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1 **Temporal variation in fine-root biomass, production and mortality in a cool temperate forest**

2 **covered with dense understory vegetation in northern Japan**

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16

17 This manuscript includes 37 pages of text, 5 tables and 6 figures.

18 Short running title: Temporal variation in fine root dynamics in a cool temperate forest

19

20 Abbreviations

21 FRP: Fine-root production, FRM: Fine-root mortality, FRB: Fine-root biomass

22 **Abstract**

23

24 To understand the temporal pattern of fine-root dynamics and the factors that affect it, we investigated
25 the seasonal and interannual variation in fine-root production (FRP) and fine-root mortality (FRM) rates,
26 as well as fine-root biomass (FRB) and necromass in a cool temperate forest in northern Japan that was
27 covered with dense understory vegetation of *Sasa senanensis*. We measured the root length density
28 (RLD) and the rate of root production and mortality over 3 years using minirhizotrons, and compared
29 these rates with temperature, precipitation, soil moisture, and plant area indices (PAI). We also measured
30 the FRB and the necromass of fine roots four times per year for 2 years using soil cores and calculated
31 dry weight-based FRP and FRM. FRB in the uppermost 15 cm of the surface-soil layer accounted for
32 41–61% of the biomass up to 60 cm soil depth, and decreased with increasing soil depth. The biomass of
33 fine roots with root diameters <0.5 mm was almost equivalent to that of roots measuring 0.5–2 mm in
34 diameter. *Sasa* roots accounted for 59–88% of the total FRB. FRB did not fluctuate seasonally, whereas
35 RLD did. The FRP rate was high in mid- to late summer and correlated significantly with air and soil
36 temperatures, indicating that temperature affects FRP. However, the relationship between FRP and soil
37 moisture was weak. FRP was significantly correlated with the PAI of oak trees and the increment in the
38 PAI of *Sasa*, suggesting that endogenous factors also affect FRP. Depending on the method used to
39 calculate turnover, mean FRP for the 3-year study period was 589 or 726 g m⁻² yr⁻¹, accounting for 36 or
40 41% of forest net primary production, respectively. The results of this study illustrate the substantial
41 seasonal and interannual fluctuations in FRP, and indicate that a significant proportion of assimilated
42 carbon was allocated to below-ground root systems in an oak-*Sasa* stand.

43

44 Keywords: fine roots, minirhizotron, oak forest, root biomass, root turnover, soil coring

45 **1. Introduction**

46

47 Despite making up only a small percentage of total tree biomass (Karizumi, 1977; Vogt et al., 1996;
48 Scarascia-Mugnozza et al., 2000; Helmisaari et al., 2002, Hertel et al., 2009), the rapid turnover of
49 fine-root biomass (FRB) means that fine roots (< 2 mm in diameter) are an important component of
50 carbon and nutrient cycling in forest ecosystems (McClaugherty et al., 1982; Hendrick and Pregitzer,
51 1992, 1993; Nadelhoffer and Reich, 1992). After reviewing studies on a global scale, Gill and Jackson
52 (2000) reported an average fine-root turnover of 0.56 yr^{-1} (maximum value: 2.6 yr^{-1}) in forest
53 ecosystems and showed that it increased with an increase in annual mean temperature. Finér et al. (2011)
54 also summarized global datasets and calculated the mean fine-root turnover of boreal, temperate, and
55 tropical forests to be 0.77, 1.21, and 1.44 yr^{-1} , respectively. Similarly, Yuan and Chen (2010) reported
56 that the average fine-root turnover in boreal forests was 1.07 yr^{-1} . These studies showed that fine-root
57 production (FRP) is an important component of total net primary production (NPP) in forest ecosystems;
58 indeed, several studies have reported that FRP contributes 40–60% of total NPP (Aber et al., 1985;
59 Hendrick and Pregitzer, 1993; Vogt et al., 1996; Tateno et al., 2004). However, considerable uncertainty
60 remains regarding the extent to which fine-root turnover and FRP can be generalized as both of these
61 factors can vary considerably, even under the same environmental conditions. In addition, since our
62 current knowledge of below-ground fine root dynamics and productivity is considerably more limited
63 than it is for above-ground biomass, further studies need to be conducted in this area.

64 Information on the temporal variation in FRB, FRP and fine-root mortality (FRM) is essential for
65 estimating fine-root turnover and FRP. Although seasonal variation in FRB has been reported to be a

66 small part of variation compared to spatial variation (Yuan and Chen, 2012), relating the temporal
67 patterns of fine-root dynamics to climatic factors at a local scale is necessary for generalizing FRP
68 characteristics and for anticipating fine-root dynamics under a changing climate (Tierney et al., 2003).
69 Minirhizotron-based techniques are useful for detecting temporal changes in fine-root dynamics because
70 they can pursue the fate of an individual root continuously under conditions in which FRP and FRM
71 occur simultaneously (Hendrick and Pregitzer, 1992; Fukuzawa et al., 2007; Satomura et al., 2007).

72 Several studies have shown that substantial FRP occurs during the growing season in forests ranging
73 from temperate to boreal (Tryon and Chapin, 1983; Joslin et al., 2001; Steinaker et al., 2010), although
74 there is a discrepancy in the peak period of root production. Of the factors that have been shown to
75 affect fine-root dynamics, soil temperature was considered to be the factor most closely correlated with
76 FRP in forests not experiencing soil drought (Tryon and Chapin, 1983; Steele et al., 1997; Steinaker et
77 al., 2010). On the other hand, soil moisture was correlated with FRP rate in temperate forests
78 experiencing severe drought in late summer (Joslin et al., 2001), illustrating the importance of
79 endogenous controls, such as timing of carbohydrate supply from leaves (Joslin et al., 2001; Tierney et
80 al., 2003). However, few studies relating seasonal patterns of FRP to shoot phenology have been
81 reported, limiting our understanding of the interactions between above- and below-ground environments
82 in areas with marked differences in seasonality (Steinaker et al. 2010). It is therefore still necessary to
83 measure fine-root dynamics and relate them to changes in environmental and endogenous factors in
84 forests with a diversity of vegetation types and climate conditions. In addition, since the pattern of
85 fine-root dynamics has been reported to differ among species (Kozłowski and Pallardy, 1997; Steinaker
86 et al. 2010; Fukuzawa et al., 2010), considering the species composition of the forest would be necessary,

87 unless the stand is in a plantation of a single species.

88 The role of understory vegetation in carbon and nutrient cycling in forests is not fully understood,
89 although some studies have suggested that it is important, especially in temperate or boreal forests
90 (Nilsson and Wardle, 2005; Moore et al., 2007; Koike et al., 2010; Cavard et al. 2011; Finér et al., 2011).

91 In northern Japan, *Sasa* dwarf bamboo grows very densely as understory vegetation in forest ecosystems.
92 Fukuzawa et al. (2007) showed that the FRB of *Sasa* spp. is larger than that of the trees in such
93 ecosystems and suggested the possibility that the leaf phenology of *Sasa* determines the pattern of FRP.
94 Their study focused on the role of *Sasa* in carbon and nutrient cycling in cool temperate forests.
95 However, because their study was based on observations from a single year with no observations from
96 autumn to winter, the resulting data had uncertainties regarding seasonal and interannual variations in
97 the pattern of fine-root dynamics. Ruess et al. (1998) reported that FRP is large in Alaskan boreal forests
98 mainly dominated by willow species, with interannual variation exceeding two-fold, and suggested that
99 this interannual variation is affected by annual differences in climatic conditions. Furthermore, even
100 under the same temperature conditions, the endogenous situation can differ between spring and autumn
101 (Tierney et al., 2003). Thus, in order to more accurately clarify the dominant factors affecting fine-root
102 dynamics and to predict their effects, examining fine-root dynamics throughout the year over multiple
103 years, and relating these observations to environmental and endogenous factors, is considered necessary.
104 Secondly, it is also necessary to evaluate mass-based FRP per unit area and compare it with
105 above-ground production in order to clarify the role of fine roots in carbon and nutrient cycling (Vogt et
106 al., 1986).

107 We hypothesized that the seasonal and interannual patterns of FRP and FRM are influenced by

108 environmental factors, such as temperature and soil moisture, and that above-ground phenological
109 fluctuations, particularly those of understory *Sasa*, also affect temporal changes in fine-root dynamics
110 and productivity of forest ecosystems.

111 The objectives of this study were as follows: (1) to determine the seasonal and interannual variation in
112 FRB, FRP and FRM in a cool temperate forest in northern Japan, and relate these fine-root parameters to
113 climatic factors, such as air and soil temperatures, precipitation, and soil moisture, as well as to
114 above-ground phenology, which is related to endogenous controls; (2) to evaluate fine-root turnover and
115 mass-based FRP and FRM in the forest, including *Sasa*, and to elucidate the contribution of fine-root
116 productivity to forest NPP.

117

118 **2. Materials and methods**

119

120 2.1. Study site

121

122 We conducted the study in a mature cool temperate forest in the Teshio Experimental Forest of
123 Hokkaido University in northern Japan (45°03'N, 142°06'E, 70 m a.s.l.). The dominant tree species,
124 which constituted 84.5 Mg ha⁻¹ of above-ground tree biomass, consisted of Mongolian oak (*Quercus*
125 *crispula*), followed by birches (*Betula ermanii* and *B. platyphylla* var. *japonica*) and Sakhalin fir (*Abies*
126 *sachalinensis*) (Koike et al., 2001). The forest floor was covered with a dense understory of evergreen
127 dwarf bamboo, *Sasa senanensis*. There is continuous snowpack from November to late April or early
128 May, with maximum snow depth (about 1.5 m) occurring in March. The bedrock is Cretaceous

129 sedimentary rock and the dominant soil is a Gleyic Cambisol (FAO, 1990) with about 10 cm of O
130 horizon with a mor humus type, 20 cm of A horizon, and 30 cm of B horizon.

131 To investigate fine-root dynamics and the environmental parameters described in the following
132 section, we established a 0.25 ha plot at the study site and selected three oak trees within the plot aged
133 approximately 160 yr and 50–60 cm in diameter at breast height (DBH). We set the observation points
134 under the tree canopy to cover both trees and *Sasa* vegetation. Observations were conducted over three
135 growing seasons, from late April 2002 to November 2004.

136

137 2.2. Minirhizotrons

138

139 We observed fine-root length-based production and mortality using minirhizotrons (BTC-100X camera
140 system and BTC I-CAP software, Bartz Technology Corp., Santa Barbara, CA, USA). In June 2001, we
141 installed transparent acrylic tubes (2 m long with a 5.08 cm inside diameter) 2 m from the three
142 observed oak trees at an angle of 45° to the soil surface, slanting toward the observed trees. We captured
143 digital images of the soil, including fine roots in contact with one side of each tube, and stored the
144 digital images on a personal computer. Each image (18 × 13.5 mm) was obtained at 3 cm depth intervals
145 within each tube to a depth of 45 cm. Minirhizotron measurements were conducted from April 2002 to
146 November 2004 at monthly intervals during the growing season. We also obtained images three times
147 during the dormant season (December, February, and early April of 2003–2004). Accordingly, we
148 analyzed 836 images over the three-year period.

149 We used MSU ROOTs Tracer software (Michigan State University, East Lansing, MI, USA) to

150 analyze the roots in the captured images. We traced the length and diameter of each individual root in
151 each image and converted the values to length per imaged area (root length density (RLD): mm cm⁻²).
152 For each tube, FRP was evaluated as the sum of the length of new roots and the increase in the length of
153 existing roots during each observation interval. Similarly, we evaluated the FRM rate as the sum of the
154 length of roots that disappeared (Tingey et al., 2000; Satomura et al., 2007). RLD, FRP, and FRM values
155 obtained from five images were averaged for each 15 cm-thick soil layer for each tube. Coarse roots, i.e.
156 roots thicker than 2.0 mm in diameter, were not evaluated in this study.

157 We calculated the turnover rate of FRP and FRM for each tube as the proportion of the cumulative
158 annual length-based root production (ALRP) to maximum RLD (RLD_{max}) or mean RLD (RLD_{mean})
159 according to equation 1, and the annual length-based mortality (ALRM) to RLD_{max} or RLD_{mean}
160 according to equation 2, respectively (Gill et al. 2002):

161 Turnover rate of production (yr⁻¹) = ALRP/RLD_{max} or ALRP/RLD_{mean} (Eq. 1)

162 Turnover rate of mortality (yr⁻¹) = ALRM/RLD_{max} or ALRM/RLD_{mean} (Eq. 2)

163 where ALRP and ALRM are expressed in mm cm⁻² yr⁻¹ and RLD_{max} and RLD_{mean} in mm cm⁻². We used
164 RLD_{max} and RLD_{mean} for each year, based on the observed seasonal change in RLD. We also calculated
165 the mean turnover rate as the ratio of mean ALRP or ALRM to mean RLD_{max} or RLD_{mean} for the three
166 years.

167

168 2.3. Soil coring

169

170 We used a soil coring technique to measure FRB and necromass. We collected soil to a soil depth of 60

171 cm using a soil auger (inner diameter, 4.2 cm) in June, August, September, and October 2003, and May,
172 July, September, and October 2004. Each soil sample was collected at a distance of 2 m from each oak
173 tree, and the average of three points was used for further analyses. We divided the 60 cm soil core to
174 four layers of 15 cm, washed them with water and then sieved them through a 0.25 mm mesh to collect
175 the roots. We categorized the roots by state (living and dead), species (*Sasa* and trees) and diameter
176 classes (<0.5 and 0.5 to 2.0 mm). We defined dead roots (necromass) as dark, inelastic roots. In
177 measuring root necromass, classification by diameter was not conducted because of the fragility of the
178 roots. We then oven-dried (70°C, 48 h) and weighed the samples. In all samples, herbaceous roots other
179 than *Sasa* were so rare that we considered their contribution to be negligible because of the dense
180 coverage by *Sasa*.

181

182 Mass-based fine-root productivity and mortality

183 Dry mass-based FRP and FRM were calculated according to Eq. 3 and Eq. 4, respectively, by assuming
184 that the turnover rate of length-based values coincides with that of the dry mass-based value (Hendrick
185 and Pregitzer, 1993). Turnover rates in Eq. 3 and Eq. 4 were obtained from Eq. 1 and Eq. 2, respectively.
186 For the calculation using RLD_{max} , we used FRB data obtained within one month after the RLD_{max} was
187 observed in December 2003 and September 2004. For the calculation of the turnover rate for 2002, we
188 used the FRB data obtained at the beginning of the next growing season (May 2003) because of the lack
189 of biomass data in 2002, even though RLD_{max} was observed in August 2002. However, this procedure
190 was not considered to produce a large error as the RLD in May 2003 was similar to that in August 2002
191 (94% of that in August 2002). For estimating dry mass-based production or mortality in each year based

192 on the turnover rate in each year using RLD_{mean} , we used the respective mean FRB in 2003 and 2004.
193 However, due to the lack of biomass data in 2002, we did not calculate mass-based FRP in 2002 using
194 RLD_{mean} . We also evaluated the 3-year mean of mass-based FRP and FRM using mean turnover rates
195 and mean FRB during the observation period using the following equations.

196

197 Mass-based FRP ($\text{g m}^{-2} \text{yr}^{-1}$) = FRB (g m^{-2}) \times Turnover rate of production (yr^{-1}) (Eq. 3)

198 Mass-based FRM ($\text{g m}^{-2} \text{yr}^{-1}$) = FRB (g m^{-2}) \times Turnover rate of mortality (yr^{-1}) (Eq. 4)

199

200 2.4. Temperature and soil moisture

201

202 We measured soil temperature hourly at a depth of 5 cm at a distance of 2 m from the observed trees,
203 with three replications from January 2002 to December 2004, using a TR-71S thermo recorder (T & D
204 Corp., Matsumoto, Japan). We measured air temperature at a height of 30 m and precipitation every 30
205 min from a meteorological tower 0.7 km away from the observation plot (Takagi et al., 2009). We
206 measured soil volumetric water content at depths of 15 cm using a TRIME-FM device (IMKO GmbH
207 Inc., Ettlingen, Germany) for time-domain reflectometry at monthly intervals during the growing season
208 in 2002 and 2004. We measured the plant area indices (PAI) of overstory trees and *Sasa* once a month
209 during the growing seasons in a representative area of the surrounding forest with three replications
210 from 2002 to 2004 using an LAI-2000 Plant Canopy Analyzer (Li-Cor, Lincoln, NE, USA) (Takagi et al.,
211 2009). For tree PAI, using the light value at an open site as a reference, we measured light values
212 beneath the tree canopy. For *Sasa*-PAI, light values were measured beneath the *Sasa* canopy near the soil

213 surface, as well as above the *Sasa* canopy as a reference. For each of the three replicates, 10
214 measurements were taken at different positions in the horizontal direction before averaging the readings.

215

216 2.5. Above-ground productivity

217

218 We measured the DBH of all trees (>5 cm at DBH) in the 0.25 ha plot and calculated the above- and
219 below-ground woody biomass from the allometric equation:

$$220 \ln Y = a \ln X + b \quad (\text{Eq. 5})$$

221 where X and Y represent DBH (in cm) and estimated biomass (in kg), respectively. We calculated the
222 trunk, branch, and coarse root biomass separately and summed the trunk and branch biomass to estimate
223 the above-ground biomass. Coefficients in this equation were determined using the dry mass data of 22
224 trees around the study site, ranging from 3.8 to 55 cm in DBH and including the three dominant tree
225 species (Takagi et al., 2010). The values of the coefficients a and b for the trunk, branches, and coarse
226 roots were 2.365, 2.713, 2.224, and -2.596 , -4.456 , and -2.918 , respectively.

227 To estimate the annual biomass increment of above-ground parts and coarse roots, we measured the
228 radii of whole tree rings (half of DBH) and tree ring widths for the previous 5 years of three mature oak
229 trees that were cut in 2001, with three replications per tree. We calculated the ratio of the mean annual
230 increments in the radii (DBH) and the ratio of the annual increments in DBH as the radius at time t
231 divided by the radius at time $t-1$. We then estimated the above-ground woody and coarse root biomass
232 increments by multiplying each biomass by the ratio of the annual increment in DBH. We collected the
233 litterfall of trees using a 0.5 m² litter trap below the canopy with nine replications in 2001.

234 Above-ground NPP of the trees was calculated as the sum of the annual above-ground woody biomass
235 increment and litterfall. We measured the above-ground biomass of understory *S. senanensis* by
236 harvesting a 1 m² area with four replications in October 2004, when biomass reached a maximum.
237 Above-ground NPP of *Sasa* was measured as the biomass of culms and leaves of the current year.

238

239

240 2.6. Statistical analysis

241

242 We analyzed the relationships between the monthly FRP or FRM rate in each soil layer, and the air and
243 soil temperatures, precipitation, soil water content, tree and *Sasa* PAI, and the increment of trees and
244 *Sasa* PAI using regression analysis. In the analysis, we used the mean air and soil temperatures and
245 mean daily precipitation during the minirhizotron observation interval, or the soil volumetric water
246 content and PAI measured in each interval. Increments in the PAI were calculated as the difference
247 between $PAI_{time; t}$ and $PAI_{time; t-1}$. We used the FRP and FRM data obtained during the snow-free periods
248 to analyze their relationship to PAI and soil moisture, because PAI and soil moisture were not measured
249 during the snow period.

250 A repeated-measures ANOVA was used to examine the effects of depth, time of observation, and their
251 interaction on the average values obtained for FRB, fine-root necromass, length-based production, and
252 mortality for each year. Between-subject effect was evaluated as soil depth; within-subject effect was
253 observation date (season). For FRB and fine-root necromass, additional analyses were also conducted by
254 adding 'year' to the between-subject factor. In the repeated-measures ANOVA, the sphericity assumption

255 was tested and degrees of freedoms were Greenhouse-Geisser adjusted if the assumption was violated.
256 The analyses were conducted with JMP software (SAS Institute, Cary, North Carolina, USA).
257 Differences in ALRP, ALRM, and turnover rates for production and mortality between years were
258 analyzed using one-way ANOVA followed by a Tukey HSD test. We used a Kruskal-Wallis Rank Sum
259 test when there was nonhomogeneity, even after log transformation. The relationship between ALRP and
260 ALRM was analyzed using Pearson's correlation.

261

262 **3. Results**

263

264 3.1. Temperatures, precipitation, and soil moisture

265

266 The annual mean air temperature in 2002, 2003, and 2004 was 5.5, 5.6, and 6.3°C, respectively, with
267 maximum monthly mean temperatures of 16.1, 17.7, and 18.3°C in August and minimum monthly mean
268 temperatures of -6.3, -8.4, and -6.4°C in January (February for 2003) (Fig. 1). The annual mean soil
269 temperature at 5 cm soil depth in 2002, 2003, and 2004 was 7.2, 7.1, and 7.6°C, respectively, with
270 maximum monthly temperatures of 15.0, 14.8, and 16.1°C in August and minimum monthly
271 temperatures of 1.9, 2.0, and 1.6°C in March (April for 2004) (Fig. 1). Soil temperature in the dormant
272 season from December to April was stable, ranging between 1 and 3°C due to the thick snowpack (about
273 1.5 m). Mean air temperature during the period of intensive FRP (May through August) in 2002, 2003,
274 and 2004 was 13.4, 13.8, and 15.3°C, respectively, and the corresponding values for mean soil
275 temperature were 11.6, 11.1, and 11.8°C, respectively.

276 Annual precipitation in 2002 was 1170 mm, of which snow accounted for 30% of the total. Total
277 precipitation during May to August in 2002, 2003 and 2004 was 419, 311, and 363 mm, respectively.
278 Soil volumetric water content was lowest in June, with values of 33.7% in 2002 and 30.1% in 2004,
279 indicating that there was no severe drought throughout the year.

280

281 3.2. Fine-root biomass and necromass

282

283 Mean FRB at a surface soil depth of 60 cm was 891 g m⁻², ranging from 767 g m⁻² in October 2004 to
284 1,108 g m⁻² in June 2003, with no significant differences ($P > 0.05$) between sampling dates (Fig. 2,
285 Table 1) or between years (data not shown). FRB, which was concentrated in the uppermost soil layer
286 (0–15 cm depth) and accounted for 41–61% of the total biomass, decreased significantly between soil
287 depths (Fig. 2, Table 1; $P < 0.001$). The amount of FRB finer than 0.5 mm in diameter was similar to
288 that of roots 0.5–2 mm in diameter, and the proportion of roots thinner than 0.5 mm in the 0 – 15 cm soil
289 layer was higher than in the other layers, with maximum and minimum values of 53 and 41% obtained
290 in the 0–15 and 30–45 cm soil layers, respectively. The FRB of *Sasa* at each sampling date accounted
291 for 59–88% of the total (trees plus *Sasa*) in each sampling date. The proportion of *Sasa* FRB was highest
292 in the 15–30 cm soil layer, with maximum and minimum values of 78 and 61% obtained in the 15–30
293 and 45–60 cm soil layers, respectively.

294 Mean fine-root necromass was 76 g m⁻², ranging from 44 g m⁻² in May 2004 to 132 g m⁻² in June
295 2003 (Fig. 3, Table 1). There was no significant difference in fine-root necromass among sampling dates.
296 The quantity of fine-root necromass was consistently less than FRB, with the biomass to necromass ratio

297 ranging from 8.4 to 20.1.

298

299 3.3. Root length density, production, mortality and turnover

300

301 In contrast to FRB, minirhizotron measurements revealed marked temporal variation in RLD (Fig. 4),
302 which increased in the growing season. Measurements in 2003–2004, which we could observe through
303 dormant season, revealed that RLD decreased during the dormant season. In addition, RLD in 2002 was
304 lower than in 2003 and 2004. Although RLD could not be observed from August 2002 to May 2003,
305 maximum RLD for 2002 was considered to have occurred in August 2002. Seasonal maximum RLD for
306 2003 and 2004 were observed in December and September, respectively. RLD_{max} of each year was used
307 to calculate turnover. However, for the 15–30 and 30–45 cm soil layers in 2002, we used the values
308 observed in May 2003 because of the slight increase in the RLD from August 2002 to May 2003. The
309 extent of temporal variation was largest in the uppermost surface soil layer (0–15 cm), and decreased
310 with increasing soil depth.

311 Length-based FRP rate was high in the growing season but low during the period from September to
312 April (Fig. 5), and there was a significant difference between observation time and soil depth (Table 1).
313 In 2002, FRP in August was significantly higher than in the other months, but it remained high from
314 May through August of 2003 and 2004. The length-based production rate decreased in September and
315 remained low during the dormant season until the next spring. The length-based FRM rate was high in
316 July, but no clear temporal patterns or significant differences were observed among observation dates
317 (Fig. 5, Table 1). FRP and FRM were high in surface soil and decreased with increasing soil depth (Fig.

318 5, Table 1).

319 ALRP in the surface soil layer (0–15 cm) was largest in 2002, with a significant difference observed
320 between 2002 and 2004 (Table 2; $P < 0.05$). On the other hand, in the 30–45 cm soil layer, ALRP in
321 2003 was significantly higher than that in 2004. No significant difference was observed in ALRP among
322 years in the 15–30 cm soil layer. ALRM did not differ significantly among years at any depth and ALRP
323 was higher than ALRM for all years and depths (Table 2). The ratio of ALRP to ALRM increased with
324 increasing soil depth, indicating that the mortality rate in particular decreased in deeper layers (Table 2).
325 There was a significant positive relationship between ALRP and ALRM in each tube and in each soil
326 layer (Fig. 6; $P < 0.0001$).

327 Turnover rates of both FRP and FRM were highest in 2002, with a significant difference ($P < 0.05$)
328 observed in production turnover in the 0–15 cm layer between 2002 and 2004 (Table 3). In the case of
329 using RLD_{mean} , significant differences ($P < 0.05$) were also observed in production turnover in layers
330 deeper than 15 cm between 2002 and 2004; mean production turnover rates for the three years were 0.8,
331 0.4, and 0.5 yr^{-1} in the 0–15, 15–30, and 30–45 cm soil layers, respectively, and mortality turnover rates
332 were 0.5, 0.08, and 0.03 yr^{-1} , respectively (Table 3). Production turnover was larger than mortality
333 turnover for every year and depth.

334

335 3.4. Fine root production and above-ground NPP

336 Using the turnover rate calculated from RLD_{max} , mass-based FRP was estimated to be 1,287, 577, and
337 287 $\text{g m}^{-2} \text{yr}^{-1}$ in 2002, 2003, and 2004, respectively. Similarly, FRM estimated from RLD_{max} was 496,
338 273, and 180 $\text{g m}^{-2} \text{yr}^{-1}$ in 2002, 2003, and 2004, respectively. Using the turnover rate calculated from

339 RLD_{mean}, the corresponding FRP was estimated to be 846 and 273 g m⁻² yr⁻¹ in 2003 and 2004,
340 respectively, and FRM from RLD_{mean} was estimated to be 373 and 164 g m⁻² yr⁻¹ in 2003 and 2004,
341 respectively. During the three years, using the turnover calculated from RLD_{max}, mean FRP and FRM
342 were 589 and 279 g m⁻² yr⁻¹, respectively, and the mean corresponding FRP and FRM calculated using
343 RLD_{mean} were 726 and 342 g m⁻² yr⁻¹, respectively (Table 4).

344 Above-ground woody biomass of trees was 11,918 and coarse root biomass was 2,617 g m⁻²; the
345 increments of above-ground woody biomass and coarse-root biomass were 72 and 16 g m⁻² yr⁻¹,
346 respectively (Table 4). Stand density, mean DBH, and basal area were 470 trees ha⁻¹, 17.7 cm, and 17.5
347 m² ha⁻¹, respectively. Litterfall of trees was 267 g m⁻² yr⁻¹. Thus, above-ground NPP of trees was 339 g
348 m⁻² yr⁻¹. On the other hand, the maximum height of *Sasa* culms was approximately 1.6 m, *Sasa* density
349 was about 31 culms m⁻², and above-ground *Sasa* biomass was 1,509 g m⁻². Above-ground NPP of *Sasa*,
350 that is, the biomass of culms and leaves that emerged during the growing season of the current year, was
351 689 g m⁻² yr⁻¹ (leaves, 230 g m⁻² yr⁻¹ and culms, 459 g m⁻² yr⁻¹, Table 4).

352

353 3.5. Relationships between fine-root dynamics and other factors

354

355 Length-based FRP rate in the 0–15 and 15–30 cm soil layers was significantly correlated with mean air
356 and soil temperature at each observation interval (Table 5). No significant relationship between
357 length-based FRP rate and precipitation was observed. There was a weak relationship between
358 length-based FRP rate and volumetric soil water content ($r = 0.32$, $P = 0.19$) at each observation interval
359 during the growing season in 2002 and 2004. No significant relationship was observed between

360 length-based FRP rate and *Sasa* PAI, except for the 30–45 cm layer. However, significant relationships
361 were observed between length-based FRP rate and tree PAI in the 0–15 cm layer ($r = 0.60$, $P = 0.014$). A
362 significant relationship was also observed between length-based FRP rate and increment of *Sasa* PAI
363 during each observation interval for the 15–30 cm layer ($r = 0.57$, $P = 0.019$). The length-based FRM
364 rate was not significantly correlated with any environmental factor, including soil or air temperature,
365 precipitation, or volumetric soil water content ($P > 0.05$), while it showed a significant relationship with
366 increment of *Sasa* PAI in the 0–15 cm layer ($r = 0.70$, $P = 0.003$).

367

368 **4. Discussion**

369

370 4.1. Seasonal variation in fine-root production and mortality with climatic factors

371

372 Although RLD exhibited seasonal variation and was highest in the growing season, no distinct temporal
373 trend was observed in FRB (Figs. 2, 4). This seasonal pattern in RLD has also been observed in other
374 studies using minirhizotrons (Hendrick and Pregitzer, 1993; Noguchi et al., 2005; Satomura et al., 2006).
375 On the other hand, as in this study, FRB has been reported to exhibit relatively little, or no clear seasonal
376 variation (Persson, 1978; Aber et al., 1985; Yuan and Chen, 2010), while other studies have recorded
377 maximum biomass in autumn as a result of production during the growing period (McClaugherty et al.,
378 1982; Brassard et al., 2009). It has been suggested that any spatial variation between sampling times due
379 to destructive sampling during FRB measurements obscures temporal variation (Santantonio and Grace,
380 1987). It is also possible that the low sampling intensity employed in this study may have masked any

381 temporal variation in FRB. However, RLD, which was determined based on minirhizotron observations
382 at the same locations used for those of FRB, exhibited a different temporal pattern. As a result, it is
383 considered that RLD, rather than the FRB measured by sequential coring, would reveal the actual
384 seasonal pattern of fine-root dynamics.

385 The root length-based production rate was high in the growing season, especially in mid- to late
386 summer, and low in the dormant season (Fig. 5). Soil temperature was an important factor controlling
387 FRP in this cool temperate forest (Table 5). This seasonal pattern of FRP is consistent with the
388 observations of numerous studies that have been conducted in cool temperate and boreal forests in the
389 absence of severe soil drought, and suggests that soil temperature is a controlling factor of fine-root
390 growth (Tryon and Chapin, 1983; Burke and Raynal, 1994; Steele et al., 1997; Ruess et al., 1998;
391 Tierney et al., 2003; Steinaker et al. 2010). Based on observations under controlled temperature
392 conditions, Alvarez-Uria and Körner (2007) suggested that low soil temperature inhibited root growth in
393 spring. However, in this study, the FRP rate was low in September and October despite still-favorable air
394 and soil temperatures, indicating that the relationship between temperature and FRP rate may change
395 between spring or early summer and late summer or autumn, as suggested by Tierney et al. (2003).
396 Although new roots would be necessary to meet the demand for water and nutrients until midsummer,
397 they would not be as necessary during the period before the dormant season, when the metabolic activity
398 of the plants would be decreasing, as they would be during the middle period of growing season.

399 In contrast, as reported by Steinaker et al. (2010) in a boreal forest, the relationship between the FRP
400 rate and precipitation or soil water content was weak in our study, indicating that soil moisture was not
401 as important a factor as temperature at this moist site. The absence of a severe drought in late summer

402 would likely be associated with continuous FRP in mid- to late summer because the lowest volumetric
403 soil water content at this site was 30%.

404 The FRP rate was also strongly related to air temperature, suggesting the importance of endogenous
405 control via photosynthesis above ground, as air temperature would not control fine roots directly
406 (Tierney et al. 2003). Joslin et al. (2001) reported that leaf phenology was also important in FRP;
407 specifically, the increase in the supply of carbohydrates after leaf expansion in early summer facilitated
408 FRP in a temperate forest in Tennessee in the USA. In cool temperate forests with dense understory
409 vegetation in Japan, the influence of dense *Sasa*, which has more FRB than the surrounding trees, is
410 considered to have a marked effect on the seasonal patterns of root production in these forests
411 (Fukuzawa et al., 2007, 2010). The mean lifespan of *Sasa* leaves is 1.98 years (Yajima et al., 1997), and
412 its new culms and leaves emerge most intensively in July. In this study, the FRP rate was more closely
413 related to the increment in *Sasa* PAI than to *Sasa* PAI itself, while Fukuzawa et al. (2007) reported a
414 significant relationship between *Sasa* PAI and FRP. This discrepancy in the relationship between
415 *Sasa*-PAI and FRP in the two studies may arise from differences in observation period: the present
416 results showed that FRP was low in autumn when *Sasa* PAI was high, which weakened the relationship,
417 while Fukuzawa et al. (2007) related the PAI to FRP using data obtained up to late summer, during the
418 increasing phase for both parameters. These results suggest that the increment in *Sasa* PAI may be a
419 better indicator of FRP than *Sasa* PAI itself, because the increment in *Sasa* PAI reflects leaf production,
420 although both the cumulative effect of emergence (production) and fall (mortality) of *Sasa* leaves are
421 included in *Sasa* PAI (Fig. 1). On the other hand, the present study also showed that FRP was
422 significantly related to tree PAI, which declined in autumn, in the topmost 15 cm soil layer. These results

423 imply that the timing of FRP is influenced by leaf phenology, as suggested by Joslin et al. (2001).
424 Interestingly, Steinaker et al. (2010) proposed that root production lagged behind shoot production by 8
425 weeks in woody plants and 2–4 weeks in grasses. Thus, a high FRP rate in midsummer (July and
426 August) is considered likely, in terms of tree roots and understory *Sasa* roots, in response to both
427 environmental and endogenous factors.

428 There was no significant relationship between FRM and any environmental factor, including
429 temperature, precipitation, or soil moisture, indicating that FRM was less affected by environmental
430 factors. FRM tended to be high in July, but seasonal variation in FRM rate was not as clear as seasonal
431 variation in FRP. In northern forests, FRM was reported to be highest in late summer to autumn (Tierney
432 et al., 2003; Tingey et al., 2005; Brassard et al. 2009), after the peak period of growth, resulting in an
433 inverse relationship between growth and mortality within a year. It has been suggested that defoliation
434 promotes FRM in citrus and apple trees due to carbon limitation (Eissenstat and Duncan, 1992;
435 Eissenstat and Yanai, 1997). In our study, carbon limitation in *Sasa* due to expansion of new leaves in
436 midsummer may have stimulated FRM.

437

438 4.2. Interannual variation in fine-root production and mortality

439

440 Interannual variation was observed in ALRP, and it was significantly higher in 2002 than in 2004 in the
441 surface 15 cm soil layer (Table 2). In 2003, ALRP was significantly higher than in 2004 in the 30–45 cm
442 soil layer, although the value was quite low compared to the upper two layers. Several previous studies
443 suggested that higher FRP in the first year of observation occurred due to compensation for trees having

444 fewer roots after tube installation, or due to increased nitrogen availability due to the promotion of
445 mineralization immediately after tube installation (Joslin and Wolfe, 1999). However, in this study, since
446 RLD observations were initiated in the year following tube installation, the disturbance effect would be
447 minimized and would not be the main cause of the high fine-root productivity observed in 2002.

448 Ruess et al. (1998) suggested that FRP is high in warmer and drier years in boreal forests. Joslin et al.
449 (2000) reported higher FRP and FRM at a wet experimental site. In our study, the mean soil temperature
450 during the growing season (May to August) of 2002 was near the average of the observed values, while
451 the mean air temperature was the lowest; however, the mean air temperature during the spring (March
452 and April) was 1.2°C higher than the mean value for 2002–2004. Higher air temperatures in spring
453 caused leaf expansion to occur earlier and promoted net ecosystem production in the early growing
454 period of 2002 on a broad scale in East Asia (Saigusa et al., 2008). Since FRP is considered to be
455 positively correlated with above-ground production (Vogt et al., 1986), it is probable that this higher net
456 ecosystem production promoted FRP in 2002, although no data for production at this site is available.

457 ALRM was lower than ALRP in each year by up to 60% (Table 2 and Fig. 6). This imbalance caused
458 an increase in RLD, especially during 2002 to 2003 (Fig. 4), although the maximum value for RLD in
459 2003 and 2004 was similar. Conflicting results have been obtained regarding the relationship between
460 production and mortality rates in previous studies, for example, similar production and mortality in a
461 temperate conifer plantation (Noguchi et al., 2005), and lower mortality in a cool temperate hardwood
462 forest and shortgrass steppe (Hendrick and Pregitzer, 1993; Gill et al., 2002). Gill et al. (2002) attributed
463 this imbalance between production and mortality to an underestimation of mortality due to the existence
464 of only young roots after tube installation. Production due to tube installation was also considered, as

465 described above. In our study, the ratio of production to mortality (P/M) did not change much over time
466 in the surface 15 cm layer, implying that tube installation did not affect FRP or FRM; however, P/M was
467 high in the 15–30 cm layer in 2002 (Table 2) owing to the low mortality in that year. Since production
468 was higher than mortality in each year, the definition used for mortality may have been a factor in the
469 imbalance (Tingey et al., 2000; Satomura et al., 2007). We defined FRM as indicating roots that
470 disappeared; consequently, this definition of mortality may have led to mortalities always being lower
471 than production.

472

473 4.3. Estimation of turnover rate in fine-roots and mass-based fine root production

474

475 Turnover rates of FRP ranged between 0.2 and 2.7 yr⁻¹ and mortality ranged between 0 and 1.6 yr⁻¹
476 (Table 3); both production and mortality turnover decreased with increasing soil depth, indicating a
477 shorter root lifespan and rapid decomposition in the surface soil layer. The present study revealed that
478 the proportion of roots thinner than 0.5 mm in FRB was highest in the topmost soil layer and it
479 decreased with increasing soil depths. However, Fukuzawa et al. (2007) quantified the proportion of the
480 corresponding diameter class in the image analysis of minirhizotron and showed that roots thinner than
481 0.5 mm accounted for 80% in the topmost soil layer (0 – 15 cm), but only for 16% in 30 – 45 cm layer,
482 therefore, the diameter of the observed roots may also be an important factor affecting the turnover of
483 fine roots (Joslin et al., 2006). High interannual variation in production and mortality turnover might
484 have been caused by high variation in FRP and FRM, and in RLD, which was influenced by climate
485 each year as described above. Therefore, here we discuss the range or the mean value of the turnover

486 rather than the interannual variation of turnover.

487 The uppermost value of 1.7 yr^{-1} obtained in our study was near the higher end of those described in
488 Gill and Jackson (2000) (0.1 and ca. 2.6 yr^{-1}), and within the range of 1.4 – 3.3 yr^{-1} as reported by Steele
489 et al. (1997). In contrast, the average production turnover values in the surface 15 cm soil layer that we
490 observed, i.e. 0.8 or 1.0 yr^{-1} , were consistent with numerous previous studies: 0.7 – 0.8 yr^{-1} (0 – 10 cm ;
491 Burton et al., 2000), 1.0 – 1.1 yr^{-1} (0 – 30 cm ; Hendrick and Pregitzer, 1993) in temperate or cool temperate
492 forests in the USA, 0.9 – 1.2 yr^{-1} in a cool temperate deciduous forest in Japan (0 – 20 cm , Satomura et al.,
493 2006), 0.9 – 1.1 yr^{-1} in European beech and spruce forests (Brunner et al., 2013), and 0.9 yr^{-1} , which is
494 the average turnover of minirhizotron studies conducted around the world (Finér et al., 2011).

495 Reports on FRM turnover rate are more limited than on production. Mean turnover of mortality in our
496 study (i.e. 0.5 or 0.7 yr^{-1} calculated using RLD_{max} or RLD_{mean} , respectively, in the surface 15 cm layer,
497 Table 3) was a little lower than the ca. 0.5 – 1.1 yr^{-1} for every 5 cm in a 0 – 15 cm layer in a cool temperate
498 forest reported by Satomura et al. (2006), but a little higher than the value of 0.4 – 0.5 yr^{-1} in a 0 – 10 cm
499 layer in a northern cool temperate hardwood forest reported by Burton et al. (2000), and higher than the
500 ca. 0.3 yr^{-1} in the 0 – 20 cm layer of a shortgrass steppe reported by Gill et al. (2002).

501 In our study, the mean FRP calculated from RLD_{max} and RLD_{mean} (589 and $726 \text{ g m}^{-2} \text{ yr}^{-1}$,
502 respectively) over three years was higher than that of other studies using minirhizotrons. For example,
503 FRP was 58 – $235 \text{ g m}^{-2} \text{ yr}^{-1}$ in jack pine, aspen and black spruce forests in Canada (Steele et al., 1997)
504 and $320 \text{ g m}^{-2} \text{ yr}^{-1}$ in a cedar plantation in central Japan (Noguchi et al., 2005). In contrast, our data were
505 more consistent with those of Hendrick and Pregitzer (1993) who obtained values in the range 730 – 808
506 $\text{g m}^{-2} \text{ yr}^{-1}$ in cool temperate forests in Michigan, USA, especially when we calculated FRP from RLD_{mean} .

507 Our estimates of FRP were also higher than the average values of 311 and 428 g m⁻² yr⁻¹ obtained for
508 boreal and temperate forests, respectively, or the average value of 420 g m⁻² yr⁻¹ obtained using a
509 minirhizotron (Finér et al. 2011), or the 201 g m⁻² yr⁻¹ average obtained for broad-leaved species in
510 boreal forests (Yuan and Chen 2010). Thus, the FRP recorded in the present study is considered to be
511 very high, even on global scale. Finér et al. (2011) showed that the factor contributing the most to FRP
512 was FRB, as opposed to temperature or precipitation, implying that the observed variation in FRB was
513 larger than that in fine-root turnover. At our experimental site, fine-root turnover was close to the global
514 average value, thus, the high FRP in this study might have been attributed to the high FRB.

515 However, the ratio of FRP (NPP_{fr}) to total NPP (NPP_{fr}/NPP_{total} , %) would be a more useful indicator
516 for understanding the role of fine roots in forest productivity, because NPP_{fr} and above-ground NPP both
517 change between sites, although few studies have measured both fine-root and above-ground production.
518 In our study, NPP_{fr}/NPP_{total} was 36 or 41% (Table 4) depending on whether RLD_{max} and RLD_{mean} were
519 used to calculate turnover, respectively. These findings indicate that methods for calculating turnover
520 rate did not markedly affect the inferred contribution of FRP to total NPP, and that a significant portion
521 of forest net primary production was allocated to below-ground root systems. Vogt et al. (1996) reported
522 that below-ground production accounted for 3–54 % of forest NPP, which means that the value in our
523 study was in the uppermost range of those in Vogt’s review. Using a minirhizotron, Hendrick and
524 Pregitzer (1993) reported that NPP_{fr}/NPP_{total} was 58–60% in a cool temperate forest in Michigan, USA,
525 but Lopez et al. (2001) reported that NPP_{fr}/NPP_{total} was only 11% in a Mediterranean oak forest in Spain.
526 On the other hand, Aber et al. (1985) reported that NPP_{fr}/NPP_{total} was 24–41% or 4–35% in broad-leaved
527 forests and 18–30% or 10–38% in conifer forests, in the northern USA using a nitrogen budget method

528 and a sequential coring (max-min) method, respectively. Tateno et al. (2004) reported that NPP_{fr}/NPP_{total}
529 was 16–56% in a cool temperate forest in western Japan using an ingrowth-core method. The values in
530 our study were similar to the upper ranges reported by these studies and confirmed the significance of
531 FRP in forest NPP in our study area.

532 One of the imitations of our study could be the low spatial sampling intensity and the location of
533 observations; i.e. we only investigated FRB and root dynamics beneath the canopy of the dominant oak
534 trees using three replications. Consequently, our results can only be applied to the narrow area
535 surrounding dominant oak trees. Further efforts are therefore required to extend the application of the
536 methods described here to a larger stand-scale and to consider a mixture of species, although this may be
537 complicated by the marked variation that would expected from such an analysis. For example, the FRB
538 of *Sasa* below canopy gaps was twice that beneath the canopy (Fukuzawa et al., unpublished data).
539 Despite being unable to separately evaluate the fine-root turnover or FRP of *Sasa* and the trees, we
540 expect that *Sasa* contributes considerably to the FRP in this stand, particularly since *Sasa* accounted for
541 considerable proportion of FRB and above-ground NPP, and because *Sasa* PAI was larger than that of
542 the trees. Relatively few studies have clarified the importance of understory vegetation (e.g. shrubs and
543 herbaceous species) on forest structure and biogeochemical cycling in boreal or temperate forests (Yarie,
544 1980; Nilsson and Wardle, 2005; Kolari and Pumpanen, 2006; Koike et al., 2010; Moore et al., 2007;
545 Cavard et al. 2011; Finér et al., 2011). Makkonen and Helmisaari (2001) reported that the FRB of
546 understory vegetation was equal to or larger than that of overstory trees in Finnish boreal Scots pine
547 forests. Finér et al. (2011) proposed that FRP could be clarified more precisely if tree roots were
548 separated from the roots of the understory vegetation. Consequently, evaluating the fine-root turnover of

549 tree and *Sasa* roots will be necessary to precisely estimate fine-root dynamics in this stand in the future.
550 On the other hand, this study has illustrated the important contribution that understory *Sasa*, which is
551 distributed throughout East Asia, makes to biomass and productivity both below- and above-ground.
552 Consequently, the contribution of understory vegetation to C cycling should be considered on a global
553 scale. Indeed, we have shown that FRP is a major component of NPP in this stand of cool temperate
554 forest.

555

556 **5. Conclusions**

557 We clarified the probable range of fine-root turnover in a cool temperate forest over a three-year. We
558 estimated that the mean fine-root turnover was 0.8 and 1.0 yr⁻¹ in surface 15 cm soil layer and that
559 mass-based FRP was 589 and 726 g m⁻² yr⁻¹ using two different calculation methods. Using each of
560 these methods, the contribution of FRP to total NPP was estimated to be 36 or 41%, depending on the
561 method used, indicating that significant portion of assimilated carbon was allocated to below-ground
562 root systems in a cool temperate forests stand covered by dense a understory of *Sasa*.

563

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565

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575

576 **References**

577

578 Alvarez-Uria, P., Korner, C., 2007. Low temperature limits of root growth in deciduous and evergreen
579 temperate tree species. *Funct. Ecol.* 21, 211-218.

580 Aber, J.D., Melillo, J.M., Nadelhoffer, K.J., McClaugherty, C.A., Pastor, J., 1985. Fine root turnover in
581 forest ecosystems in relation to quantity and form of nitrogen availability: a comparison of two
582 methods. *Oecologia* 66, 317-321.

583 Brassard, B.W., Chen, H.Y.H., Bergeron, Y., 2009. Influence of environmental variability on root
584 dynamics in northern forests. *Crit. Rev. Plant Sci.* 28, 179-197.

585 Burke, M.K., Raynal, D.J., 1994. Fine root growth phenology, production, and turnover in a northern
586 hardwood forest ecosystem. *Plant Soil* 162, 135-146.

587 Brunner, I., Bakker, M.R., Bjork, R. G., Hirano, Y., Lukac, M., Aranda, X., Borja, I., Eldhuset, T.D.,
588 Helmisaari, H.S., Jourdan, C., Konopka, B., Lopez, B.C., Perez, C.M., Persson, H., Ostonen, I., 2013.
589 Fine-root turnover rates of European forests revisited: an analysis of data from sequential coring and
590 ingrowth cores, *Plant Soil* 362, 357-372.

- 591 Burton, A.J., Pregitzer, K.S., Hendrick, R.L., 2000. Relationships between fine root dynamics and
592 nitrogen availability in Michigan northern hardwood forests. *Oecologia* 125, 389-399.
- 593 Cavard, X., Bergeron, Y., Chen, H.Y.H., Pare, D., 2011. Effect of forest canopy composition on soil
594 nutrients and dynamics of the understory: mixed canopies serve neither vascular nor bryophyte
595 strata. *J. Veg. Sci.* 22, 1105-1119.
- 596 Eissenstat, D.M., Duncan, L.W., 1992. Root-growth and carbohydrate responses in bearing citrus trees
597 following partial canopy removal. *Tree Physiol.* 10, 245–257.
- 598 Eissenstat, D.M., Yanai, R.D., 1997. The ecology of root lifespan. *Adv. Ecol. Res.* 27, 1-60.
- 599 FAO, 1990. Soil map of the world. Revised legend. Reprinted with corrections 1990. World Soil
600 Resources Reports 60. FAO-UNESCO-ISRIC, Rome.
- 601 Finér, L., Ohashi, M., Noguchi, K., Hirano, Y., 2011. Fine root production and turnover in forest
602 ecosystems in relation to stand and environmental characteristics. *For. Ecol. Manage.* 262,
603 2008-2023.
- 604 Fukuzawa, K., Shibata, H., Takagi, K., Satoh, F., Koike, T., Sasa, K., 2007. Vertical distribution and
605 seasonal pattern of fine-root dynamics in a cool-temperate forest in northern Japan: Implication of
606 the understory vegetation, *Sasa* dwarf bamboo. *Ecol. Res.* 22, 485-495.
- 607 Fukuzawa, K., Dannoura, M., Kanemitsu, S., Kosugi, Y., 2010. Seasonal patterns of root production of
608 Japanese oak seedlings and dwarf bamboo grown in rhizoboxes. *Plant Biosyst.* 144, 434-439.
- 609 Gill, R.A., Jackson, R.B., 2000. Global patterns of fine root turnover for terrestrial ecosystems. *New*
610 *Phytol.* 147, 13-31.
- 611 Gill, R.A., Burke, I.C., Lauenroth, W.K., Milchunas, D.G., 2002. Longevity and turnover of roots in the

612 shortgrass steppe: influence of diameter and depth. *Plant Ecol.* 159, 241-251.

613 Helmisaari, H. S., Makkonen, K., Kellomaki, S., Valtonen, E., Malkonen, E. 2002. Below- and
614 above-ground biomass, production and nitrogen use in Scots pine stands in eastern Finland. *For.*
615 *Ecol. Manage.* 165, 317-326.

616 Hertel, D., Moser, G., Culmsee, H., Erasmi, S., Horna, V., Schuldt, B., Leuschner, C. 2009. Below- and
617 above-ground biomass and net primary production in a paleotropical natural forest (Sulawesi,
618 Indonesia) as compared to neotropical forests. *For. Ecol. Manage.* 258, 1904-1912.

619 Hendrick, R.L., Pregitzer, K.S., 1992. The demography of fine roots in a northern hardwood forest.
620 *Ecology* 73, 1094-1104.

621 Hendrick, R.L., Pregitzer, K.S., 1993. The dynamics of fine root length, biomass, and nitrogen content in
622 two northern hardwood ecosystems. *Can. J. For. Res.* 23, 2507–2520.

623 Hendricks, J.J., Hendrick, R.L., Wilson, C.A., Mitchell, R.J., Pecot, S.D., Guo, D., 2006. Assessing the
624 patterns and controls of fine root dynamics: an empirical test and methodological review. *J. Ecol.* 94,
625 40-57.

626 Joslin, J.D., Wolfe, M.H., 1999. Disturbances during minirhizotron installation can affect root
627 observation data. *Soil Sci. Soc. Am. J.* 63, 218-221.

628 Joslin, J.D., Wolfe, M.H., Hanson, P.J., 2000. Effects of altered water regimes on forest root systems.
629 *New Phytol.* 147, 117-129.

630 Joslin, J.D., Wolfe, M.H., Hanson, P.J., 2001. Factors controlling the timing of root elongation intensity
631 in a mature upland oak stand. *Plant Soil* 228, 201-212.

632 Joslin, J.D., Gaudinski, J.B., Torn, M.S., Riley, W.J., Hanson, P.J., 2006. Fine-root turnover patterns and

633 their relationship to root diameter and soil depth in a C-14-labeled hardwood forest. *New Phytol.*
634 172, 523-535.

635 Karizumi, N., 1977. Root biomass, In: Shidei, T., Kira, T. (Eds), *Primary productivity of Japanese*
636 *forests, JIBP synthesis 16.* University of Tokyo Press, Tokyo, pp 45-52.

637 Koike, T., Hojyo, H., Naniwa, A., Ashiya, D., Sugata, S., Sugishita, Y., Kobayashi, M., Nomura, M.,
638 Akibayashi, Y., Nakajima, J., Takagi, K., Shibata, H., Satoh, F., Wang, W., Takada, M., Fujinuma, Y.,
639 Shi, F., Matsuura, Y., Sasa, K., 2001. Basic data for CO₂ flux monitoring of a young larch plantation:
640 Current status of a mature, mixed conifer-broadleaf forest stand. *Eurasian J. For. Res.* 2, 65-79.

641 Koike, T., Mori, S., Zyryanova, O.A., Kajimoto, T., Matsuura, Y., Abaimov, A.P., 2010. Photosynthetic
642 characteristics of trees and shrubs growing on the North- and South facing slopes in Central Siberia,
643 In Osawa, A., Matsuura, Y., Wein, R.W. (Eds), *Permafrost Ecosystems: Siberian Larch Forest.*
644 *Ecological studies 209:* Springer, Dordrecht, pp. 273-288.

645 Kolari, P., Pumpanen, J., 2006. Forest floor vegetation plays an important role in photosynthetic
646 production of boreal forests. *For. Ecol. Manage.* 221, 241-248.

647 Kozlowski, T.T., Pallardy, S.G., 1997. Vegetative growth, In: Kozlowski, T.T., Pallardy, S.G. (Eds),
648 *Physiology of Woody Plants.* 2nd edn. Academic Press, San Diego, pp 36-67.

649 Lopez, B., Sabate, S., Gracia, C.A., 2001. Annual and seasonal changes in fine root biomass of a
650 *Quercus ilex* L. forest. *Plant Soil* 230, 125–134.

651 Makkonen, K., Helmisaari, H.S., 2001. Fine root biomass and production in Scots pine stands in relation
652 to stand age. *Tree Physiol.* 21, 193-198.

653 McClaugherty, C.A., Aber, J.D., Melillo, J.M., 1982. The role of fine roots in the organic matter and

654 nitrogen budgets of two forested ecosystems. *Ecology* 63, 1481-1490.

655 Moore, P. T., Van Miegroet, H., Nicholas, N. S., 2007. Relative role of understory and overstory in
656 carbon and nitrogen cycling in a southern Appalachian spruce–fir forest. *Can. J. For. Res.* 37,
657 2689–2700.

658 Nadelhoffer, K.J., Raich, J.W., 1992. Fine root production estimates and below-ground carbon allocation
659 in forest ecosystems. *Ecology* 73, 1139-1147.

660 Nilsson, M.C., Wardle, D.A., 2005. Understory vegetation as a forest ecosystem driver: evidence from
661 the northern Swedish boreal forest. *Front Ecol Environ* 3, 421-428.

662 Noguchi, K., Sakata, T., Mizoguchi, T., Takahashi, M., 2005. Estimating the production and mortality of
663 fine roots in a Japanese cedar (*Cryptomeria japonica* D. Don) plantation using a minirhizotron
664 technique. *J. For. Res.* 10, 435-441.

665 Persson, H., 1978, Root dynamics in a young Scots pine stand in central Sweden, *OIKOS* 30, 508-519.

666 Ruess, R.W., Hendrick, R.L., Bryant, J.P. 1998. Regulation of fine root dynamics by mammalian
667 browsers in early successional Alaskan taiga forests. *Ecology* 79, 2706-2720.

668 Santantonio, D., Grace, J.C., 1987. Estimating fine-root production and turnover from biomass and
669 decomposition data: a compartment-flow model. *Can. J. For. Res.* 17, 900-908.

670 Saigusa, N., Yamamoto, S., Hirata, R., Ohtani, Y., Ide, R., Asanuma, J., Gamo, M., Hirano, T., Kondo,
671 H., Kosugi, Y., Li, S.G., Nakai, Y., Takagi, K., Tani, M., Wang, H.M., 2008. Temporal and spatial
672 variations in the seasonal patterns of CO₂ flux in boreal, temperate, and tropical forests in East Asia.
673 *Agric. For. Meteorol.* 148, 700-713.

674 Satomura, T., Hashimoto, Y., Koizumi, H., Nakane, K., Horikoshi, T. 2006. Seasonal patterns of fine root

675 demography in a cool-temperate forest in central Japan. *Ecol. Res.* 21, 741-753.

676 Satomura, T., Fukuzawa, K., Horikoshi, T., 2007. Considerations in the study of tree fine-root turnover
677 with minirhizotrons. *Plant Root* 1, 34-45.

678 Scarascia-Mugnozza, G., Bauer, G.A., Persson, H., Matteucci, G., Masci, A., 2000. Tree biomass, growth
679 and nutrient pools, In Schulze ED (Eds) *Carbon and Nitrogen Cycling in European Forest
680 Ecosystems*. Springer-Verlag, Berlin, Heidelberg, pp 49-62.

681 Steele, S.J., Gower, S.T., Vogel, J.G., Morman, J.M., 1997. Root mass, net primary production and
682 turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada. *Tree
683 Physiol.* 17, 577-587.

684 Steinaker, D.F., Wilson, S.D., Peltzer, D.A., 2010. Asynchronicity in root and shoot phenology in grasses
685 and woody plants. *Glob. Chang. Biol.* 16, 2241-2251.

686 Takagi, K., Fukuzawa, K., Liang, N., Kayama, M., Nomura, M., Hojyo, H., Sugata, S., Shibata, H.,
687 Fukazawa, T., Takahashi, Y., Nakaji, T., Oguma, H., Mano, M., Akibayashi, Y., Murayama, T., Koike,
688 T., Sasa, K., Fujinuma, Y., 2009. Change in CO₂ balance under a series of forestry activities in a
689 cool-temperate mixed forest with dense undergrowth. *Glob. Chang. Biol.* 15, 1275-1288.

690 Takagi, K., Kotsuka, C., Fukuzawa, K., Kayama, M., Kobayashi, M., Watanabe, T., Nomura, M.,
691 Fukazawa, T., Takahashi, H., Hojyo, H., Ashiya, D., Naniwa, A., Sugata, S., Kamiura, T., Sugishita,
692 Y., Sakai, R., Ito, K., Kobayashi, M., Maebayashi, M., Mizuno, M., Murayama, T., Kinoshita, K.,
693 Fujiwara, D., Hashida, S., Shibata, H., Yoshida, T., Sasa, K., Saigusa, N., Fujinuma, Y., Akibayashi,
694 Y., 2010. Allometric relationships and carbon and nitrogen contents for three major tree species
695 (*Quercus crispula*, *Betula ermanii*, and *Abies sachalinensis*) in northern Hokkaido, Japan. *Eurasian J.*

696 For. Res. 13,1-7.

697 Tateno, R., Hishi, T., Takeda, H., 2004. Above- and belowground biomass and net primary production in
698 a cool-temperate deciduous forest in relation to topographical changes in soil nitrogen. For. Ecol.
699 Manage. 193, 297-306.

700 Tierney, G.L., Fahey, T.J., Groffman, P.M., Hardy, J.P., Fitzhugh, R.D., Driscoll, C.T., Yavitt, J.B., 2003.
701 Environmental control of fine root dynamics in a northern hardwood forest. Glob. Chang. Biol. 9,
702 670-679.

703 Tingey, D.T., Phillips, D.L., Johnson, M.G., 2000. Elevated CO₂ and conifer roots: effects on growth,
704 life span and turnover. New Phytol. 147, 87-103.

705 Tingey, D.T., Phillips, D.L., Johnson, M.G., Rygiewicz, P.T., Beedlow, P.A., Hogsett, W.E., 2005.
706 Estimates of Douglas-fir fine root production and mortality from minirhizotrons. For. Ecol. Manage.
707 204, 359-370.

708 Tryon, P.R., Chapin III, F.S., 1983. Temperature control over root growth and root biomass in taiga
709 forest trees. Can. J. For. Res. 13, 827-833.

710 Yuan, Z.Y., Chen, H.Y.H., 2010. Fine Root Biomass, Production, Turnover Rates, and Nutrient Contents
711 in Boreal Forest Ecosystems in Relation to Species, Climate, Fertility, and Stand Age: Literature
712 Review and Meta-Analyses. Crit. Rev. Plant Sci. 29, 204-221.

713 Vogt, K.A., Grier, C.C., Vogt, D.J., 1986. Production, turnover, and nutrient dynamics of above- and
714 belowground detritus of world forests. Adv. Ecol. Res. 15, 303-377.

715 Vogt, K.A., Vogt, D.J., Palmiotto, P.A., Boon, P., O'Hara, J., Asbjornsen, H., 1996. Review of root
716 dynamics in forest ecosystems grouped by climate, climatic forest type and species. Plant Soil 187,

- 717 159-219.
- 718 Yajima, T., Watanabe, N., Shibuya, M., 1997. Changes in biomass of above- and under-ground parts in
719 *Sasa kurilensis* and *Sasa senanensis* stands with culm height. J. Jpn. For. Soc. 79, 234-238 (in
720 Japanese with English summary)
- 721 Yarie, J., 1980. The role of understory vegetation in the nutrient cycle of forested ecosystems in the
722 mountain hemlock biogeoclimatic zone. Ecology 61, 1498–1514.

723 **Figure captions**

724

725 Fig. 1 Monthly average air and soil temperatures and the increments in plant area indices (PAI) of *Sasa*
726 and trees from 2002 to 2004.

727

728 Fig. 2 Temporal variation in fine-root biomass classified by (a) soil depth layer, (b) root diameter, and
729 (c) plant type. Vertical bars represent ± 1 S.E. for total and each component, respectively (n=3).

730

731 Fig. 3 Temporal variation in fine-root necromass. Vertical bars represent ± 1 S.E. for total (n=3).

732

733 Fig. 4 Temporal variation in root length density (RLD) of fine roots in three soil layers for three years.
734 Vertical bars represent ± 1 S.E. (n=3).

735

736 Fig. 5 Fine-root production and mortality rate for three years at depths of (a) 0–15 cm, (b) 15–30 cm,
737 and (c) 30–45 cm. Vertical bars represent ± 1 S.E. (n=3).

738

739 Fig. 6 Relationship between annual length-based root production (ALRP) and annual length-based root
740 mortality (ALRM) in each tube and soil layer.

Table 1. *F* values of a repeated measures ANOVA of the effects of depth, time of the observation (season), and their interaction on fine-root biomass, necromass, and length-based production and mortality rates for each year.

	Year	Depth	Time	DepthxTime
Biomass	2003	27 ^{***}	1.07	0.79
	2004	38.6 ^{***}	0.28	0.92
Necromass	2003	1.44	1.10	0.97
	2004	11.3 ^{**}	0.65	0.34
Production	2002	29.3 ^{***}	7.64 [*]	2.54
	2003	7.86 [*]	7.44 [*]	1.14
	2004	24.3 ^{**}	5.95 [*]	2.66
Mortality	2002	28.5 ^{***}	0.39	0.39
	2003	18.8 ^{**}	2.29	3.23
	2004	2.94	1.06	0.83

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Fukuzawa et al. Table 1

Table 2. Changes in annual length-based root production (ALRP), annual length-based root mortality (ALRM), and the ratio of production to mortality (P/M) over time.

Soil depth (cm)	Year	ALRP (mm cm ⁻² yr ⁻¹)	ALRM (mm cm ⁻² yr ⁻¹)	P/M
0-15	2002	13.8 (1.94) ^a	7.96 (2.36) ^a	1.91
	2003	10.8 (1.82) ^{ab}	7.19 (1.52) ^a	1.58
	2004	5.85 (0.87) ^b	3.70 (1.56) ^a	2.27
15-30	2002	3.86 (1.39) ^a	0.21 (0.14) ^a	25.3
	2003	5.59 (0.72) ^a	1.19 (0.57) ^a	7.16
	2004	1.68 (0.72) ^a	0.88 (0.57) ^a	12.2
30-45	2002	1.11 (0.56) ^{ab}	0 ^a	-
	2003	2.44 (0.43) ^a	0.02 (0.02) ^a	34.3
	2004	0.57 (0.14) ^b	0.27 (0.26) ^a	10.2

Mean values are shown with +1 SE in parentheses (n=3). Different superscript letters indicate significant difference between years at each soil depth.

Fukuzawa et al. Table 2

Table 3. Mean fine-root turnover, or ratio of the mean annual length-based root production (ALRP) or mean annual length-based root mortality (ALRM) to the mean root length density in different years of the study.

Depth (cm)	Year	Turnover (yr ⁻¹)			
		Production		Mortality	
		ALRP/RLD _{max}	ALRP/RLD _{mean}	ALRM/RLD _{max}	ALRM/RLD _{mean}
0-15	2002	1.65 (0.33) ^a	2.65 (0.64) ^a	0.95 (0.27) ^a	1.57 (0.54) ^a
	2003	0.79 (0.05) ^{ab}	1.00 (0.02) ^{ab}	0.53 (0.08) ^a	0.67 (0.11) ^a
	2004	0.43 (0.03) ^b	0.44 (0.01) ^b	0.30 (0.15) ^a	0.30 (0.13) ^a
	3 years	0.84 (0.05)	1.04 (0.11)	0.53 (0.08)	0.66 (0.13)
15-30	2002	0.73 (0.14) ^a	1.66 (0.80) ^a	0.03 (0.03) ^a	0.05 (0.04) ^a
	2003	0.56 (0.15) ^a	0.72 (0.26) ^{ab}	0.10 (0.03) ^a	0.12 (0.04) ^a
	2004	0.16 (0.06) ^a	0.17 (0.06) ^b	0.09 (0.08) ^a	0.09 (0.08) ^a
	3 years	0.42 (0.08)	0.52 (0.12)	0.08 (0.03)	0.10 (0.03)
30-45	2002	0.81 (0.15) ^a	2.76 (1.23) ^a	0 ^a	0 ^a
	2003	0.69 (0.15) ^a	1.01 (0.28) ^{ab}	0.01 (0.01) ^a	0.01 (0.01) ^a
	2004	0.19 (0.10) ^a	0.20 (0.11) ^b	0.05 (0.05) ^a	0.05 (0.05) ^a
	3 years	0.49 (0.09)	0.62 (0.10)	0.03 (0.02)	0.03 (0.02)

Values are means +1 SE in parentheses (n=3). Results of two calculations using root length density (RLD_{max} or RLD_{mean}) are shown. Different superscript letters denote a significant difference among years at each soil depth.

Table 4. Estimated forest net primary production (NPP) showing each component (above-ground NPP for each species and parts, and coarse and fine-root production).

Parts	NPP (g m ⁻² yr ⁻¹)
<i>Above-ground</i>	
Tree litterfall	267 (75)
Woody biomass increment	72 (19)
Above-ground tree total	339
<i>Sasa</i>	
<i>Sasa</i> leaves	230 (37)
<i>Sasa</i> culms	459 (105)
Above-ground <i>Sasa</i> total	689
<i>Below-ground</i>	
Woody coarse root increment	16 (4)
Fine root production (NPP _{fr}) ^b	589 (107), 726 (132)
Total	1632, 1769
NPP _{fr} /NPP _{total} (%)	36, 41

Values are means +1 SD in parentheses.

^an=3 for above-ground woody and woody coarse-root biomass increments, n=4 for above-ground *Sasa* NPP, n=6 for NPP_{fr}, and n=9 for tree litterfall.

^bNPP_{fr} calculated from RLD_{max} are shown, followed by that calculated from RLD_{mean}.

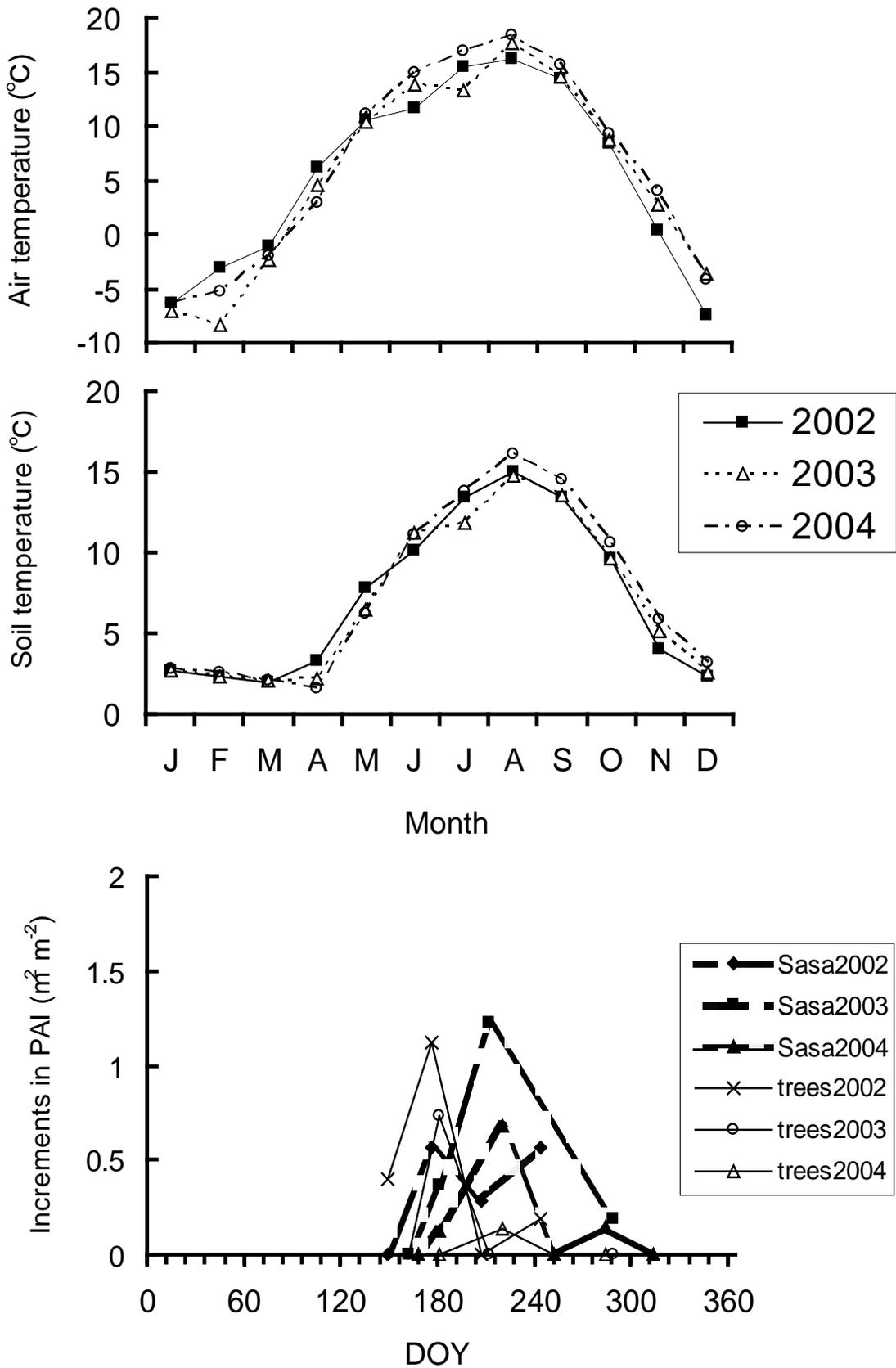
Table 5. Regression analysis of fine root production (FRP), fine root mortality (FRM), and environmental and endogenous factors.

Depth (cm)	Regression equation	N	Adj. R ²	P value
Fine root production (mm cm ⁻² d ⁻¹)				
0 - 15	Ln(FRP) = 0.107(ST) - 4.51	18	0.24	*
	Ln(FRP) = 0.0921(AT) - 4.45	18	0.42	**
	Ln(FRP) = 0.789(treePAI)-4.845	14	0.36	*
15 - 30	Ln(FRP) = 0.260(ST) - 7.50	18	0.50	***
	Ln(FRP) = 0.143(AT) - 6.53	18	0.30	*
	Ln(FRP) = 2.39(Δ SasaPAI) - 5.30	14	0.33	*
30 - 45	Ln(FRP)=5.69(SasaPAI) - 27.7	14	0.65	***
Fine root mortality (mm cm ⁻² d ⁻¹)				
0 - 15	Ln(FRM) = 1.17(Δ SasaPAI)-4.32	14	0.50	**

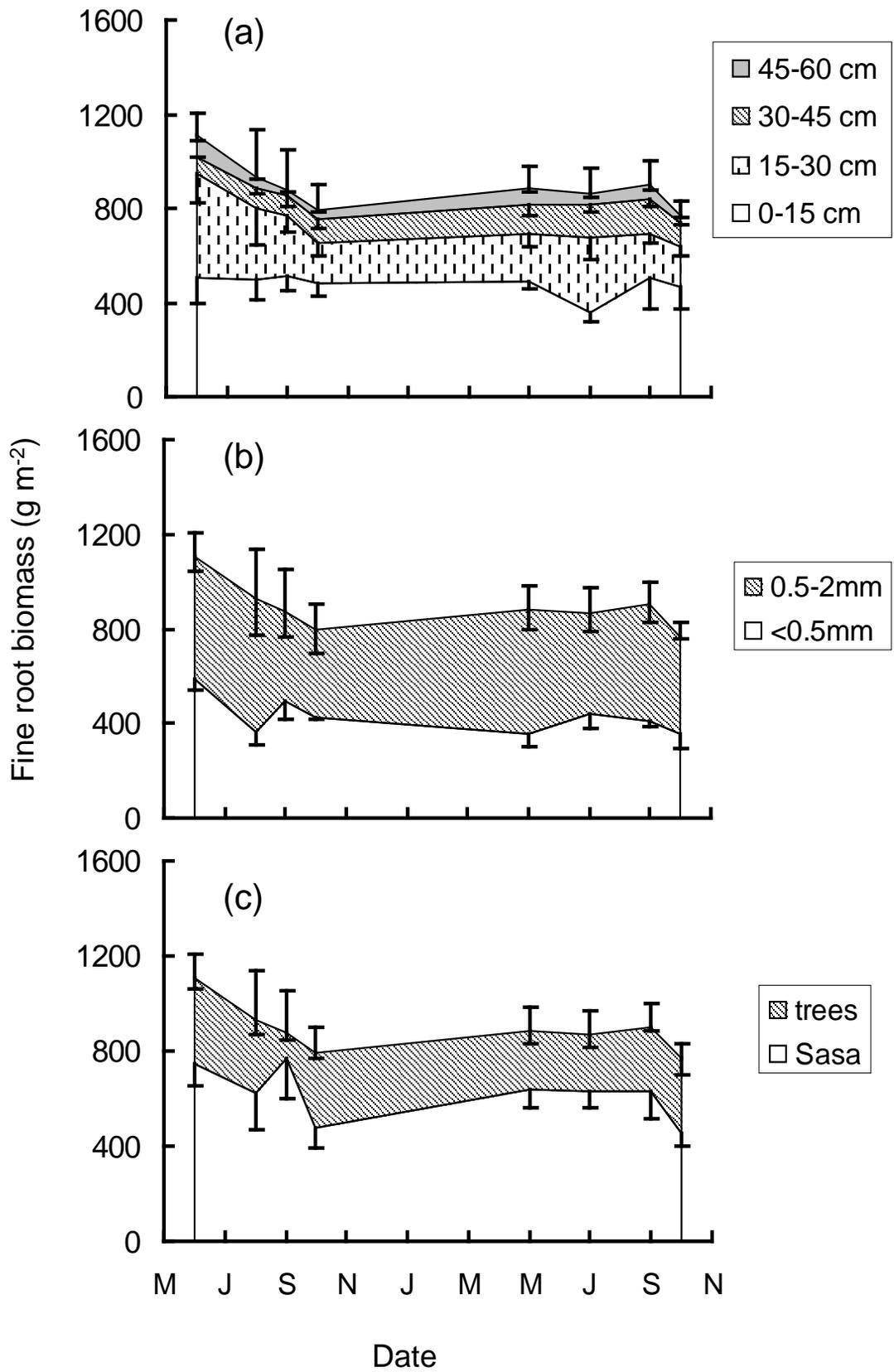
N: Number of observation for each regression.

ST: mean soil temperature, AT: mean air temperature, Δ Sasa PAI: increment in *Sasa* PAI. FRP and FRM were log-transformed. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

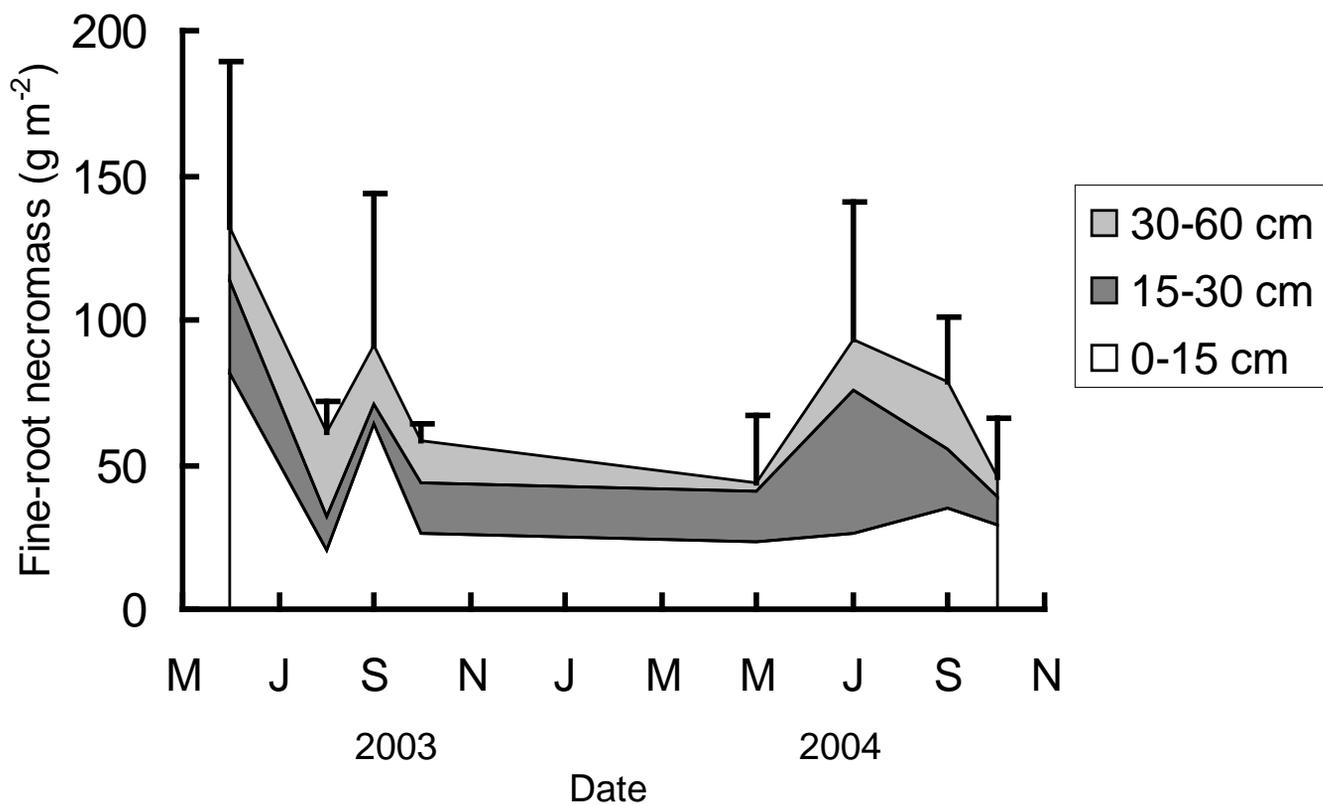
Fukuzawa et al. Table 5



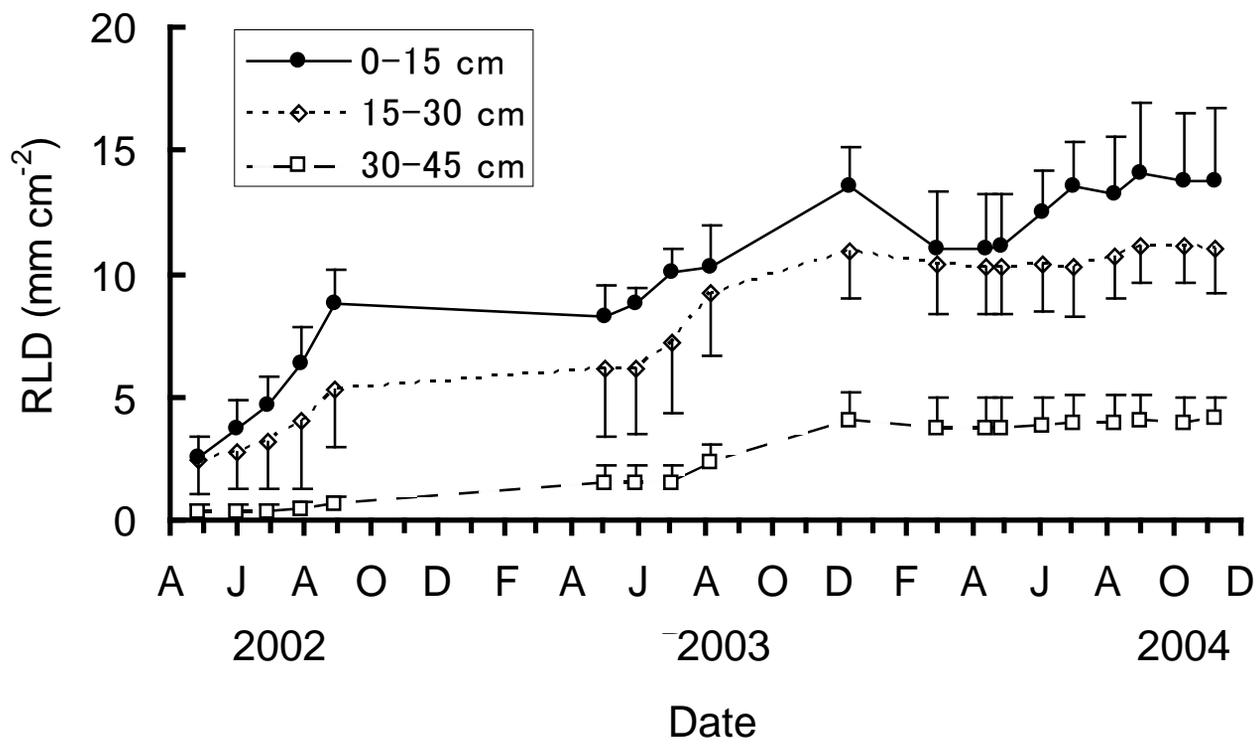
Fukuzawa et al. Fig. 1



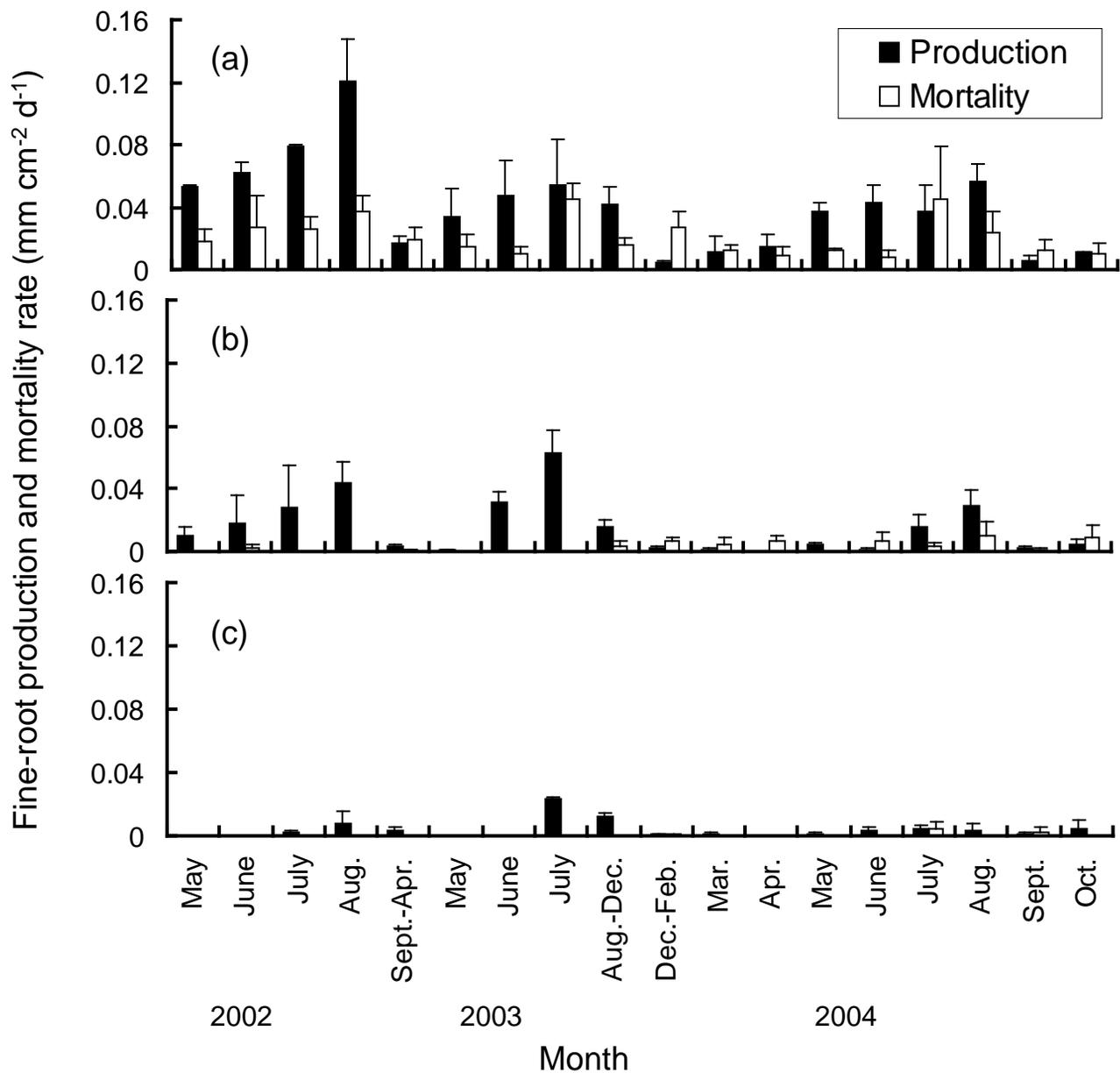
Fukuzawa et al. Fig. 2



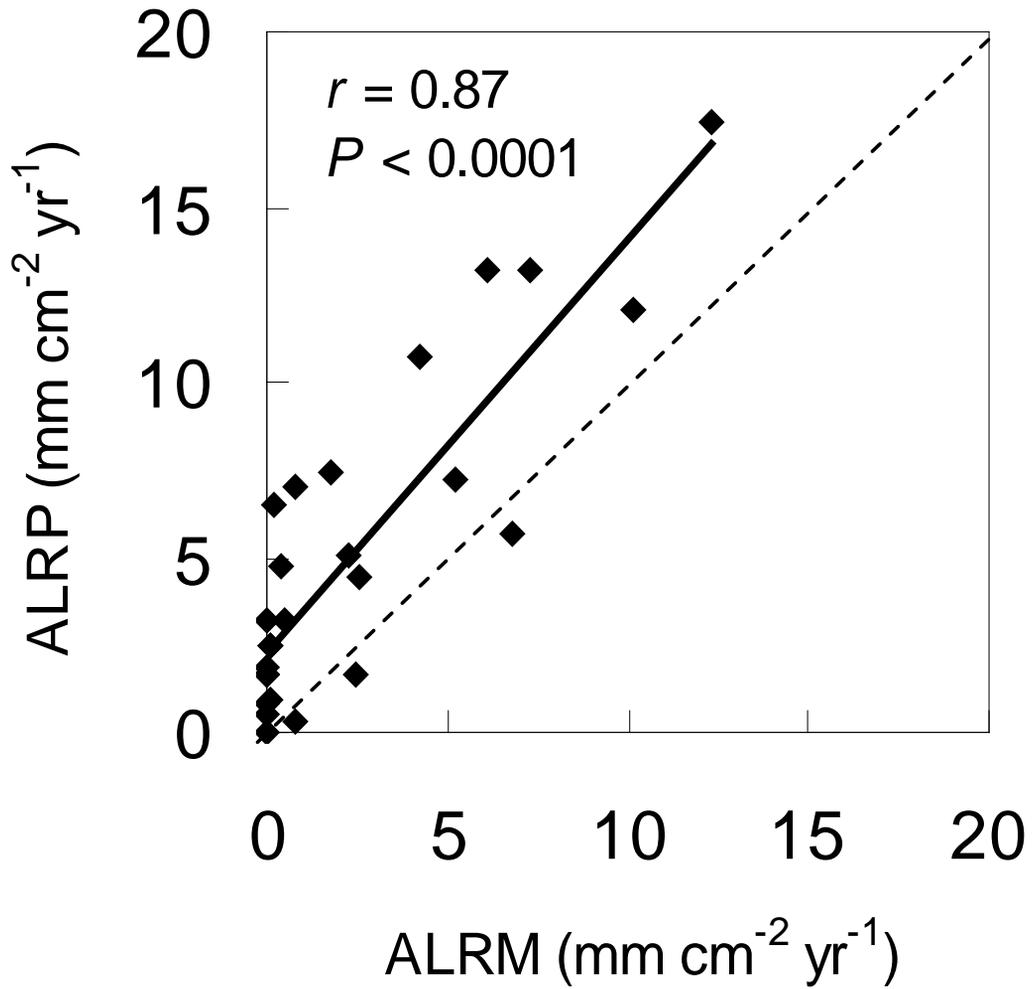
Fukuzawa et al. Fig. 3



Fukuzawa et al. Fig. 4



Fukuzawa et al. Fig. 5



Fukuzawa et al. Fig. 6