Presence of understory dwarf bamboo determines ecosystem fine root production in a cool-temperate forest in northern Japan

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Abstract

Fine root biomass (FRB) and production (FRP) are crucial in forest carbon and nutrient cycling, but the factors controlling FRB and FRP are not well understood. Here, we examined FRB, FRP, aboveground environmental and stand factors, and soil environmental factors in four stands in a forest covered with dense understory vegetation of dwarf bamboo, *Sasa senanensis* (hereafter, Sasa). The four stands had different tree species composition and included a primary forest (PF), secondary forest (SF), conifer plantation (CP), and Sasa area (SA). We quantified the FRB and FRP of trees and Sasa separately using the ingrowth core method. Total FRP was higher in stands with substantial presence of Sasa (99–130 g m^{-2} yr^{-1}) than in CP with scarce Sasa (69 g m^{-2} yr^{-1}). Despite being occupied by Sasa alone, SA had high FRP, suggesting that the presence of Sasa regardless of trees is a key determinant of ecosystem FRP. Tree FRB increased with increasing tree aboveground biomass, tree density, or basal area at breast height, but Sasa FRB and total FRB decreased. Total FRP was also lower at higher values of these aboveground stand factors. In Sasa, specific root length was significantly higher, and root tissue density was significantly lower, than in trees, indicating the capacity of Sasa for explosive growth. Positive correlations between Sasa FRB or FRP and soil inorganic N or ammonium contents (i.e., N availability) were detected. We conclude that Sasa is important in determining FRB and FRP in this northern forest with understory vegetation.

Keywords: fine root biomass, species diversity, *Sasa senanensis*, tree aboveground biomass, soil nitrogen availability

Introduction

Forest is a huge carbon (C) sink in terrestrial ecosystems, accounting for 80% of

50 aboveground C and 40% of belowground C (Dixon et al. 1994). Although fine root
51 biomass (FRB) accounts for only 5% of total forest biomass (Vogt et al. 1996), fine root
52 production (FRP) accounts for up to 76% of total net primary production (NPP) in
53 forests (Gower et al. 1996), implying that fine roots are essential for the transfer of C
54 and nutrients from vegetation to soil. In addition, uptake of water and nutrients by fine
55 roots is crucial for plant survival and biogeochemical cycles (e.g., nitrogen (N)
56 leaching). Therefore, fine root dynamics influences ecosystem functioning and services
57 of forests (e.g., C sequestration and nutrient retention).

58 Multiple environmental and stand factors affect FRB, FRP, and root turnover
59 rate. For example, FRB is higher in warm than in cool biomes, such as boreal forests, at
60 a global scale (Vogt et al. 1996). Positive relationships have been demonstrated between
61 FRB, FRP, and turnover rate, and air temperature and precipitation in boreal forests
62 (Yuan and Chen 2010), and between turnover rate and air temperature on a global scale
63 (Gill and Jackson 2000). FRB, FRP, or both are controlled by soil environmental
64 factors, namely pH, and N and phosphorus (P) contents (Godbold et al. 2003; Yuan and
65 Chen 2010), or N availability (i.e., inorganic N content: Aber et al. 1985; Nadelhoffer
66 2000). They are also controlled by stand factors, namely stand age (Yuan and Chen
67 2010) and basal area at breast height (BA, Finér et al. 2011a, b). Chen et al. (2004)
68 demonstrated a positive relationship between FRB and BA, suggesting that the former
69 can be predicted from the latter. Positive relationships have been reported between FRB
70 and FRP (Finér et al. 2011b) and between FRP and root turnover rate (McCormack et
71 al. 2014). However, understanding the relationship among these three parameters is
72 insufficient because FRB is influenced not only by FRP but also by root turnover rate
73 (Aber et al. 1989), and reports on FRP and turnover rate are scarce. Fine root dynamics

depends on climatic, aboveground stand, and soil environmental factors. Site-scale analysis allows us to disregard climatic factors and focus on stand factors.

Although high plant species diversity increases aboveground NPP in grasslands (Tilman et al. 1996), the relationship between species diversity and FRP is not well understood. In forest ecosystems, some studies revealed FRP increases with increasing diversity of tree species (e.g., Brassard et al. 2013). However, reports of the species diversity–FRP relationship in forest ecosystems are scarce and more studies in diverse ecosystems are necessary.

Root traits affect foraging for soil nutrients. Thin roots with great surface area in contact with soil are advantageous for nutrient foraging, but such roots are ephemeral because of their vulnerable structure (Eissenstat and Yanai 1997). Specific root length (SRL: root length per unit weight) is an indicator of this trade-off: high-SRL (thin) roots are advantageous for nutrient foraging, whereas low-SRL (thick) roots have structural and maintenance advantages (Eissenstat and Yanai 1997; Ostonen et al. 2007). McCormack et al. (2012) demonstrated an inverse relationship between SRL and root lifespan and attributed the short lifespan of thin roots (high SRL) to low C investment in such roots. Root tissue density (RTD: root weight per unit volume) is another useful root trait indicator: roots with low RTD have an ability to explore for nutrients and are productive but short-lived (Ryser 1996). Measurements of root traits and those of FRB and FRP would provide useful insight into the mechanisms of fine root dynamics.

Fine root phenology is also important because it explains the detailed mechanism of fine root dynamics and influences water and nutrient dynamics in the soil. Tierney et al. (2003) suggested that environmental and endogenous factors affect the timing of FRP. Species-specific patterns have been demonstrated in a pot

experiment (Makoto et al. 2020) and by literature analysis of ecosystem observation (Abramoff and Finzi 2015). However, information on the timing of FRP of distinct plant species or forms in the same fields is scarce.

Some cool-temperate or boreal forests have understory vegetation (e.g., herbs, shrubs). Reportedly, FRB and FRP cannot be predicted well unless understory vegetation roots are considered (Finér et al. 2011a, b); understory vegetation increases total FRB (Finér et al. 2007; Helmisaari et al. 2007; Hansson et al. 2013). However, the role of understory vegetation in fine root dynamics (e.g., FRB, FRP, turnover rate, root phenology) is not clear in the majority of studies because separating roots of understory vegetation from tree roots is difficult and labour intensive. It is possible that this role depends on understory species.

On Hokkaido Island, northern Japan, dwarf bamboo, *Sasa* spp. (hereafter Sasa; Gramineae) covers 89% of the forest area (Toyooka 1983). *Sasa senanensis* allocates half of biomass to belowground parts (Fukuzawa et al. 2015) and its FRB accounts for 59%–88% of the total FRB in a cool-temperate forest in northern Hokkaido (Fukuzawa et al. 2013). However, it is unclear whether total FRB or FRP and the proportion of Sasa roots to total roots change depending on stand type (e.g., tree species, tree aboveground biomass, BA, tree density, and soil environment). Such information could facilitate general understanding of the fine root dynamics in various tree–Sasa ecosystems in northern Japan. Furthermore, the FRP and the temporal patterns of production and turnover of Sasa and tree roots have not been identified. Root traits would influence fine root dynamics, however the differences in root traits between Sasa and trees in forests have not been clarified.

121 In the present study, we chose four stands covered with understory vegetation:
122 three stands with different tree species composition and a Sasa area without trees. To
123 predict the ecosystem FRB and FRP from the aboveground stand characteristics (tree
124 density, BA, tree aboveground biomass, canopy openness), and soil environment, and
125 clarify the contribution of Sasa to total FRB and FRP in tree–Sasa ecosystems, we
126 quantified the FRB and FRP of trees and Sasa separately and investigated the
127 relationship between FRBs or FRPs of trees, Sasa, and total and the stand
128 characteristics. To understand the behaviour of the roots of trees and Sasa, we
129 investigated seasonal changes and annual values of FRB and FRP and root traits of each
130 plant form in four stand types. We hypothesized that (1) understory Sasa contributes to
131 the total FRB and FRP and influences the relationship between them and tree
132 aboveground stand factors (tree density, BA, tree aboveground biomass); (2) root traits
133 (i.e., SRL and RTD) differ between trees and Sasa; (3) timing of FRP differs among
134 stands as a reflection of different plant composition; and (4) FRB and FRP correlate
135 with soil environmental factors, especially with soil N availability.

136 **Materials and Methods**

137 ***Study site***

138 We established study plots in four stands in the Teshio Experimental Forest, Hokkaido
139 University (45°03′N, 142°06′E) in northern Hokkaido, Japan. The stands are located on
140 a flat ridge (70–80 m a.s.l.) within 1 km of each other. The selected representative
141 stands were (1) conifer plantation (CP) of mature *Abies sachalinensis*, (2) primary forest
142 stand (PF) dominated by *Quercus crispula* and composed of multiple broadleaved and
143 conifer species, (3) secondary forest stand (SF) dominated by 69-year-old *Betula*

144 *platyphylla*, and (4) Sasa area (SA) completely dominated by *S. senanensis* except for
145 scarce young trees (Table S1). In 2005–2014, the mean annual air temperature was
146 5.7 °C and the total annual precipitation was 1190 mm at the meteorological station ca.
147 16 km south-west of the site (Teshio Experimental Forest); 30% of total annual
148 precipitation fell as snow during November to April. The bedrock is Cretaceous
149 sedimentary rock and the dominant soil is a Gleyic Cambisol (FAO, 1990).

150 In each stand, we randomly selected five individual target trees and established a
151 plot for tree surveys (circles [10-m radius] around each target tree: type I) and a plot for
152 fine root dynamics and aboveground and belowground environment (ca. 5 × 5 m: type
153 II) with a centre 2 m away from each target tree (also within the type I plot) during
154 July−August 2013. The target tree species were *A. sachalinensis* in CP, *Q. crispula* in
155 PF, and *B. platyphylla* in SF. In SA, we randomly selected five plots in the Sasa
156 vegetation community (ca. 1.5–1.7 m height).

157 ***Stand structure and aboveground biomass***

158 We determined the overstory tree density and tree aboveground biomass in each plot in
159 April 2014. We counted the trees to obtain tree density (trees ha^{-1}) and measured the
160 diameter at breast height (1.3 m, DBH) of all individual trees in each type I plot. Then
161 we calculated BA (m^2 ha^{-1}) as the sum of the basal areas at breast height of individual
162 trees. To estimate tree aboveground biomass, we used the following allometric equation
163 obtained from 22 individual trees with a wide DBH distribution (*Q. crispula*, *B.*
164 *ermanii*, and *A. sachalinensis*) in the Teshio Experimental Forest (Takagi et al. 2010).

165 $$\ln Y = a \ln X + b \quad (1)$$

where X is DBH (cm), Y is aboveground biomass (kg), and a and b are constants (a = 2.428, b = −2.282, r^2 = 0.994). To evaluate the aboveground biomass of Sasa, we harvested its aboveground parts including culms and leaves in 50 cm × 50 cm quadrats in each plot in September 2014 after current-year leaves had completely expanded. We dried the culms and leaves separately (70 °C, 48 h) and weighed them.

Aboveground and belowground environments

We determined canopy openness, an indicator of light availability for the understory layer, in the centre of each type II plot; at 1.5 m above the ground, we took photographs in the zenith direction using a camera with a fish-eye converter (E4500 & FC-E8 0.21x, Nikon Corp., Tokyo, Japan; shutter speed, 1/250; aperture value, 2.6) in 2013 (September and November) and in 2014 (May and July) in the absence of direct solar radiation, and used the CanopOn2 software (URL: http://takenaka-akio.org/etc/canopon2/). We converted the hemispherical photos into black-and-white images and calculated the proportion of white area to estimate canopy openness. We measured soil temperature at 5-cm depth at two randomly selected plots for each stand at 1-h intervals from November 2013 to September 2014 using a thermometer with a data logger (UA-001-64, Onset Computer Corp., Bourne, MA, USA). We measured the mean soil volumetric water content of the surface 15 cm of soil using a time-domain reflectometer (TRIME-FM, IMKO GmbH Inc., Ettlingen, Germany) in September and November 2013. We measured soil gravimetric water content in collected soil (see below for the sampling method) by weighing soil before and after oven-drying (105 °C, 24 h) in September 2014. We also measured the thickness of the Oe/Oa layer at the

points of soil environmental measurements in 2013 (August and November) and in 2014 (May and July).

Fine root biomass, production, and turnover

To measure FRB, we used in situ core sampling at the points of soil environmental measurements in each type II plot (one core at each time point) in 2013 (26 August and 6 November) and 2014 (21 May and 2 July). We removed the fresh litter (L) layer and collected the Oe/Oa layer and the 0–10 cm surface soil by auger (inner diameter: 4.4 cm). In each plot, sequential collection points were more than 20 cm apart from each other.

To measure FRP, we used in situ ingrowth cores (diameter: 4.4 cm, depth: 10 cm, 152 cm^3, lateral face: 4-mm polyethylene mesh). We collected soil to a depth of 10 cm at the representative point in each stand and sieved the soil through a 4-mm mesh to remove roots, used it to fill the ingrowth cores, and installed them into the 10-cm deep hole created by the FRB measurement in the soil. To measure FRP in the Oe/Oa layer, we put humus-filled ingrowth cores prepared similarly to those filled with soil on the installed soil-filled ingrowth cores. We established the ingrowth cores in both the Oe/Oa and soil layers (one core for each time period, each layer, and each plot) during 26 August–30 October 2013, 6 November 2013–14 May 2014, 21 May–1 July 2014, and 2 July–16 September 2014 to identify seasonal trends. To calculate annual FRP, we summed the FRP of each observation interval. We calculated fine root turnover (yr^{-1}) from FRP (g m^{-2} yr^{-1}) and FRB (g m^{-2}) according to the following equation (Dahlman and Kucera 1965; Gill and Jackson 2000):

$$\text{Fine root turnover} = \text{Annual FRP}/\text{annual mean FRB} \quad (2)$$

212 Annual mean FRB was the temporal mean value calculated from the four collection
213 times. For both FRB and FRP, we separated roots from soil by washing. We sieved soil
214 through a 2-mm mesh and additionally used a 0.5-mm sieve attached below as a
215 backup. We distinguished Sasa roots from tree roots by their light colour and branching
216 style (Fig. S1). We selected roots <2 mm in diameter. We captured the images of the
217 roots from each plot spread in a water-filled transparent acrylic box and measured total
218 root length and root volume with a WinRHIZO root image analysis system (REG 2009,
219 Regent Instruments Inc., Quebec, Canada) attached to a scanner (V700 Photo, Epson,
220 Suwa, Japan). After imaging, we dried the roots (70 °C, 48 h) and weighed them. We
221 calculated SRL (m g^{-1}) and RTD (g cm^{-3}) from the length, volume, and weight of roots
222 in each plot.

223 ***Soil chemical properties***

224 We determined soil C and N content, N availability, and soil environmental factors in
225 the centre of each plot. We collected cores of the 0–10 cm surface soil layer after
226 removing the Oe/Oa layer in September 2014 using an auger and removed gravel, roots,
227 and coarse organic debris by sieving through a 2-mm mesh. To evaluate soil N
228 availability, we extracted soil with KCl (fresh soil:2N KCl = 1:10, w/v; shaking for 1 h)
229 and filtered the suspension (No. 5C, Advantec Inc., Tokyo, Japan). We measured nitrate
230 and ammonium concentrations in the extract colorimetrically using a flow-injection N
231 analyser (AACS-4, BL-TEC Inc., Osaka, Japan), calculated their contents per weight of
232 dry soil, and added them to obtain inorganic N content. We extracted soil with water
233 (dry soil:deionized water = 1:2.5, shaking for 1 h) and determined the pH of the
234 suspension with a glass electrode (MM-60, TOA-DKK Inc., Tokyo, Japan). We ground

235 oven-dried soil with an automated mortar (AMM-140D, Nitto Kagaku Co., Ltd.,
236 Nagoya, Japan) and analysed C and N contents with a CHNS/O analyser (PE2400II,
237 Perkin Elmer Inc., Waltham, MA, USA).

238 ***Statistical analysis***

239 We used two-way ANOVA to analyse the effects of stand type, season and their
240 interaction on FRB, fine root length (FRL), and weight- and length-based FRP of total
241 vegetation. We also used two-way ANOVA to analyse the effects of stand type, plant
242 form (trees or Sasa), and their interaction on fine root turnover rate. We used the Tukey
243 HSD test for multiple comparisons of FRB and FRL among stands and seasons. We
244 used one-way ANOVA to analyse the effect of stand type on tree and Sasa aboveground
245 biomass, the annual weight-based FRP of total vegetation, volumetric soil water
246 content, soil ammonium and inorganic N contents, and soil pH. Before one-way
247 ANOVA, we performed a square-root transformation for tree and Sasa aboveground
248 biomass to ensure variance homogeneity. We used the Tukey HSD test after one-way
249 ANOVA to compare stands. Because of the non-normal distribution or non-
250 homogeneity of variance even after transformation, we used the Kruskal–Wallis test to
251 analyse the effect of stand type on the annual length-based FRP of total vegetation, BA,
252 tree density, Sasa culm density, canopy openness, Oe/Oa layer thickness, gravimetric
253 soil water content, soil total C and N contents, soil C/N, and soil nitrate content, and
254 then the Steele–Dwass test for the comparison among stands. We used three-way
255 ANOVA to analyse the effects of plant form, soil layer, and stand type and their
256 interactions on SRL and RTD. We conducted polynomial regression analysis using the
257 least-squares method to identify the relationships between aboveground stand factors

258 and FRB (mean of four seasons) or weight-based annual FRP in each plot. We assumed
259 first- and second-order linear models and selected them on the basis of the Akaike
260 information criterion (AIC). We applied a general linear mixed model (GLMM) using
261 the maximum-likelihood method with a gamma error distribution and a log link to
262 analyse the effects of soil properties on FRB and FRP of trees, Sasa, and total. We
263 specified each soil property as a fixed effect and site (stand) as a random effect. We
264 determined the significance of each fixed effect using analysis of deviance (type II test).
265 In GLMM, we omitted soil temperature data from the analysis because of limited
266 replication. We conducted correlation analysis for the relationship between stand mean
267 FRB, FRP, and stand mean for each soil property. All statistical analyses were
268 performed in R software (Version 4.0.3; R Core Team 2020).

269 **Results**

270 ***Aboveground stand factors and environment***

271 The BA, tree density, and tree aboveground biomass were significantly higher in CP
272 than in PF and SA (Table S2). These three parameters were significantly lower in SA
273 than in the other stands. Sasa culm density and its aboveground biomass were
274 significantly higher in SA than in CP, but no significant difference was found between
275 SA and PF or SF (Table S2). Canopy openness was significantly lowest in CP and was
276 100% in SA (Table S2, Fig. S2).

277 ***Soil environmental factors***

278 The thickness of the Oe/Oa layer was significantly lower in CP than in the other stands
279 (Table S2). Mean annual soil temperature was lowest in CP, followed by SA, PF, and

280 SF (Table S2), with especially low temperature from December to April in CP (Fig. S3).
281 In SF, soil volumetric water content was significantly lower than in the other stands, but
282 soil gravimetric water content tended to be high (Table S2). Soil total C content and
283 C/N ratio were significantly higher in SF than in the other stands, whereas soil total N
284 content was not significantly different among stands (Table S2). Soil ammonium
285 content was significantly higher in SA and PF than in CP (Table S2). Soil inorganic N
286 content was significantly higher in SA and SF than in CP. Soil nitrate content was
287 significantly higher in SF and SA than in PF, but the absolute values and ranges were
288 smaller than those of ammonium, indicating that ammonium is the dominant form of
289 inorganic N at the study site. Soil pH was significantly higher in SA than in CP and SF,
290 and in PF than in SF (Table S2).

291 ***Fine root biomass and length***

292 FRB differed significantly among stands, but not among seasons, and no interaction
293 effect was observed (Table S3a). FRB was significantly higher in PF than in SF and CP
294 and was significantly lower in CP than in the other stands (Fig. S4a). The average
295 proportion of Sasa FRB to total FRB was extremely low in CP (8%), extremely high in
296 SA (95%), and intermediate in PF and SF (Fig. S5a), indicating that CP and SA are
297 composed of almost *A. sachalinensis* and Sasa, respectively. Despite the absence of
298 trees in SA, its total FRB was similar to those of PF and SF and was significantly higher
299 than that of CP (Fig. S4a).

300 FRL was significantly affected by both stand and season, with no significant
301 interaction effect (Table S3b). FRL was significantly higher in SA than in PF and CP
302 and was significantly lower in CP than in the other stands (Fig. S4b). FRL was

303 significantly higher in early July 2014 than in late August and November 2013 (Fig.
304 S4b).

305 ***Fine root production and turnover rate***

306 Weight-based FRP was significantly affected by stand and season, with significant
307 stand × season interaction (Table S3c). It was high in summer (July–September) in each
308 stand, but the seasonal changes (whether FRP just peaked in summer or was
309 continuously high during spring to summer [May–September]) depended on stands (Fig.
310 S6a). Most FRP was found in soil, whereas FRP in the Oe/Oa layer was considerably
311 lower (Fig. S6a), perhaps because of a methodological limitation of the use of ingrowth
312 cores for estimating FRP in the Oe/Oa layer, such as dry layer or roots in the Oe/Oa
313 layer originating from those in soil. The proportion of Sasa in weight-based FRP (Fig.
314 S7a) was similar to that of FRB (Fig. S5). Length-based FRP was also significantly
315 affected by stand and season, with significant stand × season interaction (Table S3d),
316 and the trends among stands and seasons were similar to those of weight-based FRP
317 (Fig. S6b). The proportion of Sasa in length-based FRP was similar to or slightly higher
318 than that of weight-based FRP (Fig. S7b). Seasonal trends of weight- or length-based
319 FRP of trees and Sasa were similar to those of the total FRP in PF and SF, where trees
320 and Sasa co-exist (Fig. S6).

321 Weight-based annual FRP was significantly lower in CP than in SF and PF (Fig.
322 1a). Length-based annual FRP was significantly lower in CP than in the other stands
323 (Fig. 1b). Fine root turnover rate was not significantly affected by stand, plant form, or
324 their interaction (Table S4). We found positive relationships between FRB and FRP of
325 trees, Sasa, and total (Fig. 2).

326 ***Root traits***

327 The SRL was affected by plant form, layer (Oe/Oa layer vs. soil layer), and stand (Table
328 S5a). The plant × layer, plant × stand, layer × stand, and plant × layer × stand
329 interactions were significant. The SRL was significantly higher in Sasa than in trees,
330 and in the Oe/Oa layer than in the soil layer (Table S5a, Fig. S8a). RTD was
331 significantly affected by plant form, layer, and stand, and the plant × layer and plant ×
332 stand interactions were significant (Table S5b). RTD was significantly lower in Sasa
333 than in trees, and in the Oe/Oa layer than in the soil layer (Table S5b, Fig. S8b).

334 ***Relationship between fine root dynamics and aboveground structure and***
335 ***environmental conditions***

336 Tree FRB increased with increasing tree aboveground biomass, tree density, and BA
337 (Fig. 3a–c), whereas Sasa and total FRB significantly decreased (Fig. 3a–c). On the
338 other hand, Sasa and total FRB were high at high canopy openness (Fig. 3d) and Sasa
339 FRB had a significant positive relationship with Sasa aboveground biomass (Fig. S9a),
340 indicating that understory light affects not only Sasa aboveground biomass but also Sasa
341 FRB.

342 Trends of the relationships between FRPs of trees and Sasa and aboveground
343 stand factors were similar to those of FRB, but total FRP was highest in the middle
344 range of the aboveground stand factors (Fig. 4a–c). Sasa FRP was high at higher canopy
345 openness, but there was a significant negative relationship between tree FRP and
346 canopy openness (Fig. 4d).

347 In GLMM analysis, soil pH significantly negatively affected total and Sasa FRP,
348 soil ammonium content significantly positively affected tree FRB and FRP, Oe/Oa layer

349 thickness significantly positively affected tree FRB, and Soil C and N contents
350 significantly positively affected total and tree FRP (Table S6). Other soil properties did
351 not significantly affect total, Sasa, or tree FRB or FRP. We found significant or
352 marginal positive correlations between the mean values of soil inorganic N or
353 ammonium contents and Sasa FRB or FRP (Fig. S10a, b, k, l) and marginal positive
354 correlations between Oe/Oa layer thickness or soil temperature and total FRP (Fig.
355 S10o, q). We also found tendencies of positive correlations with $|r| \geq 0.7$ between the
356 mean values of soil inorganic N or ammonium contents and total FRB (Fig. S10a, b),
357 between Oe/Oa thickness or soil temperature and total FRB (Fig. S10e, g), between soil
358 pH and Sasa FRB or FRP (Fig. 10d, n), and tendencies of negative correlations between
359 the mean values of soil inorganic N or ammonium contents and tree FRP (Fig. S10k, l)
360 and between soil pH or soil water content and tree FRP (Fig. S10n, p).

361 **Discussion**

362 ***Understory vegetation changes the relationship between FRB and stand factors***
363 Tree FRB and FRP increased with tree aboveground biomass, tree density, and BA
364 (Figs. 3, 4). These trends of tree FRB agree with previous studies (Karizumi 1974; Finér
365 et al. 2011a; Zhou et al. 2018). In contrast, total FRB had negative relationships with
366 these parameters because of a strong negative relationship between them and Sasa FRB
367 (Fig. 3). Sasa FRB was positively correlated with Sasa aboveground biomass, which
368 was dependent on understory light (Table S2; Fig. S9a). Finér et al. (2011a)
369 demonstrated that aboveground stand factors (e.g., tree density, BA, tree aboveground
370 biomass) explained tree FRB but not total FRB, which included the FRB of understory
371 vegetation, indicating that understory vegetation weakens the relationship between FRB

372 and aboveground stand factors. On the other hand, the present study showed a negative
373 relationship between total FRB and the aboveground stand factors in the presence of
374 understory Sasa, because inverse relationships between trees and Sasa complement each
375 other in this forest ecosystem (Fig. S9b, c; Fukuzawa et al. 2007, 2013). The regression
376 lines of total FRP against tree aboveground biomass, BA, and tree density had maxima
377 at around the intermediate values of these factors and were asymmetric (Fig. 4),
378 indicating that total FRP was higher at lower values of these factors. However, total
379 FRP did not differ significantly among PF, SF, and SA (Fig. 1). In this study, a
380 significant positive relationship was observed between FRB and FRP (Fig. 2). Similar
381 turnover rates among stands and plant forms (Tables S5, S6) also support this
382 relationship. Using a global dataset, Finér et al. (2011b) showed that FRP is explained
383 by FRB, and the present study confirms their result.

384 ***Understory vegetation determines ecosystem FRP***

385 Weight-based annual total FRP was higher in stands with a substantial presence of Sasa
386 than in the stand composed of a single tree species with scarce Sasa (CP), and FRP in
387 SA, with negligible trees, was as high as that in PF and SF, where trees and Sasa co-
388 exist (Fig. 1). These results suggest that the presence of Sasa, regardless of the presence
389 or absence of trees, is a key determinant of ecosystem FRP. A large contribution of Sasa
390 to total FRB (up to 57%), FRL (up to 75%), or FRP (59% and 72% for weight-based
391 and length-based FRP, respectively) in stands with trees (Figs. 1, S5, S7) agrees with
392 the reports of 71% and 59%–88% Sasa contribution in this forest (Fukuzawa et al. 2007,
393 2013), which may be the upper limit of the contribution of understory vegetation
394 worldwide, and a report by Helmisaari et al. (2007) that showed a contribution of up to

395 50% by understory vegetation to total FRB in boreal forests in northern Finland.
396 Seasonal mean FRB (891 g m^{-2}) was higher in a 60-cm soil profile in a forest covered
397 with Sasa (Fukuzawa et al. 2013) than global mean FRB estimates (526–776 g m^{-2}) for
398 the whole rooting depths in any of boreal, temperate, or tropical forests (Finér et al.
399 2011a).

400 An increase in FRP with increasing tree species diversity has been reported in a
401 boreal forest in Canada (Brassard et al. 2009, 2013; Ma and Chen 2017). Meta-analysis
402 also revealed an increase in FRP with increasing species diversity in multiple
403 ecosystems including grasslands and forests (Ma and Chen 2016). In contrast, the
404 positive effect of species diversity is small in young plantations (Domisch et al. 2015;
405 Ma and Chen 2016). Brassard et al. (2013) suggested greater soil volume filling by a
406 mixture of species with species-specific spatial and temporal patterns of root placement
407 and proliferation, i.e., niche differentiation, as a cause of the increase in FRP with
408 increasing tree species diversity. Ma and Chen (2017) also proposed that FRP can
409 increase as a result of horizontal soil volume filling. Alternative mechanisms include the
410 lack of pathogen-constrained root growth, which are typical in monocultures (de Kroon
411 et al. 2012) and sampling effect, which results in an apparently greater probability of
412 dominance by highly productive species with increasing species diversity (Wardle
413 1999). In the present study, the presence of Sasa increased total FRP in forest stands (PF
414 and SF) in comparison with the single-tree species stand (CP) by adding Sasa FRP to
415 the stable tree FRP (Fig. 1). This addition may be attributed to the complete cover of the
416 land surface by Sasa. However, similar vertical root distributions of trees and Sasa
417 (Fukuzawa et al. 2007) suggest that they would use the same vertical niche. On the
418 other hand, the present study did not reveal higher FRP in mixtures of trees and Sasa

419 (PF and SF) than in SA (Fig. 1, Table S1); thus, we conclude that these mixtures do not
420 always promote FRP. Then why was FRP in SA high despite its almost single-species
421 composition?

422 SRL was significantly higher in Sasa than in trees (Fig. S8, Table S5), although
423 we did not separate tree roots by species. Eissenstat (1991) highlighted the positive
424 relationship of SRL with FRP and turnover rate, suggesting that roots with higher SRL
425 are more productive. RTD was significantly lower in Sasa than in trees (Fig. S8, Table
426 S5). Although RTD is often negatively correlated with SRL (Withington et al. 2006),
427 Kramer-Walter et al. (2016) proposed that RTD is independent from SRL and that
428 species with low RTD are fast-growing highly productive species. Our data on SRL and
429 RTD indicate that Sasa grows faster and is more productive than trees, which is related
430 to its ability of foraging for water and nutrients. This feature of root traits in Sasa is
431 consistent with that of graminoids in a global dataset (Freschet et al. 2017), although we
432 detected no difference in root turnover rate between trees and Sasa (Table S4). We
433 speculate that Sasa, which has a capacity for explosive growth reflected in these root
434 traits, increases FRP in SA, where nutrients, water, and light conditions are favourable
435 because of the occupation by Sasa alone. This perspective would be important for
436 evaluation of the fine root dynamics and ecosystem functioning in forests with a
437 mixture of tree and grass species, such as cool-temperate forests in northern Japan.

438 A limitation of this study is that only a 10-cm-deep surface soil layer was
439 analysed, although fine roots are also distributed in deeper layers. Fukuzawa et al.
440 (2007) have surveyed a 60-cm soil profile in this forest and reported that 60% of fine
441 roots are concentrated in a 15-cm-deep soil layer. They also revealed similar vertical
442 patterns of the fine root biomass of the trees and Sasa as described above. These results

443 imply that the fine root dynamics of the surface soil layer represents that of the whole
444 soil layer (although the absolute FRP value may be underestimated) and suggest that the
445 fine root dynamics of the whole soil layer can be extrapolated from the data on the
446 interaction between trees and Sasa obtained in the present study.

447 ***Relationship between fine root dynamics and soil properties***

448 The relationships between FRB or FRP and soil N availability (i.e., inorganic N
449 content) in previous studies are controversial. Some studies reported negative
450 relationships between FRB and soil N availability or N content in forests and suggested
451 that plants can take up enough nutrients with fewer roots in fertile soil (Nadelhoffer
452 2000; Yuan and Chen 2010), whereas other studies suggested that roots often proliferate
453 within nutrient (including N)-rich patches (Pregitzer et al. 1993; Hodge 2004). FRP is
454 considered to increase with increasing soil N availability (Aber et al. 1989; Nadelhoffer
455 2000; Yuan and Chen 2012). However, meta-analysis of northern boreal or temperate
456 forests showed an unclear effect of soil N availability on FRB and FRP (Brassard et al.
457 2009). In the present study, soil ammonium content significantly positively affected tree
458 FRB and FRP after eliminating the effect of stand type (Table S6). Comparison of the
459 stand means revealed positive correlations between Sasa FRB or FRP and soil inorganic
460 N or ammonium contents (Fig. S10a, b, k, l). No significant relationships were found
461 between FRB or FRP and soil nitrate content (Fig. S10c, m) because of low variation of
462 the latter among stands and its low contribution to inorganic N at the study site. The
463 above positive correlations are consistent with the reports of Pregitzer et al. (1993) and
464 Hodge (2004).

465 Generally, soil N availability increases with nitrate leaching after disturbances
466 such as the forest clear-cutting that created SA (Bormann and Likens 1994). However,
467 Fukuzawa et al. (2006, 2015) showed that Sasa FRB increases and compensates for the
468 reduction of tree roots immediately after selective or clear-cutting and mitigates nitrate
469 leaching from the cleared site. Watanabe et al. (2016) reported a positive prompt
470 response of Sasa aboveground biomass to N fertilization in forest. Favourable nutrients,
471 water, and light without competition would enhance the above- and belowground
472 growth of Sasa due to its ability to respond quickly to disturbances, as mentioned above.
473 We cannot determine whether increased soil N availability would be maintained for the
474 long term since it was increased by the disturbance or could be attributed to high
475 productivity or a specific interaction in the rhizosphere (e.g., mycorrhizal colonization
476 and root exudates) of this species. In the future, long-term changes in N dynamics in
477 Sasa area after disturbances, and mechanisms of root and nutrient cycling should be
478 clarified to characterize the ecosystem functioning in northern forests with mosaic
479 structure including the Sasa areas (Inoue et al. 2017). Nevertheless, the present study
480 revealed higher FRP and N availability in SA than in the tree stands.
481 Soil pH significantly negatively affected total and Sasa FRP (Table S6), but Sasa
482 FRB and FRP tended to increase with increasing soil pH, whereas tree FRB and FRP
483 tended to decrease in the comparisons among stands (sites) (Fig. S10d, n). The reason
484 for this discrepancy between within-site and between-site relationships is unclear, but it
485 might have been caused by a large variation among sites (Table S2). High soil pH
486 stimulates root growth in various crop plants (Haynes, 1982) and is associated with high
487 FRB in boreal forests (Yuan and Chen, 2010). A negative effect of excess aluminium
488 ion on root growth at low pH is considered as a primary factor in relation to soil

489 acidification (Hirano et al. 2007). In contrast, Godbold et al. (2003) reported high root
490 growth, especially in the organic layer, at an acidic site in German Norway spruce
491 forests. The opposite responses of tree FRB or FRP and those of Sasa to soil pH in the
492 present study indicate that the effect of soil pH on root growth is not uniform. On the
493 other hand, the positive relationship of Sasa FRB and FRP and soil pH is likely
494 attributable to the cation-rich litter supply from Sasa, which prevents soil acidification
495 in Japanese forests (Takamatsu et al. 1997).

496 ***Seasonal pattern of FRB and FRP***

497 FRB did not significantly differ among seasons (Table S3a; Fig. S4a). These data agree
498 with many previous studies (Aber et al. 1985; Yuan and Chen 2010). The absence of a
499 trend may be caused by larger spatial heterogeneity during destructive root sampling
500 than temporal variations (Fukuzawa et al. 2013). On the other hand, FRL was
501 significantly affected by seasons, with high values in summer, despite destructive root
502 sampling (Table S3b; Fig. S4b); these data agree with the seasonal pattern of root length
503 in minirhizotron studies (Noguchi et al. 2005; Fukuzawa et al. 2013).

504 FRP was affected by season, with a significant stand × season interaction (Table
505 S3c, d). FRP was high in PF and SA in spring and summer (May–September), but in
506 summer (July–September) in SF and CP (Fig. S6). In SF, the lowest soil volumetric
507 water content and the highest gravimetric water content indicated low soil bulk density.
508 In addition, soil C content in SF was high, therefore high soil permeability may
509 suppress root growth during the dry spring–early summer. The root growth pattern in
510 CP is that of *A. sachalinensis* with a small contribution from Sasa. Abramoff and Finzi
511 (2015) suggested that root growth in conifer species peaks later than in deciduous

species. On the other hand, our data for SA suggest that a longer photosynthesis period in open sites enables Sasa to extend the root growth period (Fukuzawa et al. 2021).

Conclusion

The present study demonstrated that the total FRB and FRP do not parallel aboveground stand factors and the presence of Sasa regardless of the presence of trees is a key determinant of ecosystem FRP in a northern cool-temperate forest with dense understory vegetation. Lower Sasa FRP in the presence of trees suggests the competition effect for Sasa. The SRL was significantly higher in Sasa than in trees, and RTD was significantly lower, indicating that Sasa is a fast-growing highly productive species. We conclude that the roots of Sasa which has a capacity for explosive growth significantly affect fine root dynamics in forest ecosystems with dense understory vegetation. Our findings will be important for evaluation and prediction of biogeochemical cycling and ecosystem functioning in forests with understory vegetation.

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Declaration of interest statement

Conflict of interest: The authors declare that they have no conflicts of interest.

Availability of data and material All data are available at https://db.cger.nies.go.jp/JaLTER/metacat/metacat/JaLTER-Hokkaido-Kita.1146.3/jalter.

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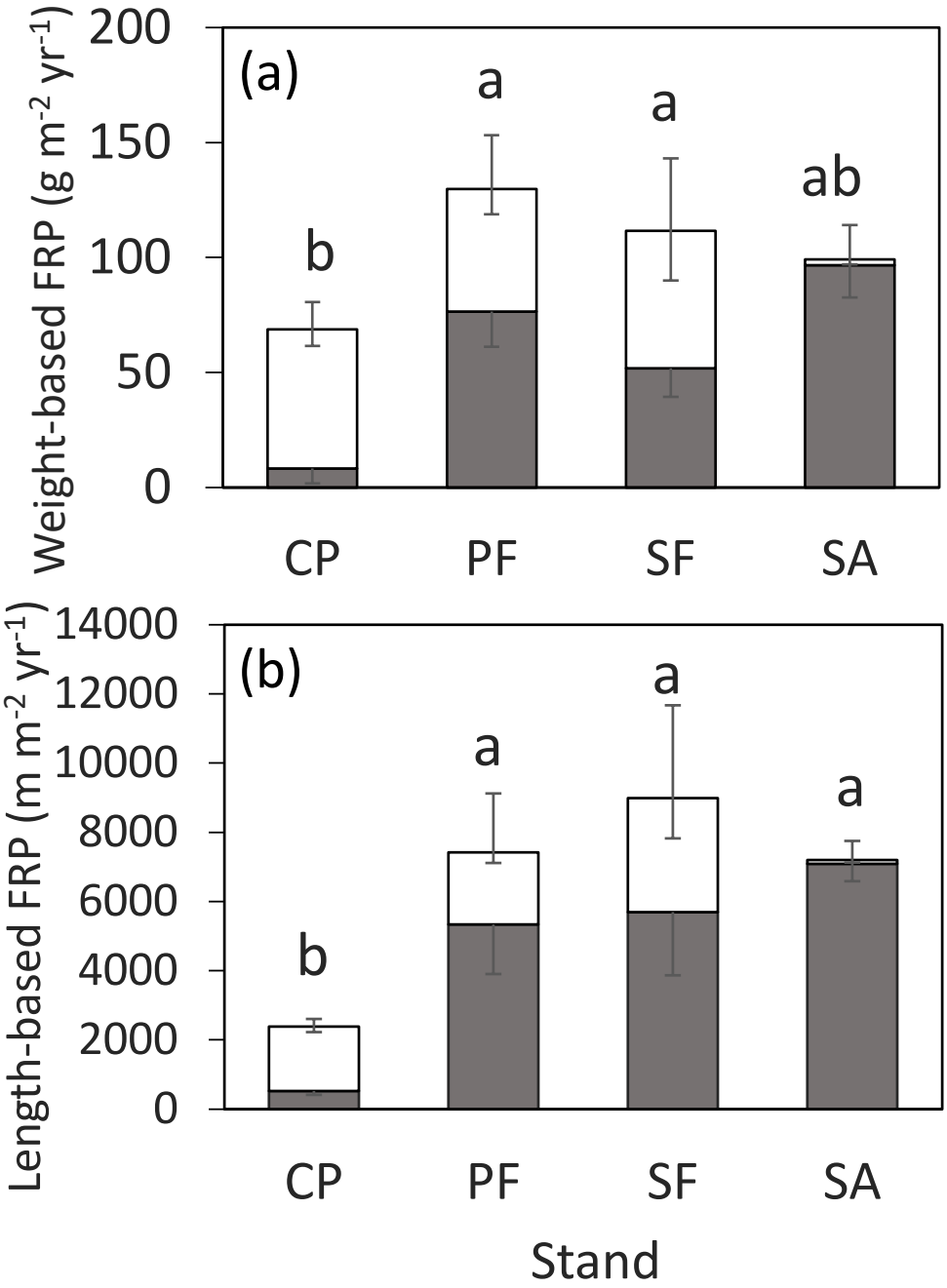
Figures



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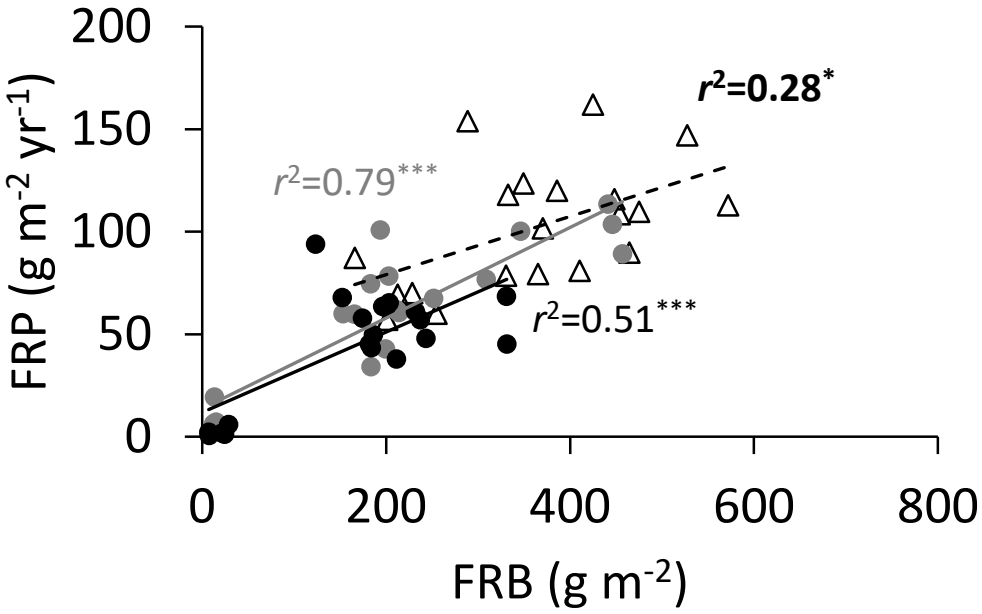

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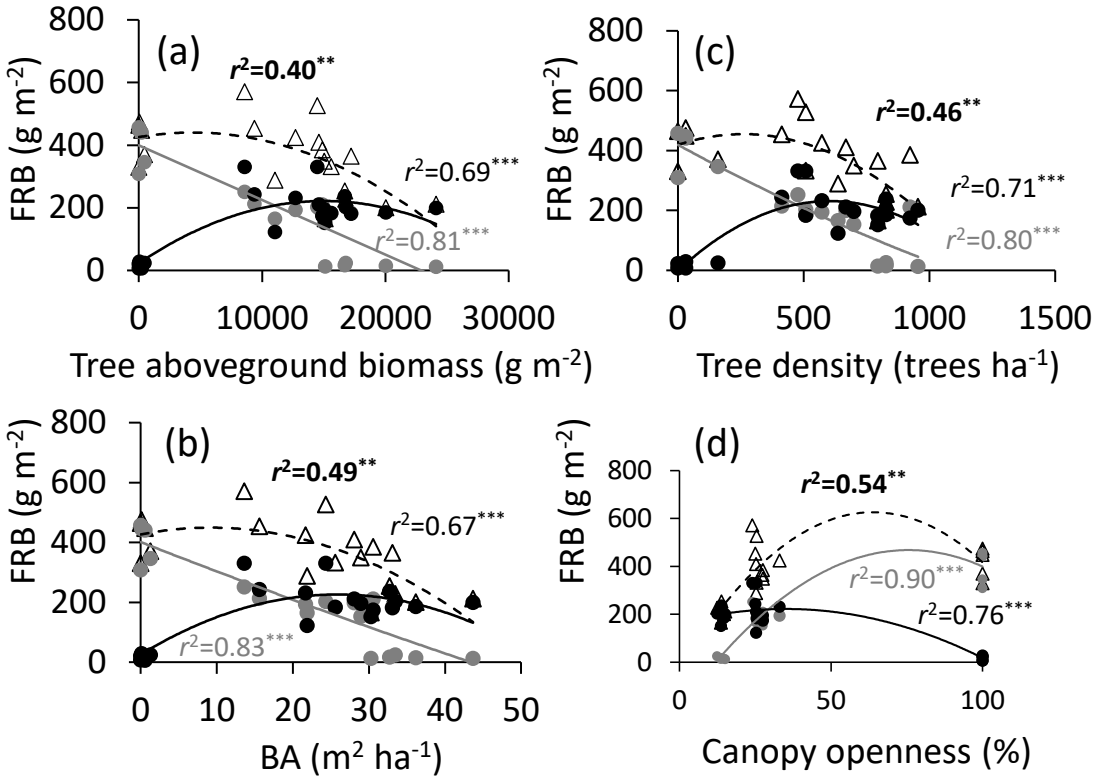

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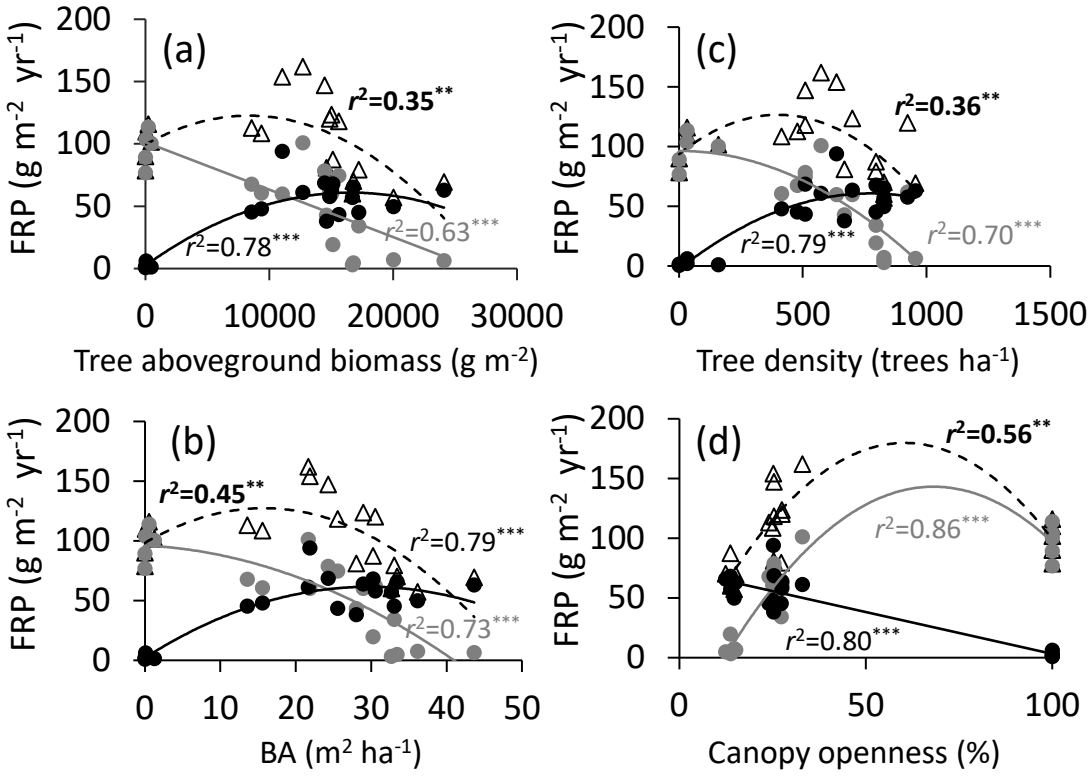

Yanagawa et al. Fig. 4

Figure captions

Figure 1. Annual weight-based (a) and length-based (b) fine root production (FRP) in each stand. Grey, Sasa; white, trees. Positive and negative error bars denote SD of total and of each plant form, respectively (n = 5). Total value is the sum of Oe/Oa and soil layers. Lowercase letters represent significant differences among stands ($P < 0.05$). CP, conifer plantation; PF, primary forest stand; SF, secondary forest stand; SA, Sasa area.

Figure 2. Relationships between fine root biomass (FRB) and fine root production (FRP) of trees, Sasa, and total. Trees, black circles and solid line; Sasa, grey circles and solid line; total, triangles and dashed line. The r^2 values are indicated in the corresponding shades (trees and Sasa) and in bold (total). *** $P < 0.001$; * $P < 0.05$.

Figure 3. Relationships between fine root biomass (FRB) and aboveground stand characteristics: tree aboveground biomass (a), tree density (b), basal area (BA) (c), and canopy openness (d). Trees, black circles and solid line; Sasa, grey circles and solid line; total, triangles and dashed line. The r^2 values are indicated in the corresponding shades (trees and Sasa) and in bold (total). Straight and curved lines denote the selected first-order or second-order linear models, respectively. *** $P < 0.001$; ** $P < 0.01$.

Figure 4. Relationships between fine root production (FRP) and aboveground stand characteristics: tree aboveground biomass (a), tree density (b), basal area (BA) (c), canopy openness (d). Trees, black circles and solid line; Sasa, grey circles and solid line; total, triangles and dashed line. The r^2 values are indicated in the corresponding shades (trees and Sasa) and in bold (total). Straight and curved lines denote the selected first-order or

second-order linear models, respectively. *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

Presense of understory dwarf bamboo determines ecosystem fine root production in a cool-temperate forest in northern Japan

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(a)

(b)

Figure S1. Photographs of Sasa (*Sasa senanensis*) (a) and tree (b) roots.

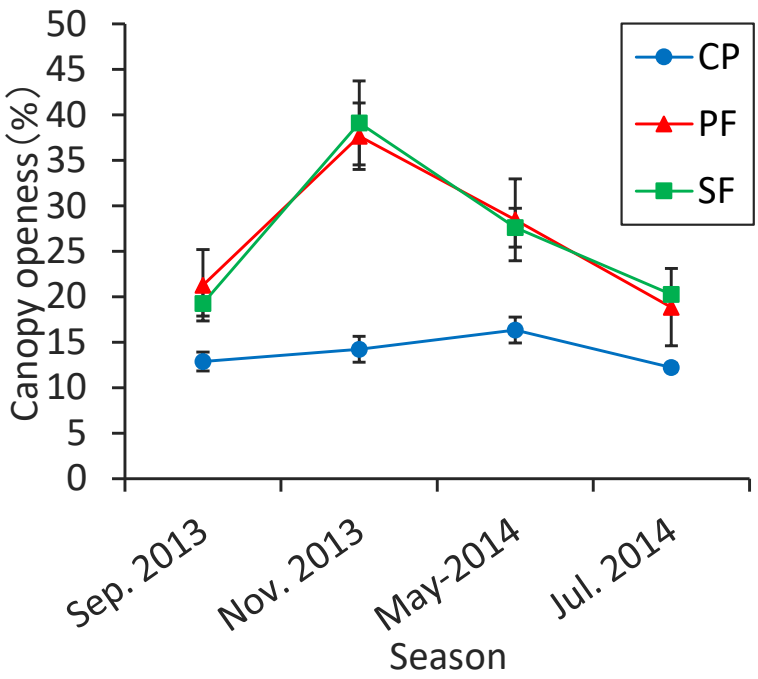

Figure S2. Canopy openness in each stand in four seasons. In the Sasa area, canopy openness was 100% at all times and the data are not shown. Error bars denote SD (n = 5). CP, conifer plantation; PF, primary forest; SF, secondary forest.

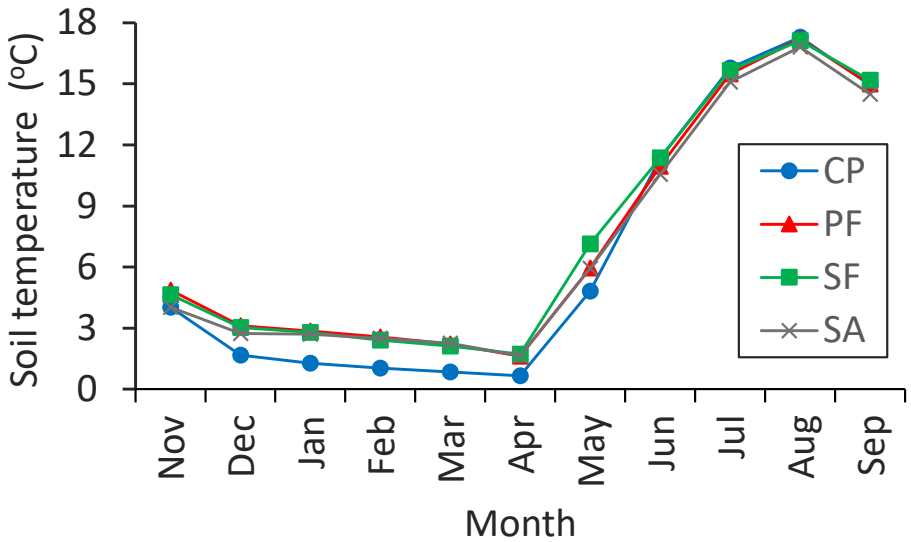

Figure S3. Mean monthly soil temperature in each stand from November 2013 to September 2014. CP, conifer plantation; PF, primary forest; SF, secondary forest; SA, Sasa area.

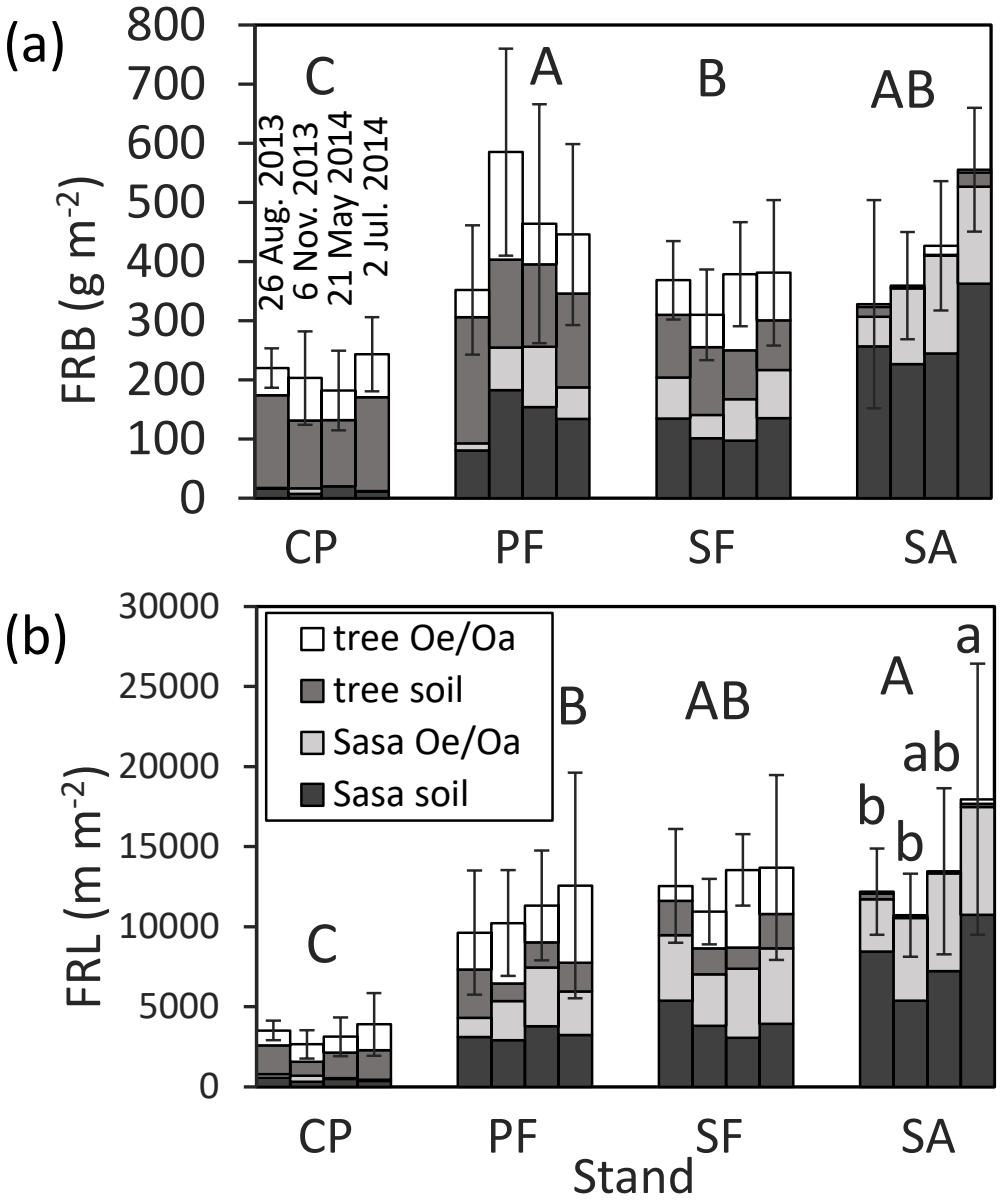

Figure S4. Seasonal changes in fine root biomass (FRB) (a) and fine root length (FRL) (b) in each stand. Error bars denote SD of total FRB or FRL (n = 5). Soil depth was 0–10 cm. Different capital and lowercase letters indicate significant differences (P < 0.05) among stands and seasons in the whole dataset, respectively. CP, conifer plantation; PF, primary forest; SF, secondary forest, SA, Sasa area.

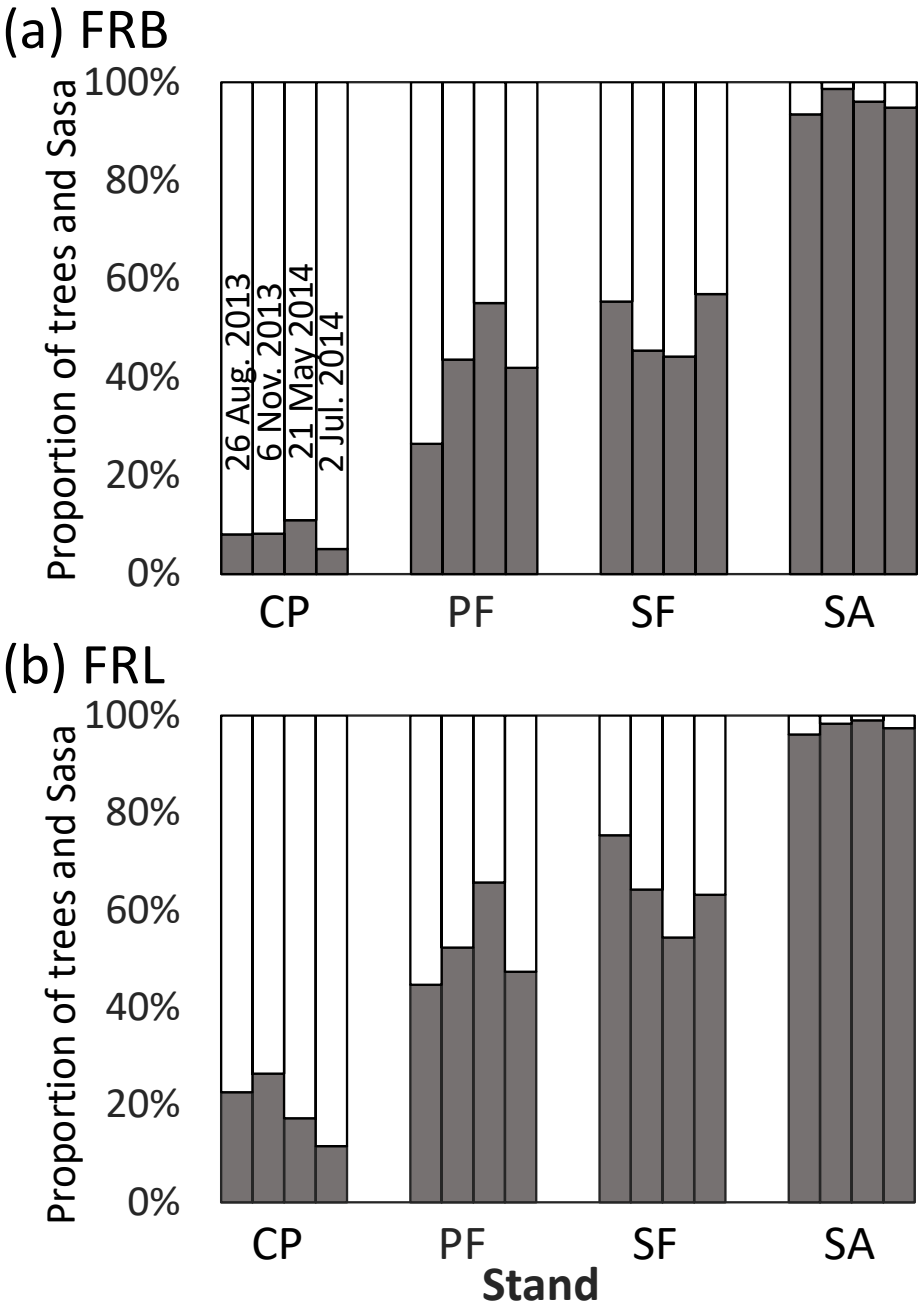

Figure S5. Proportion of trees and Sasa roots in fine root biomass (FRB) (a) and fine-root length (FRL) (b) for all layers (Oe/Oa and soil). Grey, Sasa; white, trees. CP, conifer plantation; PF, primary forest; SF, secondary forest, SA, Sasa area.

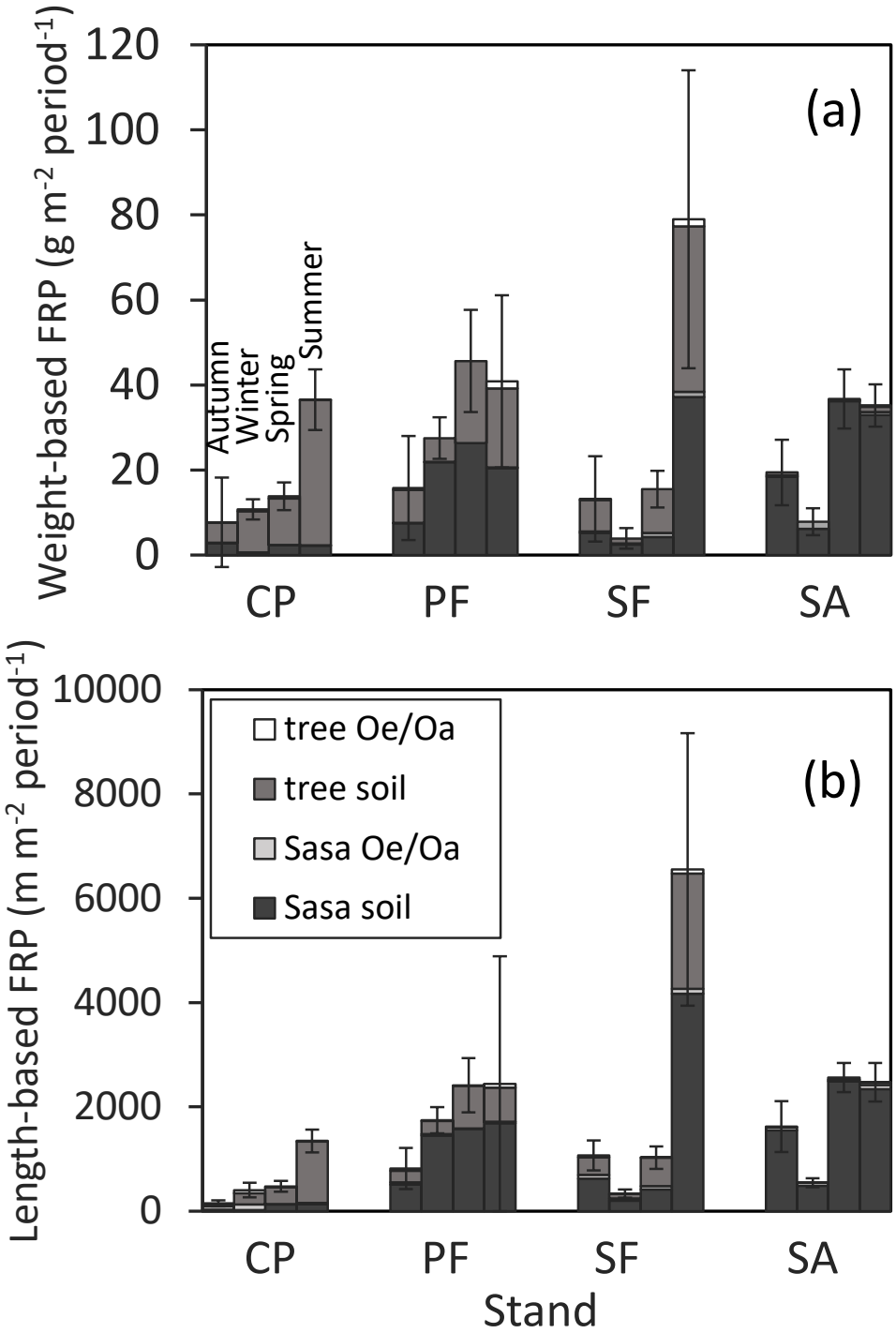

Figure S6. Seasonal changes in weight-based (a) and length-based (b) fine root production (FRP) in each stand. Error bars denote SD of total FRPs (n = 5). Soil depth was 0–10 cm. CP, conifer plantation; PF, primary forest; SF, secondary forest, SA, Sasa area. Autumn, 26 August–30 October 2013; Winter, 6 November 2013–14 May 2014; Spring, 21 May–1 July 2014; Summer, 2 July–16 September 2014.

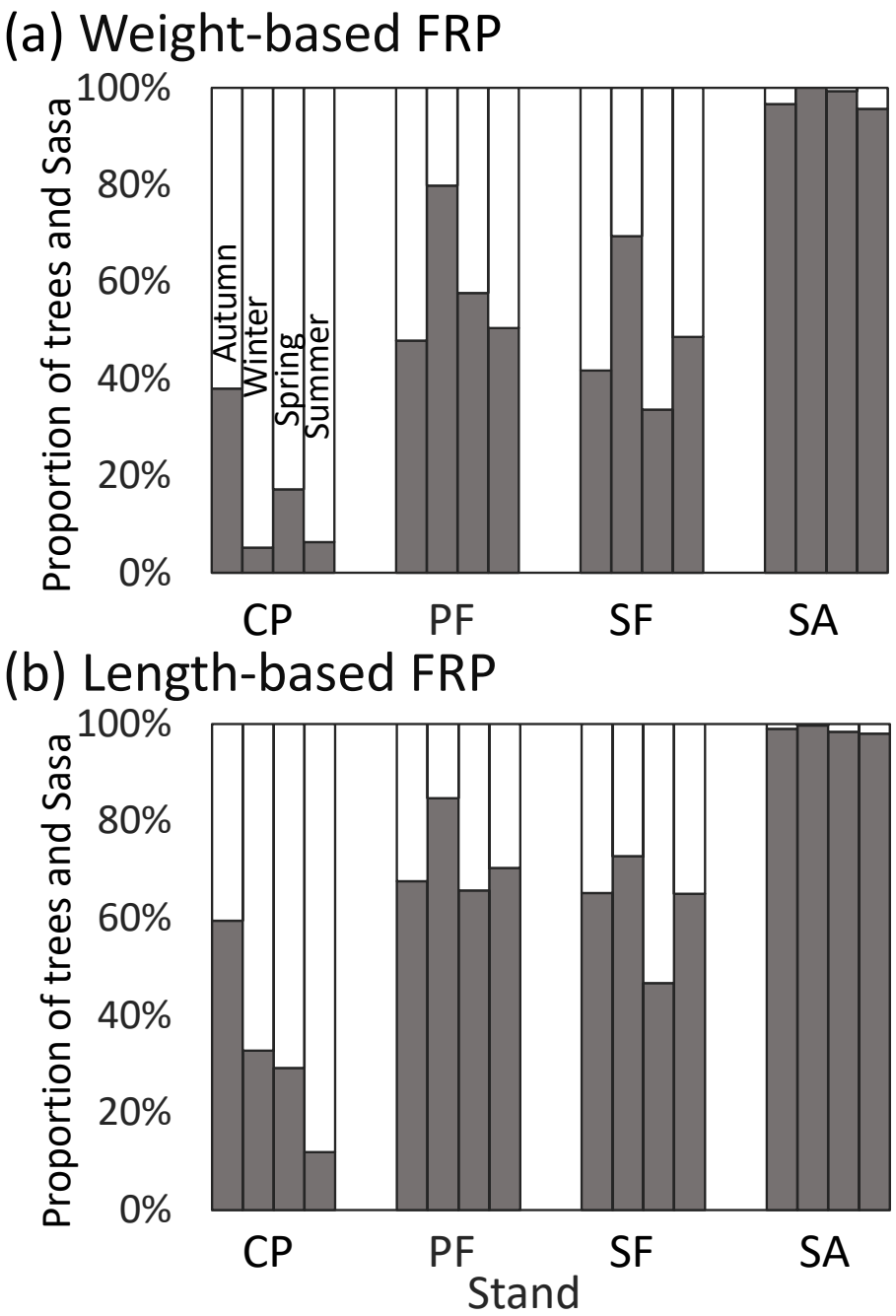

Figure S7. Proportion of trees and Sasa roots in weight-based (a) and length-based (b) fine root production (FRP) for all layers (Oe/Oa and soil). Grey, Sasa; white, trees. CP, conifer plantation; PF, primary forest; SF, secondary forest, SA, Sasa area. Autumn, 26 August–30 October 2013; Winter, 6 November 2013–14 May 2014; Spring, 21 May–1 July 2014; Summer, 2 July–16 September 2014.

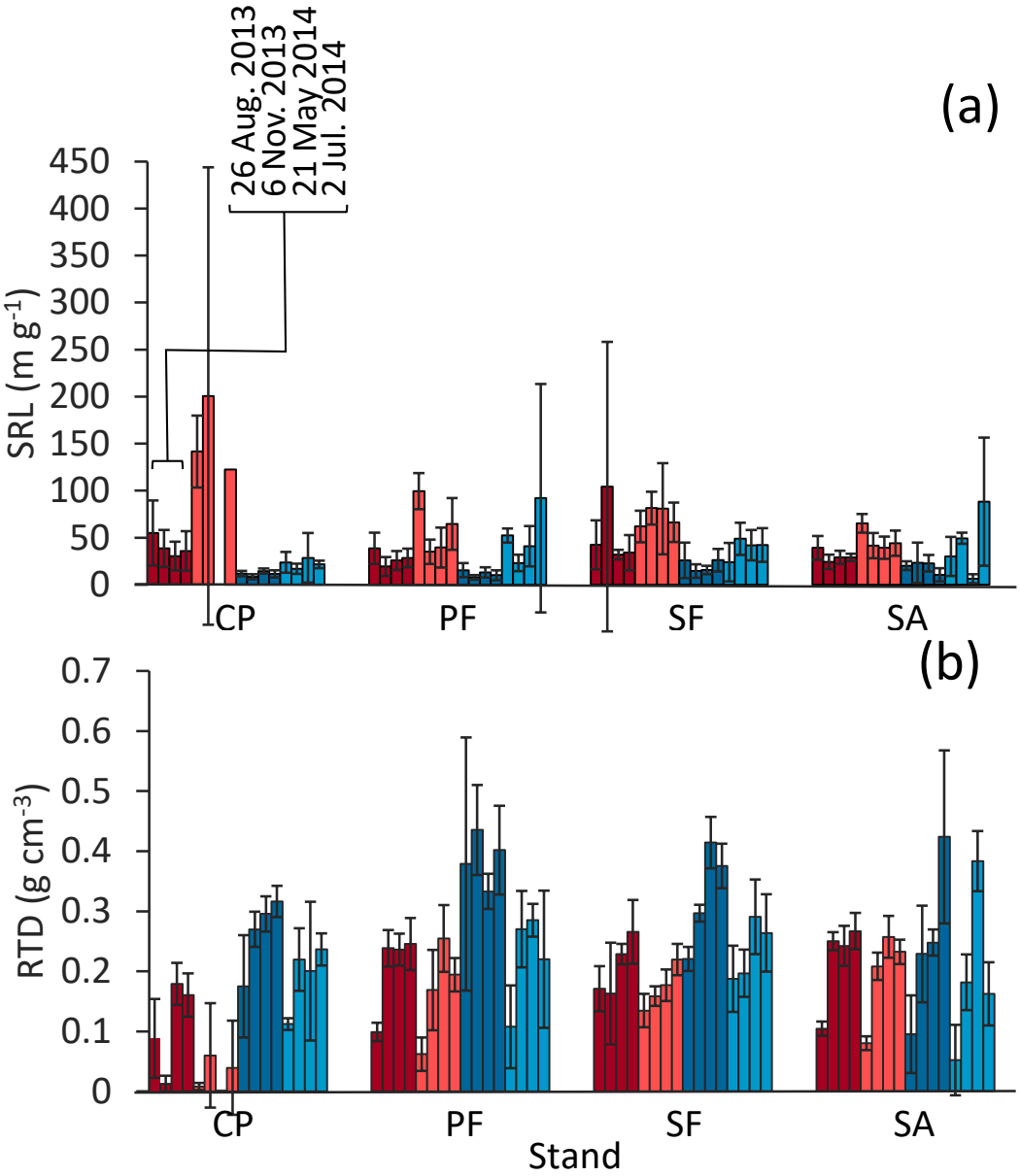

Figure S8. Root traits of trees and Sasa in soil and Oe/Oa layers in four seasons. Specific root length (SRL) (a) and root tissue density (RTD) (b). Error bars denote SD (n = 5). CP, conifer plantation; PF, primary forest stand; SF, secondary forest stand; SA, Sasa area.

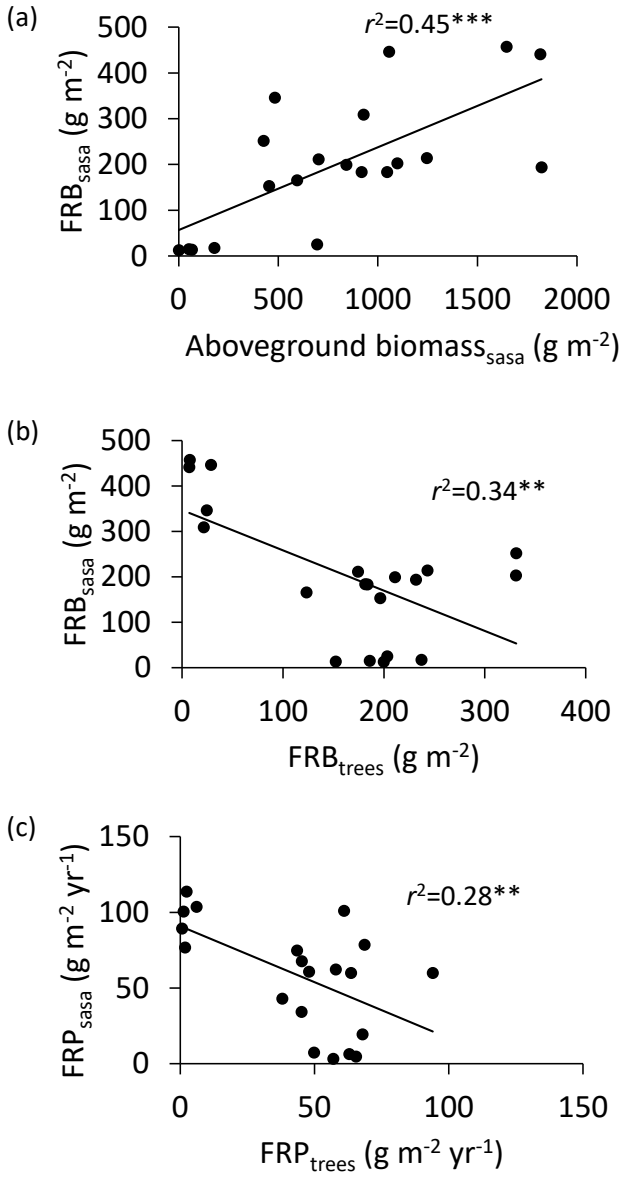

Figure S9. Relationships between Sasa aboveground biomass and Sasa fine root biomass (FRB_{sasa}) (a), between tree fine root biomass (FRB_{trees}) and FRB_{sasa} (b), and between tree fine root production (FRP_{trees}) and Sasa fine root production (FRP_{sasa}) (c). ***$P < 0.001$; **$P < 0.01$.

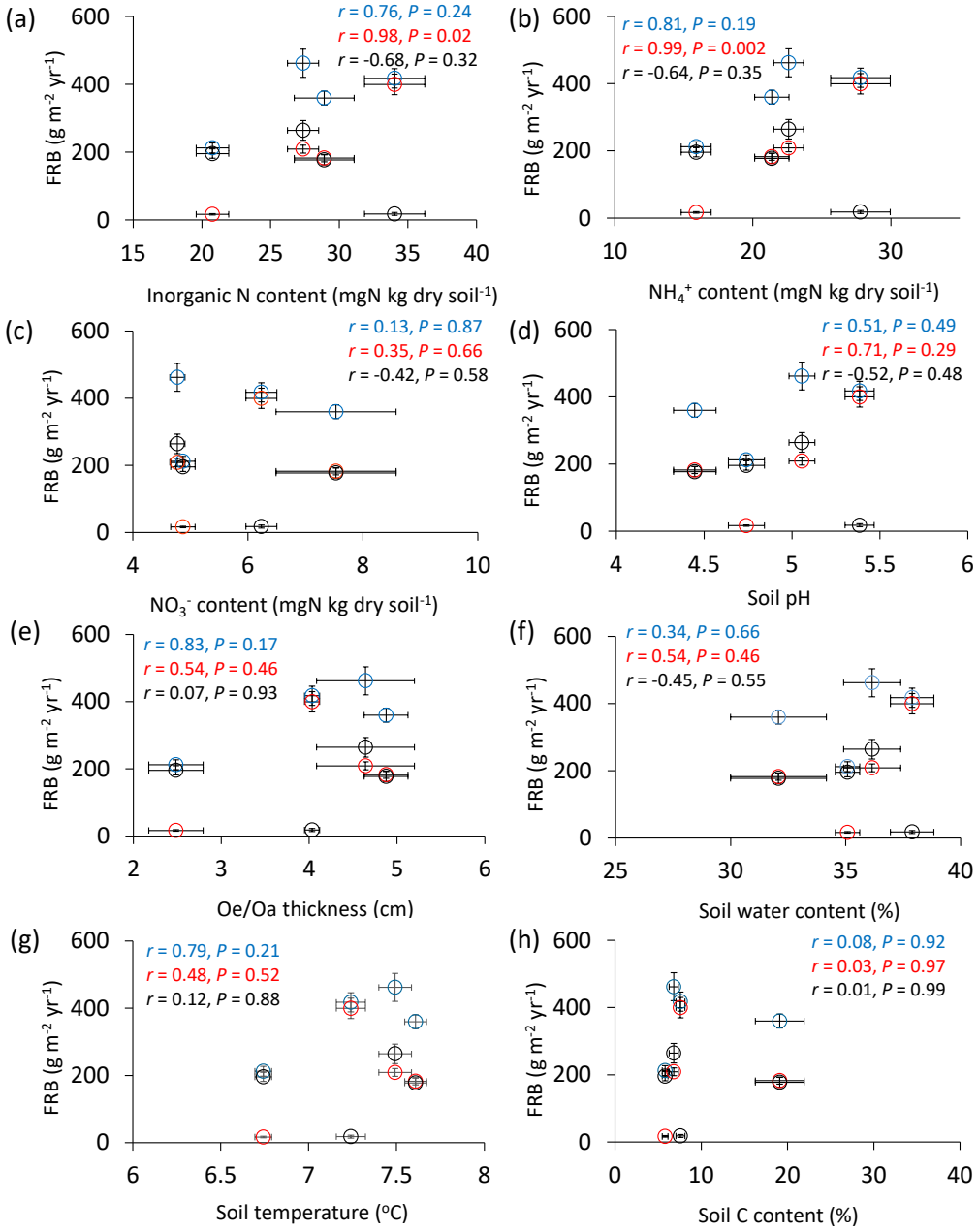

Figure S10. Relationships between site mean fine root biomass (FRB) and production (FRP) and site mean soil environmental factors: soil inorganic N content (a, k), soil ammonium content (b, l), soil nitrate content (c, m), soil pH (d, n), Oe/Oa layer thickness (e, o), soil water content (f, p), soil temperature (g, q), soil C content (h, r), soil N content (i, s), and soil C/N (j, t). Trees, black circles; Sasa, red circles; total, blue circles. Vertical and horizontal bars denote standard errors (n = 5). The r values and P values from correlation analysis for trees, Sasa, and total are indicated in the corresponding shades.

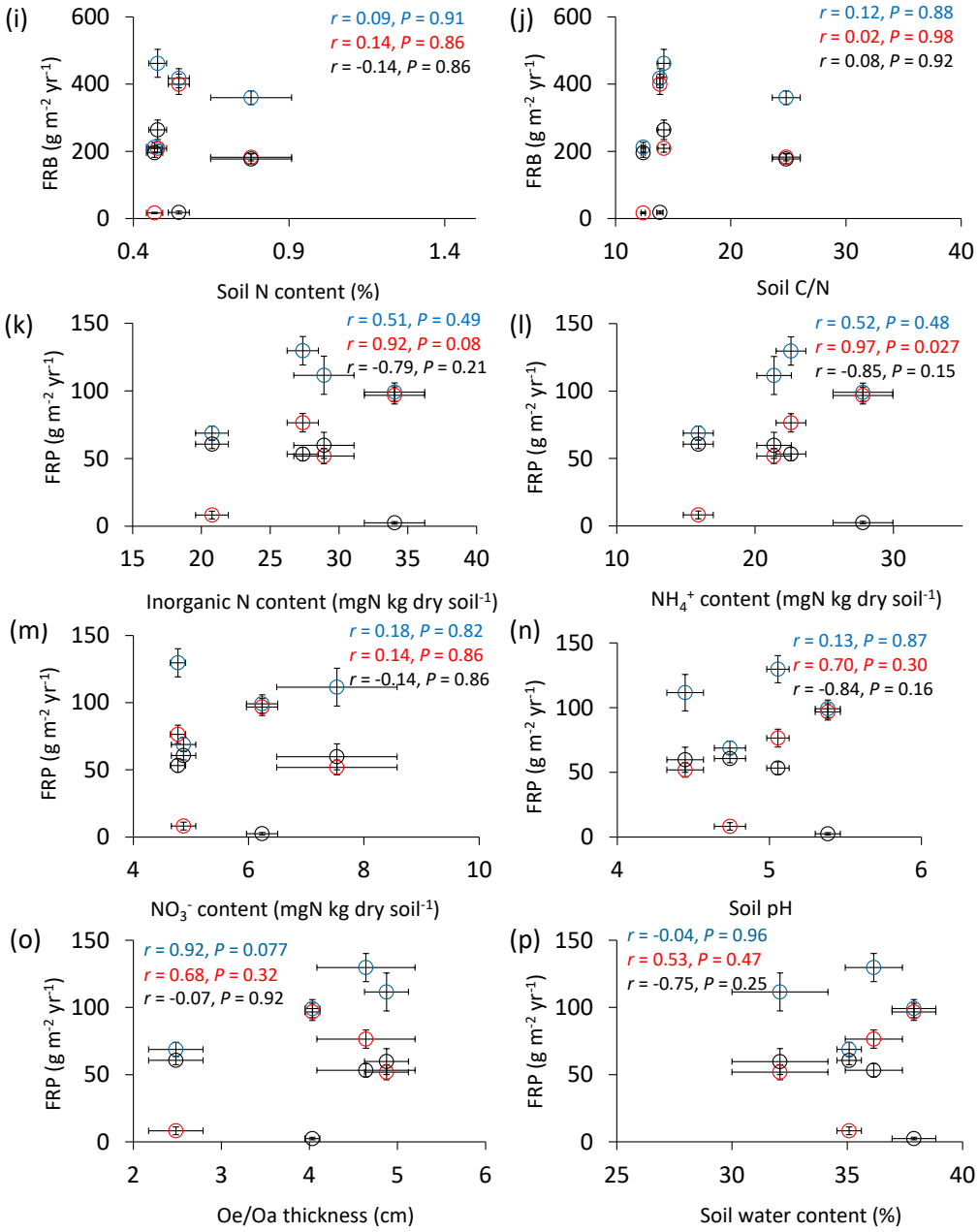

Figure S10. (Continued)

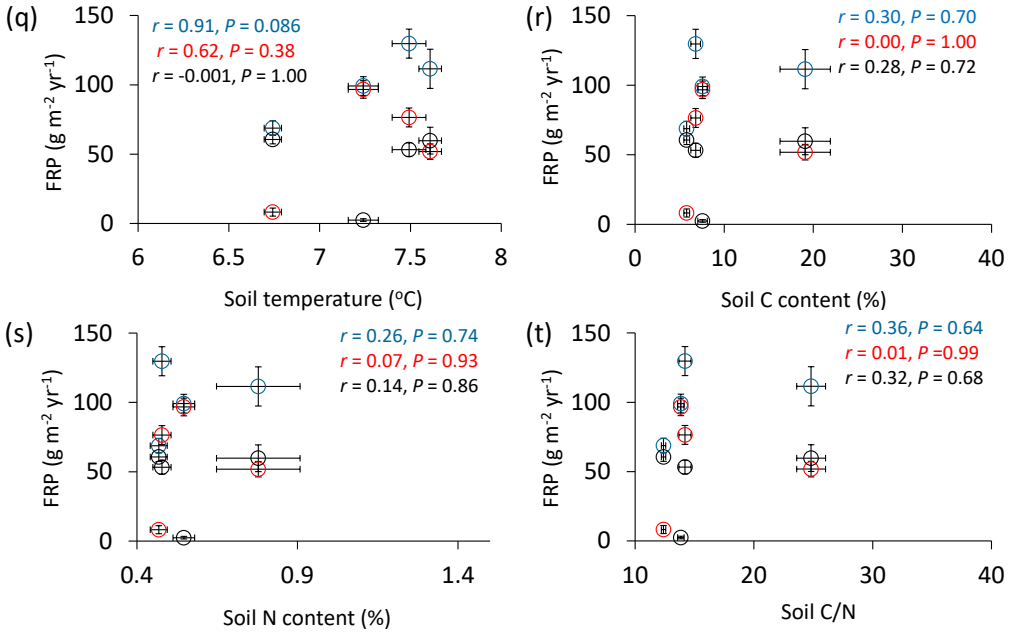

Figure S10. (Continued)

Table S1. Overview of stand characteristics.

Stand type	Abbreviation	Tree species composition	Stand history	Stand age (yrs)
Conifer plantation	CP	*Abies sachalinensis*	1929 forest fire (in part) 1975 soil scarification planting	39
Primary conifer-broadleaf mixed forest	PF	*Quercus crispula* *Magnolia obovata* *Alnus hirsuta* *Tilia japonica* *Acer pictum* *Phellodendron amurense* *Sorbus commixta* *Abies sachalinensis* *Betula ermanii* *Prunus ssiori*	1975 tree cutting (only for wind-fallen trees) 2001 selective tree cutting (in part)	>100
Secondary forest	SF	*Betula platyphylla* *Betula ermanii*	1929 forest fire 1945 forest fire	69
Sasa area	SA	*Phellodendron amurense* *Hydrangea paniculata*	2003 clear-cutting	10

Table S2. Aboveground stand characteristics and soil environmental factors in each stand.

Stand	CP	PF	SF	SA
Aboveground stand characteristics				
BA (m^2 ha^{-1})	35.2 ± 5.2 [a]	20.2 ± 5.3 [b]	28.5 ± 4.2 [ab]	0.39 ± 0.54 [c]
Tree density (trees ha^{-1})	847 ± 62 [a]	497 ± 58 [b]	745 ± 116 [a]	45 ± 66 [c]
Tree aboveground biomass (g m^{-2})	18549 ± 3584 [a]	12141 ± 3086 [b]	14551 ± 2224 [ab]	144 ± 199 [c]
Culm density of Sasa (culms m^{-2})	12 ± 11 [b]	48 ± 23 [ab]	58.4 ± 13 [a]	85.6 ± 41 [a]
Sasa aboveground biomass(g m^{-2})	440 ± 688 [b]	2410 ± 1218 [a]	1274 ± 435 [ab]	2344 ± 752 [a]
Canopy openness (%)	13.9 ± 1.0 [c]	26.6 ± 3.7 [b]	26.6 ± 1.2 [b]	100 ± 0 [a]
Soil environmental factors				
Oe/Oa layer thickness (cm)	2.5 ± 0.7 [b]	4.6 ± 1.2 [a]	4.9 ± 0.6 [a]	4.0 ± 0.2 [a]
Mean annual soil temperature (^oC)	6.7	7.5	7.6	7.2
Soil water content (volume) (%)	35.8 ± 1.3 [a]	35.0 ± 3.0 [a]	23.6 ± 3.8 [b]	37.6 ± 1.4 [a]
Soil water content (weight) (%)	33.6 ± 1.6 [a]	38.4 ± 7.0 [a]	49.0 ± 10.8 [a]	38.4 ± 4.1 [a]
Soil total C content (%)	5.8 ± 0.7 [b]	6.8 ± 1.2 [b]	19.1 ± 6.3 [a]	7.6 ± 1.2 [b]
Soil total N content (%)	0.47 ± 0.06 [a]	0.48 ± 0.06 [a]	0.78 ± 0.29 [a]	0.55 ± 0.08 [a]
Soil C/N	12.4 ± 0.4 [c]	14.2 ± 1.1 [bc]	24.8 ± 2.7 [a]	13.9 ± 0.6 [b]
NO_3^- (mgN kg dry $soil^{-1}$)	4.9 ± 0.5 [ab]	4.8 ± 0.29 [b]	7.5 ± 2.3 [a]	6.2 ± 0.6 [a]
NH_4^+ (mgN kg dry $soil^{-1}$)	15.9 ± 2.4 [c]	22.6 ± 2.4 [ab]	21.4 ± 2.8 [bc]	27.8 ± 4.8 [a]
Inorg-N (mgN kg dry $soil^{-1}$)	20.8 ± 2.7 [b]	27.4 ± 2.5 [ab]	28.9 ± 4.9 [a]	34.0 ± 4.9 [a]
Soil pH (H_2O)	4.7 ± 0.2 [bc]	5.1 ± 0.2 [ab]	4.5 ± 0.3 [c]	5.4 ± 0.2 [a]

Mean ± SD (n = 5). Different lowercase letters denote significant difference among stands (P < 0.05).

CP, conifer plantation; PF, primary conifer-broadleaf mixed forest; SF, secondary forest; SA, Sasa area.

BA, sum of basal tree area at breast height; NO_3^-, soil NO_3^- content; NH_4^+, soil NH_4^+ content; Inorg-N, soil inorganic N content.

Table S3. Two-way ANOVA of the effects of stand type (stand), season, and their interaction on (a) fine root biomass (FRB), (b) fine root length (FRL), (c) weight-based fine root production (FRP) and (d) length-based FRP.

Factor	*df*	*F-value*	*P-value*
(a) FRB			
stand	3	17.4	***
season	3	1.96	
stand×season	9	1.94	
(b) FRL			
stand	3	56.2	***
season	3	5.49	**
stand×season	9	1.08	
(c) Weight-based FRP			
stand	3	5.47	**
season	3	35.9	***
stand×season	9	7.23	***
(d) Length-based FRP			
stand	3	15.4	***
season	3	37.6	***
stand×season	9	12.8	***

***$P < 0.001$; **$P < 0.01$.

Table S4. Fine root turnover rate (yr^{-1}) of trees and Sasa at 0–10 cm soil depth in each stand with the results of two-way ANOVA for the effects of stand type (stand), plant form (plant), and their interaction on fine root turnover.

Stand	Trees	Sasa
CP	0.45 (0.08)	0.56 (0.51)
SF	0.62 (0.30)	0.42 (0.12)
PF	0.32 (0.08)	0.57 (0.15)
SA	0.28 (0.27)	0.35 (0.04)

Factor	*df*	*F-value*	*P-value*
stand	3	1.45	ns
plant	1	0.60	ns
stand×plant	3	1.45	ns

Mean with SD (n = 5) in parentheses. CP, conifer plantation; PF, primary forest stand; SF, secondary forest stand; SA, Sasa area. ns, not significant ($P \geq 0.05$).

Table S5. Results of three-way ANOVA for the effects of plant form (plant), soil layer (layer), stand type (stand), and their interaction on specific root length (SRL) and root tissue density (RTD).

Factor	*df*	*F-value*	*P-value*
(a) SRL			
plant	1	44.9	***
layer	1	53.3	***
stand	3	4.21	**
plant×layer	1	5.40	*
plant×stand	3	11.9	***
layer×stand	3	4.54	**
plant×layer×stand	3	8.41	***
(b) RTD			
plant	1	73.8	***
layer	1	39.0	***
stand	3	12.8	***
plant×layer	1	6.54	*
plant×stand	3	8.03	***
layer×stand	3	2.12	
plant×layer×stand	3	2.12	

***$P < 0.001$; **$P < 0.01$; *$P < 0.05$.

Table S6. Analysis of deviance for soil properties after GLMM for total, Sasa, and tree fine root biomass (FRB) and fine root production (FRP).

Factor	FRB_{total}	FRB_{Sasa}	FRB_{trees}		FRP_{total}		FRP_{Sasa}		FRP_{trees}	
Inorg N content	ns	ns	ns		ns		ns		ns	
NH_4^+ content	ns	ns	*	+	ns		ns		***	+
NO_3^- content	ns	ns	ns		ns		ns		ns	
Soil pH	ns	ns	ns		*	–	**	–	ns	
Oe/Oa layer thickness	ns	ns	***	+	ns		ns		ns	
Soil water content	ns	ns	ns		ns		ns		ns	
Soil C content	ns	ns	ns		**	+	ns		*	+
Soil N content	ns	ns	ns		**	+	ns		**	+
Soil C/N	ns	ns	ns		ns		ns		ns	

***$P < 0.001$; **$P < 0.01$; *$P < 0.05$; ns, not significant

GLMM, Generalized linear mixed model.

Estimated direction in GLMM: + positive; – negative.