software package (Origin Pro 2015J; Origin
225 Lab Corporation, Northampton, MA, USA).

226

227 **Results**

228 *Environmental conditions*

229 Mean air temperature at 1.5 m aboveground and total precipitation measured in the nearby re-growing forest site
230 during the growing season from May to October 2015 were 14.0°C and 822 mm, respectively, which are within
231 the range of 1 SD from their decadal means of $14.4 \pm 0.5^\circ\text{C}$ and 949 ± 188 mm between 2006 and 2015. Daily
232 mean T_s peaked in August (Fig. 2a). Mean T_s was 8.8°C in the DF site and 7.5°C in the EF site from November
233 2014 to November 2015. The higher T_s in the DF site was mainly caused by more incident solar radiation on the
234 forest floor through the defoliated canopy in spring. In 2015, SWC showed a seasonal variation with a minimum
235 in August, which was opposite to T_s (Fig. 2b).

236 Mean T_s was not significantly different among four treatments at both sites; however, it was significantly lower
237 in the EF site (Table 1). In contrast, mean SWC significantly increased after trenching (TC), though no significant
238 difference was found between the sites.

239

240 *Decomposition of dead roots*

241 Dead roots decayed exponentially. The decomposition constant k was higher in the DF site than in the EF site and
242 was highest for fine roots, followed by medium and coarse roots in both sites (Table 2). Using Eq. 6, annual R_d
243 was calculated for each root class using the k values and initial root biomass and totaled 131 and 89 g C m⁻² year⁻¹,
244 respectively, in the DF and EF sites (Table 2), accounting for 20% and 16% of the initial carbon content. The
245 contribution of fine root decomposition to the total R_d was 34% and 52%, respectively, in the DF and EF sites.

246

247 *Soil CO₂ efflux*

248 Soil CO₂ efflux was measured before the treatment and showed no significant difference among four collars in all
249 five replications in each site (ANOVA, $P > 0.05$), which indicates that correction for spatial variation in CO₂ efflux
250 was unnecessary. Also, no significant difference was found between CO₂ effluxes from CC and SC collars in 2015
251 even after the start of soil core sampling (paired t -test, $P > 0.05$); mean CO₂ effluxes (± 1 SD) were 4.97 ± 4.30
252 (CC) and 4.77 ± 3.34 (SC) $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the DF site, 3.91 ± 2.76 (CC) and 4.02 ± 2.69 (SC) $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the
253 EF site. These results indicate that the effect of core sampling on CO₂ efflux was negligible. Thus, CO₂ efflux from
254 SC was used as R_s to minimize spatial discrepancy between flux measurement and root sampling.

255 Soil CO₂ efflux showed a similar seasonal variation in both sites with a peak in late July (Fig. 3). Soil CO₂
256 efflux was significantly correlated to T_s ($P < 0.001$) in an exponential manner (Eq. 3) on every collar ($R^2 > 0.55$).
257 Figure 4 shows the mean relationships for SC and TC. The Q_{10} values (mean ± 1 SD, $n = 5$) calculated using the
258 fitting parameter (b) were 2.7 ± 0.5 (SC) and 3.0 ± 0.5 (TC) in the DF site, and 2.4 ± 0.2 (SC) and 2.4 ± 0.2 (TC)
259 in the EF site. The results were significantly higher ($P < 0.05$) in the DF site but not significantly different ($P >$
260 0.05) between SC and TC. Soil CO₂ efflux was normalized for mean T_s (R_b) according to Eq. 4 using T_b of 14°C
261 and 12°C, respectively, in the DF and EF sites (Table 1). In both sites, R_b had no significant relationship with SWC
262 ranging between 0.1 and 0.6 m³ m⁻³ (Fig. 5). Also, adding SWC did not improve adjusted R^2 than T_s alone. Thus,
263 using Eq. 3, hourly CO₂ efflux was estimated from T_s monitoring data for each collar and summed up over an
264 annual period starting in November 2014. The annual values ($n = 5$) were 1255 ± 401 (SC), 1044 ± 334 (LC), and
265 776 ± 83 (TC) g C m⁻² year⁻¹ in the DF site, and 1139 ± 386 (SC), 1027 ± 323 (LC), and 835 ± 172 (TC) g C m⁻²
266 year⁻¹ in the EF site. The SD was lower in TC than in SC, because spatial variations in root respiration were

267 excluded in TC. Annual R_s , R_l , R_h , and R_r were calculated from the annual soil CO₂ effluxes and R_d (Table 3). Here,
268 R_r includes not only the respiration of tree fine roots but also those of tree medium and coarse roots, and herbaceous
269 roots. The contributions of R_r to R_s were 49% and 35%, respectively, in the DF and EF sites. Also, R_d accounted
270 for 10% and 8% of R_s , respectively, in the DF and EF sites.

271

272 *Fine root dynamics*

273 Tree fine root biomass (B) showed a clear seasonal variation with a peak in September in the DF site (Fig. 6a),
274 whereas seasonality was indeterminable in herbaceous fine root biomass. In the EF site, B had less seasonality
275 (Fig. 6c). No herbaceous fine root biomass was found in the EF site. Peak B was 482 and 559 g DM m⁻²,
276 respectively, in the DF and EF sites (Figs. 6b and 6c). On average, 56% and 49% of B existed in the root mat in
277 the DF and EF sites, respectively. In TC, B in May and June 2015 were 32.0 ± 6.6 and 11.6 ± 1.4 g DM m⁻²,
278 respectively, in the DF site ($n = 5$), and 41.8 ± 10.2 and 16.4 ± 3.0 g DM m⁻², respectively, in the EF site ($n = 5$).
279 B decreased significantly between May and June ($P < 0.001$) in both sites. In June 2015, B in the trenched collars
280 (TC) decreased to 3% in comparison with the non-trenched collars (SC) in both sites.

281 No herbaceous fine root was found in the ingrowth cores even in the DF site, probably because herbaceous
282 plants were picked out periodically. Tree fine root production (P) showed a distinct seasonality with a peak between
283 2.3 to 2.5 g DM m⁻² day⁻¹ in summer (mid-June to early August) in both sites (Figs. 6d and 6e). The seasonal
284 variations of B and P were similar in the DF site (Figs. 6b and 6d). Even during winter and early spring between
285 November 21, 2014 and May 1, 2015, P was measured at 0.14 ± 0.08 and 0.22 ± 0.14 g DM m⁻² day⁻¹ in the DF
286 and EF sites, respectively; P was not significantly different between the sites ($P = 0.26$). The P was positively
287 correlated ($P < 0.05$) with mean T_s during core-sampling intervals (Fig. 7) but showed no significant relationship
288 with SWC ($P > 0.05$, data not shown). In both sites, R_r was significantly correlated with P (Fig. 8, $P < 0.05$), but
289 not with B ($P > 0.05$, data not shown).

290 Annual P was not significantly different between the DF and EF sites (Table 4). Although the root mat was only
291 4 cm thick, P in the root mat accounted for 45 to 48% of total P . Mean B was significantly larger in the EF site (P
292 < 0.01), although the difference was not significant if herbaceous fine root biomass was included ($P > 0.05$). In

293 the DF site, herbaceous fine root biomass accounted for 25% (110 g DM m⁻²) of total *B*. In November 2014, fine
294 root accounted for 20% and 33% of total tree root biomass, respectively, in the DF and EF sites (Table 2). The tree
295 fine root turnover rate was $1.08 \pm 0.36 \text{ year}^{-1}$ in the DF site, which was significantly larger than $0.68 \pm 0.12 \text{ year}^{-1}$
296 in the EF site ($P < 0.05$).

297

298 *Partitioning root respiration into growth and maintenance components*

299 R_r was partitioned into R_g and R_m using Eq. 8. In both sites, no significant correlation was found between P and B
300 ($P > 0.05$). Despite a relatively high R^2 (≥ 0.87), the fitting was not significant ($P \geq 0.065$) because of the small
301 number of samples ($n = 5$) for both sites (Table 5). All four parameters were not significantly different between
302 the sites ($P \geq 0.55$). The Q_{10} of R_m calculated from f (temperature coefficient) were 3.3 and 2.6, respectively, for
303 DF and EF. Using these parameters, annual R_g and R_m were calculated (Table 6). The annual totals ($R_g + R_m + h$)
304 were 638 and 396 g C m⁻² year⁻¹, respectively, in the DF and EF sites. These totals exceeded R_r by 28 and 3 g C m⁻²
305 year⁻¹, respectively, in the DF and EF sites. The contribution of R_g to the total was almost the same (19 vs. 22%),
306 though R_m was larger in the EF site (26 vs. 46%). As a result, h contributed more in the DF site.

307

308 **Discussion**

309 *Soil respiration and root respiration*

310 Root respiration (R_r) was calculated as the residual of total soil respiration (R_s) after subtracting leaf litter
311 decomposition (R_l) and soil heterotrophic respiration (R_h) (Eq. 2). Thus, R_r corresponds to mycorrhizosphere
312 respiration, which consists of not only respiration of living root tissue but also rhizomicrobial and mycorrhizal
313 respiration (Moyano et al. 2009). There was no significant difference in soil CO₂ efflux between control (CT) and
314 sampling collars (SC) even after soil sampling. Thus, soil CO₂ efflux on SC was treated as R_s , because it enabled
315 us to directly compare soil CO₂ efflux and fine root dynamics in the same collar.

316 Trenching is a commonly used method to estimate soil heterotrophic respiration, although it potentially causes
317 biases owing to dead root decomposition, lack of water uptake by roots, and lack of root litter input (Epron et al.
318 1999; Hanson et al. 2000; Subke et al. 2006). In this study, dead root decomposition (R_d) was quantified by the

319 litter bag method. Soil water content (SWC) was significantly higher in TC (Table 1), but no relationship with soil
320 CO₂ efflux was found using bivariate models and temperature-normalized CO₂ efflux (Fig. 5), suggesting that an
321 increase in SWC minimally affected soil CO₂ efflux. Tree fine root biomass (*B*) in TC was only 3% in comparison
322 with SC in June 2015, which indicates that trenching worked effectively. In contrast, belowground microbial
323 respiration was probably underestimated to a small extent due to the lack of root litter input (Subke et al. 2006).
324 Also, trenching killed ectomycorrhizal fungi and consequently might have enhanced the decomposition of soil
325 organic matter by saprotrophic fungi (Gadgil effect) (Fernandez and Kennedy 2016).

326 The annual R_s of 1255 and 1139 g C m⁻² year⁻¹ (Table 3) estimated from hourly T_s , were relatively large but
327 within the range of reported values from temperate forests (Subke et al. 2006), which were 828 ± 267 g C m⁻² year⁻¹
328 for coniferous forests and 976 ± 514 g C m⁻² year⁻¹ for deciduous forests, respectively (mean \pm 1 SD, $n = 28$).
329 Our results were also larger than the annual R_s of 760 ± 40 g C m⁻² year⁻¹ measured for 8 years in a Japanese larch
330 plantation in central Japan (Teramoto et al. 2017), which had an annual air temperature (8.6°C) similar to our site
331 (8.3°C). Before the typhoon disturbance, annual R_s was 934 g C m⁻² year⁻¹ in the DF site in 2003 (Liang et al.
332 2010), which was smaller by 321 g C m⁻² year⁻¹ than in 2015 despite having similar annual mean soil temperatures
333 (8.6°C in 2003 and 8.8°C in 2015). The larger R_s in 2015 was partly due to higher soil temperature during the
334 summer. In 2015, soil temperature in July and August were higher on average by 2.4°C because of a sparser canopy.
335 The annual contributions of R_r to R_s (R_r / R_s) were 0.49 and 0.35, respectively, in the DF and EF sites (Table 3).
336 These ratios were compatible with results from a meta-analysis (Subke et al. 2006), where R_r / R_s was calculated
337 to be 0.43 ± 0.21 for deciduous forests and 0.49 ± 0.14 for coniferous forests ($n = 28$, respectively).

338 The decomposition of dead tree roots was well explained with the rate constant of k (Table 2). The k was higher
339 in the DF site than in the EF site (0.16–0.42 vs. 0.10–0.29 year⁻¹) and highest for fine roots. A study conducted in
340 a beech forest in France showed k values of 0.38 year⁻¹ for fine roots and 0.22 year⁻¹ for coarse roots (> 2 mm)
341 (Epron et al. 1999), which is similar to the result in the DF site. Also, a meta-analysis reported that mean k values
342 for fine roots were 0.44 and 0.17 year⁻¹, respectively, for broadleaf and coniferous forests, and k values became
343 lower with root diameter (Silver and Miya 2001). Annual R_d were 131 and 89 g C m⁻² year⁻¹, respectively, for DF
344 and EF sites (Table 3), which accounted for 10% and 8% of annual R_s , respectively. If the R_d was neglected in Eq.

345 2, R_r would be calculated to be 479 and 304 g C m⁻² year⁻¹, respectively, for DF and EF sites, which would
346 underestimate R_r by 21% and 23%. In a beech forest, (Epron et al. 1999) reported that R_r was 40% underestimated
347 by annual R_d of 160 g C m⁻² year⁻¹.

348

349 *Fine root dynamics*

350 We applied the sequential coring method for tree fine root biomass (B) and the ingrowth core method for tree fine
351 root production (P) for a total soil depth of 14 cm. In this area 83–85% of fine roots existed in the surface 15 cm
352 of the soil layer (Sakai et al. 2007), suggesting underestimation of B and P in this study. The ingrowth core method
353 has been widely applied mainly because of its easy applicability (Addo-Danso et al. 2016). However, the ingrowth
354 core method tends to underestimate P in comparison with the minirhizotron method, which yields more reliable
355 estimates (Addo-Danso et al. 2016; Finér et al. 2011b; Hendricks et al. 2006; Majdi et al. 2005). Thus, our P results
356 could be underestimated.

357 In both sites, P showed a clear seasonality with a peak in summer and was found to be 0.14–0.22 g DM m⁻²
358 day⁻¹ even during a period from winter through early spring (Fig. 6). The period ranged from November 21, 2014
359 to May 1, 2015, in which albedo indicated that snow covered the ground from December 2 to April 4 in a nearby
360 re-growing forest site (Hirano et al. 2017). Mean soil temperature in the period was 1.4 and 0.4°C, respectively, in
361 the DF and EF sites. A delay in temperature rise in April in the EF site (Fig. 2) was caused by delayed thaw due to
362 a dense canopy, indicating that snow covered the ground until April 20 in the EF site. In addition, larch trees were
363 still leafless on May 1, 2015. In this area larch trees usually begin to leaf out in early May (Hirano et al. 2003a).
364 Therefore, despite including early spring after thaw the measured P suggests that tree fine roots grew during winter
365 (Radville et al. 2016).

366 The seasonal P was well explained by soil temperature (T_s) (Fig. 7). Similar seasonal variations were reported
367 from many boreal and temperate forests (Brassard et al. 2009; Fukuzawa et al. 2013; Noguchi et al. 2005; Steinaker
368 et al. 2010; Tierney et al. 2003). Also, B increased in summer in the DF site, whereas no clear seasonal variation
369 was found in the EF site (Fig. 6). Although summer B was comparable, winter B was greater in the EF site. The
370 discrepancy in seasonality was probably attributed to the life span of fine roots. Mean life span, as the reciprocal

371 of a turnover rate, was 0.93 and 1.47 year, respectively, in the DF and EF sites (Table 4). In the EF site, the longer
372 life span may not have decreased B even in winter. In boreal and temperate forests, some studies reported seasonal
373 variations similar to the DF site (Brassard et al. 2009; Coleman et al. 2000), but other studies found no seasonality
374 (Fukuzawa et al. 2013; Makkonen and Helmisaari 1998; Noguchi et al. 2005).

375 Annual mean B was 340 and 516 g DM m⁻², respectively, in the DF and EF sites (Table 4). These values are
376 smaller than mean values of 505 g DM m⁻² in deciduous broadleaf forests and 607 g DM m⁻² in evergreen conifer
377 forests in temperate regions (Finér et al. 2011a). The reasons for the smaller B are possibly because of the thin
378 surface soil in both sites, tree thinning by the typhoon in the DF site, and possibly limited sampling depth. Annual
379 P in the two sites were almost the same (368 vs. 352 g DM m⁻² year⁻¹) despite the large difference of B . As a result,
380 turnover rates, which are defined as the ratio of annual P and mean B , were significantly higher in the DF site (1.09
381 year⁻¹) than in the EF site (0.68 year⁻¹). If the maximum B is used instead of mean B (Brunner et al. 2013), turnover
382 rates of the two sites are almost identical (0.30 vs. 0.31 year⁻¹). Although the ingrowth core method was used in
383 this study, the annual P was similar to the mean P of temperate forests (337 g DM m⁻² year⁻¹), which was measured
384 by various methods, especially using the sequential coring method (Finér et al. 2011b). Also, the P of this study
385 was slightly larger than that measured by the minirhizotron method from a cedar plantation (320 g DM m⁻² year⁻¹)
386 in central Japan (Noguchi et al. 2005). A review paper showed that the turnover rates from mean B were 1.10 year⁻¹
387 for both deciduous *Fagus sylvatica* and evergreen *Picea abies* (Brunner et al. 2013). These turnover rates are
388 almost identical with the DF turnover rate. The turnover rate of the EF site was smaller than that of *Picea abies*.

389

390 *Growth and maintenance respiration*

391 R_r was partitioned into growth (R_g) and maintenance respirations (R_m) of tree fine roots using a model (Eq. 8) by
392 multiple regression. The defects of the model include the lack of respiration due to root-derived compounds
393 (rhizomicrobial and mycorrhizal respiration) and ion uptake. In addition, respiration except tree fine roots were
394 not included in the analyses. Moreover, B and P were probably underestimated because of the limited sampling
395 depth of 14 cm and the use of the ingrowth core method. These facts certainly resulted in considerable uncertainty.
396 Rhizomicrobial and mycorrhizal respiration may be related to P and B , because they depend on rhizodeposits and

397 carbohydrates derived from roots (Moyano et al. 2009). Ion uptake respiration is expected to correlate to tree
398 photosynthesis (Lambers et al. 2008). Although we did not consider ion uptake respiration, gross primary
399 production (GPP) of the larch forest growing in the DF site before the typhoon disturbance peaked in June-July
400 (Hirano et al. 2003a; Hirata et al. 2007). Also, in an evergreen conifer forest of *Pinus resinosa* in Japan, GPP
401 peaked in June-August (Mizoguchi et al. 2012). These seasonal variations of GPP are like those of *P* with a peak
402 in summer (Fig. 6). Thus, ion uptake respiration was probably partly included in R_g . The residual (h) was much
403 larger in the DF site (Table 6), which is consistent with the fact that B accounted for only 20% of total tree root
404 biomass (Table 2), and herbaceous root biomass accounted for 24% of total fine root biomass (Table 4).

405 The sums of R_g and R_m , which were rough estimates of tree fine root respiration, were similar between the DF
406 and EF sites (287 vs. 268 g C m⁻² year⁻¹; Table 6), although their contributions to total root respiration were different
407 (45 vs. 68%). (George et al. 2003) used short-term chamber measurements and published information to partition
408 fine root respiration into growth, maintenance, and ion uptake (only nitrogen) components in deciduous
409 (*Liquidambar styraciflua*) and evergreen (*Pinus taeda*) forests. They reported that annual fine root respiration in
410 the deciduous and evergreen forests were 245 and 639 g C m⁻² year⁻¹, respectively, and maintenance respiration
411 accounted for 86 and 98% of the total fine root respiration, respectively. Although annual P (345 g DM m⁻² year⁻¹)
412 of the deciduous forest was almost identical to that (368 g DM m⁻² year⁻¹) of the DF site (Table 4), growth
413 respiration (24 g C m⁻² year⁻¹) was only 20% of the DF's R_g (Table 6). Their ion uptake respiration was less than
414 4% of total fine root respiration. When limited to the growing season between May and November, tree fine root
415 respiration (R_g plus R_m) were calculated to be 260 and 230 g C m⁻², respectively, in the DF and EF sites. These
416 values are similar to those estimated from chamber measurements for *Quercus rubra* (229 g C m⁻²), *Tsuga*
417 *canadensis* (242 g C m⁻²), and *Fraxinus alba* (270 g C m⁻²) in the Harvard Forest (Abramoff and Finzi 2016).

418 The R_g accounted for 42 and 32% of the total fine root respiration in the DF and EF sites, respectively (Table
419 6). The higher contribution in the DF site might be due to its higher turnover rate (Lambers et al. 2008). Growth
420 (g_R) and maintenance (m_R) coefficients (Eq. 7) of whole root respiration for some species have been determined
421 from growth chamber or greenhouse experiments. Using the units of mmol O₂ (g DM)⁻¹ for g_R and nmol O₂ (g
422 DM)⁻¹ s⁻¹ for m_R , and explicitly including the respiration of ion uptake in g_R , whole root g_R and m_R , respectively,

423 were 11 and 26 for *Dactylis glomerata*, 19 and 21 for *Festuca ovina*, 12 and 6 for *Quercus suber*, and 18 and 22
424 for *Triticum aestivum* (Lambers et al. 2008). For *Eucalyptus* sp. cuttings, g_R and m_R of whole root respiration were
425 $5.2 \text{ mmol CO}_2 (\text{g DM})^{-1}$ and $9.7 \text{ nmol CO}_2 (\text{g DM})^{-1} \text{ s}^{-1}$, respectively, at 22°C (Thongo M'Bou et al. 2010), in
426 which ion uptake respiration was not separated from R_g . As for fine roots in field conditions (George et al. 2003),
427 g_R coefficients were $5.1 (P. taeda)$ and $5.8 \text{ mmol CO}_2 (\text{g DM})^{-1} (L. styraciflua)$, and m_R coefficients were $8.9 (P.$
428 $taeda)$ and $10.2 \text{ nmol CO}_2 (\text{g DM})^{-1} \text{ s}^{-1} (L. styraciflua)$ at 25°C . In our study for tree fine roots, $g_R (= c)$ were 26.7
429 and $20.0 \text{ mmol CO}_2 (\text{g DM})^{-1}$, respectively, in the DF and EF sites. In addition, $m_R (= d \cdot \exp(f \cdot T_s))$ were 5.5 (DF)
430 and 2.7 (EF) $\text{nmol CO}_2 (\text{g DM})^{-1} \text{ s}^{-1}$ at 22°C , and 7.9 (DF) and 3.6 (EF) $\text{nmol CO}_2 (\text{g DM})^{-1} \text{ s}^{-1}$ at 25°C . The m_R
431 increases with T_s according to Q_{10} of 3.3 and 2.6, respectively, in the DF and EF sites. Although the respiratory
432 quotient should be considered, g_R of our study was relatively higher than those of the other species. However, our
433 study's m_R were lower. Most of the differences in the coefficients possibly arose from differences in chemical
434 composition of the roots, different rates of alternative pathway respiration, and different methods used (Lambers
435 et al. 2008). In addition, differences between whole root respiration and fine root respiration would be another
436 reason for the different coefficients.

437

438 **Conclusions**

439 We conducted a year-round field experiment to measure the production and biomass of tree fine roots, and soil
440 respiration simultaneously in adjoining deciduous and evergreen forests on the same soil type. The periodic
441 measurement of the three items was made in the same collar to minimize inconsistency among items by spatial
442 positions. Using the field data, we partitioned tree fine root respiration into its growth and maintenance components
443 on an annual basis by multiple regression using an empirical model. Growth (g_R) and maintenance (m_R) coefficients
444 of the model were not significantly different between the forests. In comparison with reported values from
445 laboratory or greenhouse experiments, in our study g_R was higher, but m_R was lower. Considerable uncertainty in
446 the partitioning arose from a small sample size, the existence of thicker roots, and uncertainty in field measurement.
447 However, the results suggest the availability of the approach using the model in field. To obtain more reliable
448 results, ion uptake respiration should be incorporated into the model.

449

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456

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646 **Table 1** Soil temperature (T_s) at a depth of 5 cm and soil water content (SWC) of 5-cm-thick surface soil in chamber
647 collars with four different treatments (CC, SC, LC and TC). T_s and SWC were measured simultaneously with
648 soil CO₂ efflux once or twice a month between May 2015 and November 2015. Mean \pm 1 SD of all
649 measurements is shown ($n = 12$). Different letters in the same row denote significant difference among the
650 treatments and between the sites ($P < 0.05$) according to Tukey's HSD after ANOVA ($P < 0.01$).

Treatment	Site	T_s (°C)	SWC (m ³ m ⁻³)
CC	DF	14.7 \pm 0.9a	0.25 \pm 0.05a
	EF	12.4 \pm 0.4b	0.28 \pm 0.04a
SC	DF	14.7 \pm 0.9a	0.27 \pm 0.07a
	EF	12.5 \pm 0.4b	0.26 \pm 0.07a
LC	DF	14.6 \pm 0.8a	0.29 \pm 0.08a
	EF	12.5 \pm 0.4b	0.25 \pm 0.06a
TC	DF	14.4 \pm 0.8a	0.43 \pm 0.09b
	EF	12.3 \pm 0.3b	0.35 \pm 0.06b
ANOVA (P value)	Site	<0.0001	0.25
	Treatment	0.85	0.0004
	Interaction	0.98	0.35

651
652 **Table 2** Biomass of tree fine (< 2 mm), medium (< 10 mm) and coarse (> 10 mm) roots sampled in November
653 2014 from 30-cm-thick surface soil. Mean \pm 1 SD ($n = 5$) is shown. The decomposition constant (k)
654 determined by curve fitting to Eq. 5 (R^2) and annual decomposition (R_d) of tree dead roots in trenched
655 collars (TC) were also shown. Numbers in parentheses denote the percentage against Total.

Site	Root class	Initial biomass (g DM m ⁻²)	k (yr ⁻¹)	r^2	RD (g C m ⁻² yr ⁻¹)
DF	Fine	262 \pm 128 (20)	0.42	0.98	45
	Medium	278 \pm 152 (22)	0.25	0.91	31
	Coarse	750 \pm 636 (58)	0.16	0.97	55
	Total	1290 (100)			131
EF	Fine	362 \pm 104 (33)	0.29	0.98	46
	Medium	454 \pm 194 (42)	0.14	0.91	30

Coarse	276 ± 384 (25)	0.10	0.91	13
Total	1092 (100)			89

656

657 **Table 3** Annual sums (g C m⁻² year⁻¹) of soil respiration (R_s), leaf litter decomposition (R_l), root respiration (R_r),
658 belowground heterotrophic respiration (R_h), soil CO₂ efflux on trenched collars (R_{TC}), and decomposition
659 of tree dead roots in trenched collars (R_d) from November 2014 through November 2015 (mean ± 1 SD, n
660 = 5). Numbers in parentheses denote the percentage against R_s .

Site	R_s	R_l	R_r	R_h	R_{TC}	R_d
DF	1255 ± 401	211 ± 224	610 ± 447	434 ± 257	776 ± 83	131
	(100)	(17)	(49)	(35)	(62)	(10)
EF	1139 ± 386	112 ± 118	393 ± 356	634 ± 248	835 ± 172	89
	(100)	(10)	(35)	(56)	(73)	(8)

661

662 **Table 4** Summary of tree fine root dynamics in the root mat and A horizon. Annual production (P), biomass change
663 (ΔB), mortality (M), mean biomass (B) and turnover rates between November 2014 and November 2015
664 are shown as mean ± 1 SD ($n = 5$). Numbers in parentheses denote herbaceous fine root biomass.

Site	Root distribution	P (g DM m ⁻² year ⁻¹)	ΔB (g DM m ⁻² year ⁻¹)	M (g DM m ⁻² year ⁻¹)	Mean B (g DM m ⁻²)	Turnover rate (year ⁻¹)
DF	Root mat	178 ± 24	-25 ± 43	204 ± 66	190 ± 58 (64 ± 14)	0.94 ± 0.42
	A horizon	190 ± 22	39 ± 73	151 ± 63	150 ± 44 (46 ± 14)	1.27 ± 0.44
	Total	368 ± 42	14 ± 67	355 ± 73	340 ± 58 (110 ± 20)	1.08 ± 0.36
EF	Root mat	158 ± 42	-58 ± 42	216 ± 49	258 ± 32	0.61 ± 0.17
	A horizon	194 ± 46	10 ± 71	185 ± 87	258 ± 40	0.75 ± 0.18
	Total	352 ± 62	-48 ± 96	400 ± 126	516 ± 38	0.68 ± 0.12

665

666 **Table 5** Fitted parameters of the model (Eq. 8) (± 1 standard error).

	DF	EF
c (g C g DM ⁻¹)	0.32 ± 0.33	0.24 ± 0.20
d (g C g DM ⁻¹ day ⁻¹)	0.00041 ± 0.0019	0.00036 ± 0.0010

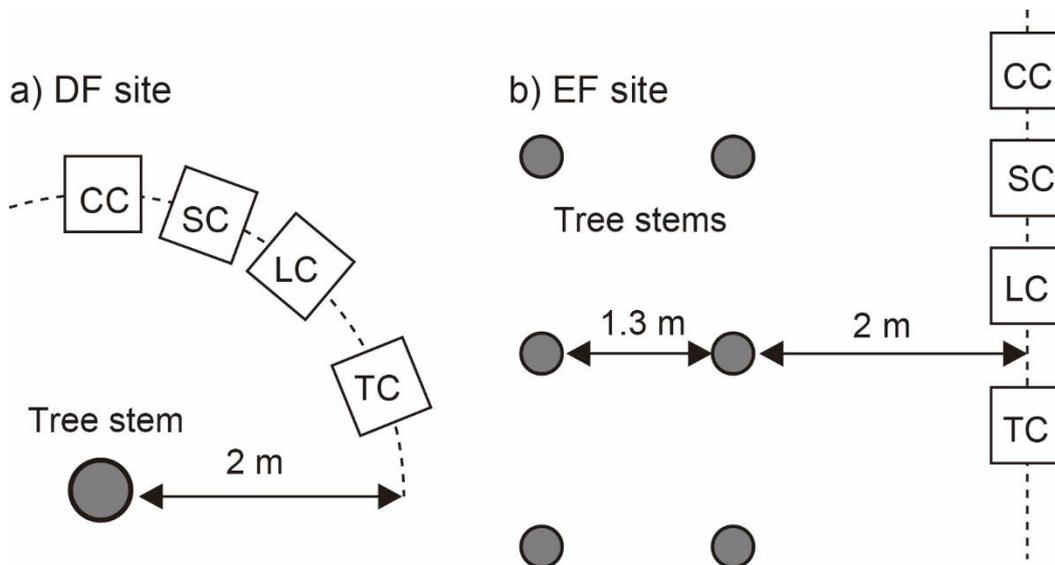
f ($^{\circ}\text{C}^{-1}$)	0.12 ± 0.21	0.094 ± 0.12
h ($\text{g C m}^{-2} \text{ day}^{-1}$)	0.94 ± 0.66	0.35 ± 0.68
Adjusted R^2	0.87	0.93
P value	0.087	0.065

667

668 **Table 6** Annual sums ($\text{g C m}^{-2} \text{ year}^{-1}$) of root respiration (R_r) in Table 3, tree fine root growth respiration (R_g),
669 maintenance respiration (R_m), residual (h), and total ($R_g + R_m + h$) from November 2014 through November
670 2015. These values were calculated using Eq. 8 with parameters in Table 5. Numbers in parentheses denote
671 the percentage against the total. Uncertainties (± 1 SD) were propagated from those of parameters and
672 measurements.

	DF	EF
R_r	610	393
R_g	121 (19)	86 (22)
R_m	166 (26)	182 (46)
h	351 (55)	128 (32)
Total	638 (100)	396 (100)

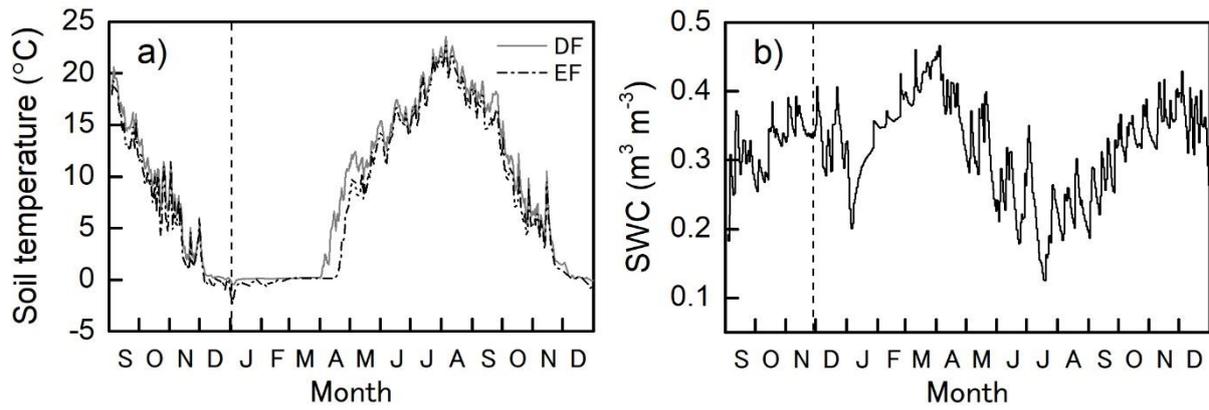
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674

675 **Fig. 1** Layout of collars for control (CC), sampling (SC), litter removal (LC), and trenching (TC) treatments.

676



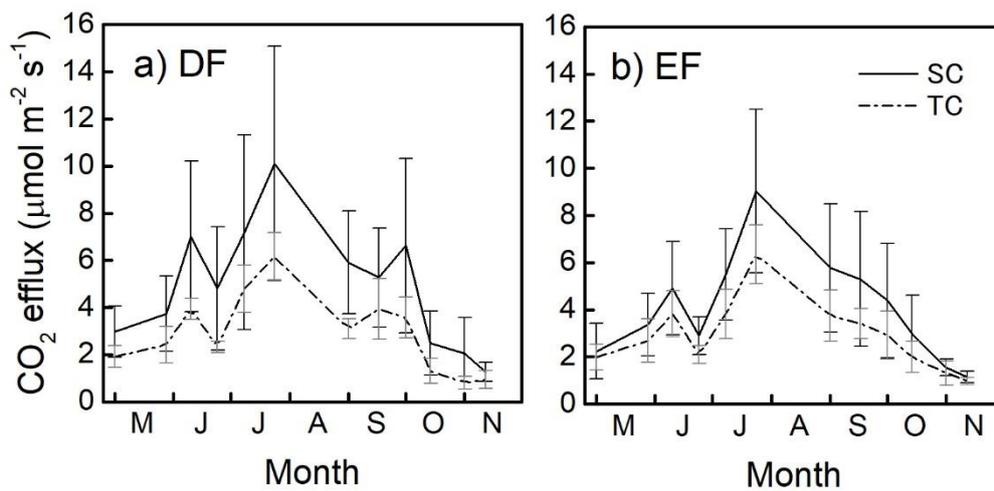
677

678 **Fig. 2** Seasonal variations in daily mean a) soil temperature (T_s) at a depth of 5 cm ($n = 2$) and b) soil water content

679 (SWC) at a depth of 3 cm ($n = 4$) from September 2014 through December 2015. SWC was measured at a

680 nearby re-growing forest site.

681

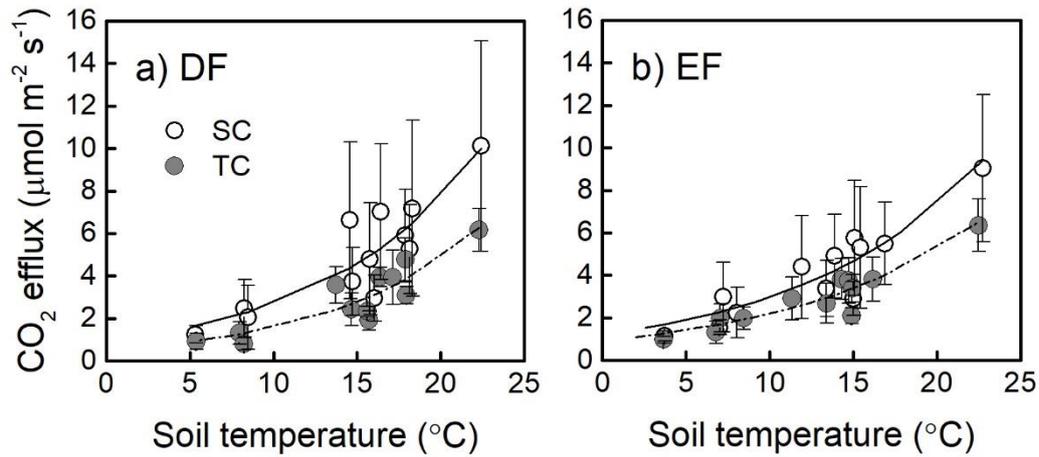


682

683 **Fig. 3** Seasonal variations in soil CO₂ efflux measured on SC and TC collars in a) DF and b) EF sites. Mean \pm 1

684 SD are shown ($n = 5$).

685



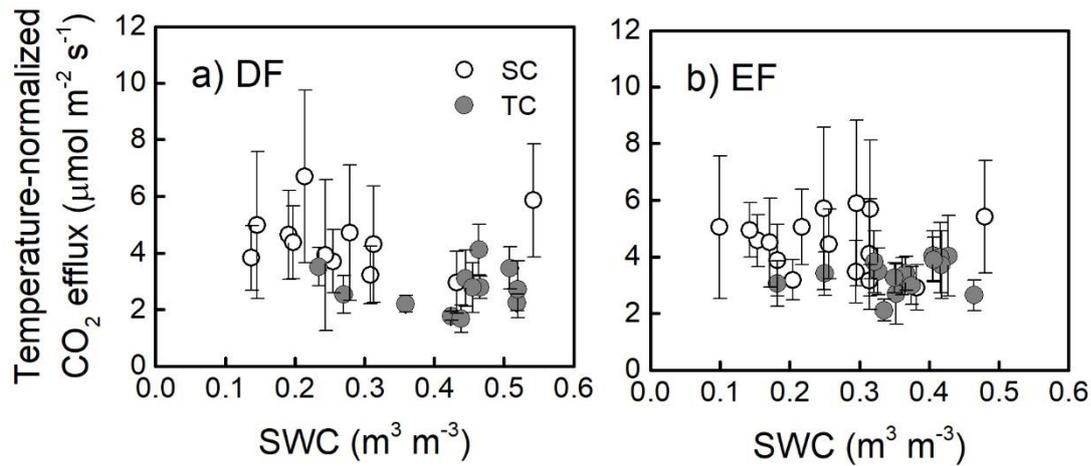
686

687 **Fig. 4** Relationship between soil CO₂ efflux and soil temperature at a depth of 5 cm for SC and TC collars in a)

688 DF and b) EF sites. Mean ± 1 SD are shown (*n* = 5). An exponential equation (Eq. 3) is fitted significantly (*P*

689 < 0.001).

690

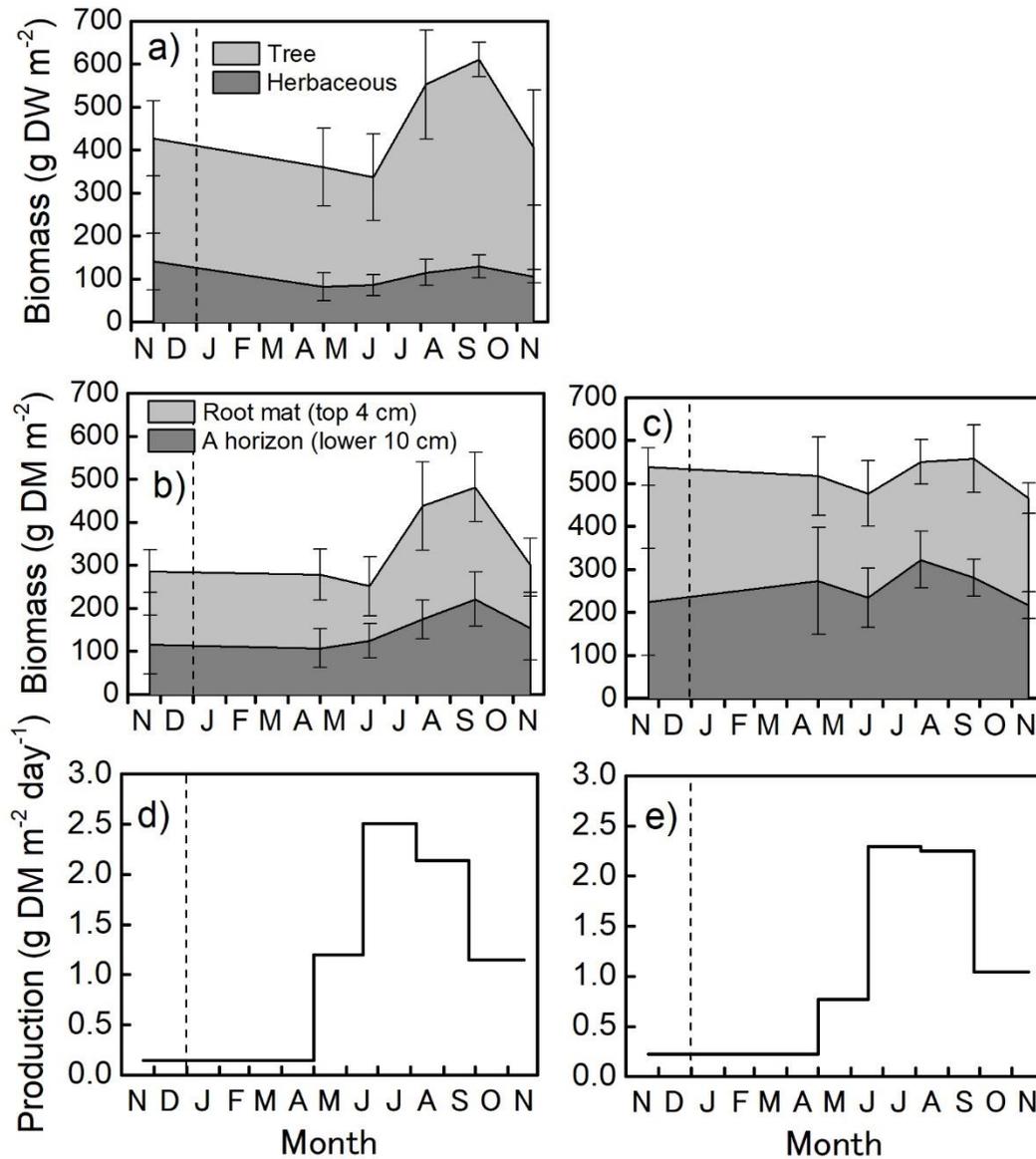


691

692 **Fig. 5** Temperature-normalized soil CO₂ efflux (*R_b*) against soil water content (SWC) of 5-cm-thick surface soil

693 for SC and TC collars in a) DF (at 14°C) and b) EF (at 12 °C) sites. Mean ± 1 SD are shown (*n* = 5).

694



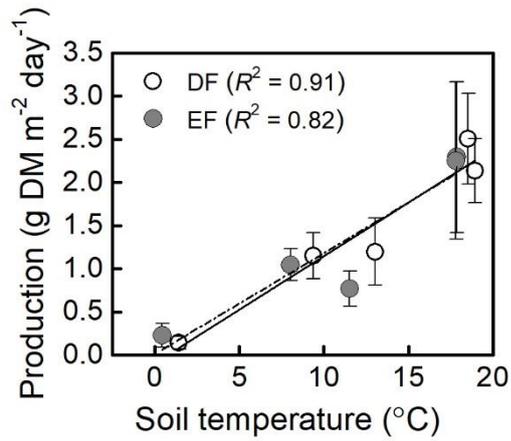
695

696 **Fig. 6** Seasonal variations in a) fine root biomass in DF site, b) tree fine root biomass (*B*) in DF site, c) *B* in EF

697 site, d) tree fine root production (*P*) in DF site and e) *P* in EF site from November 2014 through November

698 2015. Mean \pm 1 SD are shown ($n = 5$) in a) – c).

699

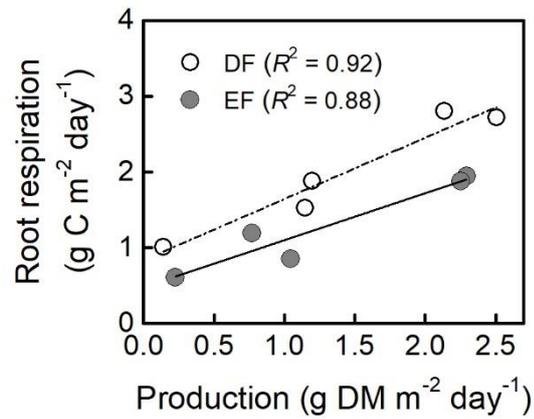


700

701 **Fig. 7** Relationship between tree fine root production (P) and soil temperature at a depth of 5 cm. Mean \pm 1 SD

702 are shown ($n = 5$). A line is fitted significantly ($P < 0.05$).

703



704

705 **Fig. 8** Relationship between root respiration (R_r) and tree fine root production (P). A line is fitted significantly (p

706 < 0.05).