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1 **Roles of dominant understory *Sasa* bamboo in carbon and nitrogen**  
2 **dynamics following canopy tree removal in a cool-temperate forest in**  
3 **northern Japan**

4

5 **Running title:** Role of understory *Sasa* in forest

6

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15

16 **Abstract**

17 To clarify the role of dense understory vegetation in the stand structure, and in carbon (C)  
18 and nitrogen (N) dynamics at forest ecosystems with various conditions of overstory trees,  
19 we 1) quantified the above- and below-ground biomasses of understory dwarf bamboo  
20 (*Sasa senanensis*) at the old canopy-gap area and the closed-canopy area and compared the  
21 stand-level biomasses of *S. senanensis* with that of overstory trees; 2) determined the N  
22 leaching, soil respiration rates, fine-root dynamics, plant area index (PAI) of *S. senanensis*,  
23 and soil temperature and moisture at the tree-cut patches (cut) and the intact closed-canopy  
24 patches (control). The biomass of *S. senanensis* in the canopy-gap area was twice that at the  
25 closed-canopy area. It equated to 12% of total biomass above ground but 41% below  
26 ground in the stand. The concentrations of  $\text{NO}_3^-$  and  $\text{NH}_4^+$  in the soil solution and soil  
27 respiration rates did not significantly changed between cut and control plots, indicating that  
28 gap creation did not affect the C or N dynamics in the soil. Root length density and PAI of *S.*  
29 *senanensis* were significantly greater at the cut plots, suggesting that promotion of *S.*  
30 *senanensis* growth following tree-cutting. The levels of soil temperature and soil moisture  
31 were not changed following tree-cutting. These results show that *S. senanensis* is a key  
32 component species in this cool-temperate forest ecosystem and plays significant roles in  
33 mitigating the loss of N and C from the soil following tree-cutting by increasing its leaf and  
34 root biomass and stabilizing the soil environment.

35 **Keywords:** biomass, nitrogen leaching, soil solution, soil respiration, fine roots

36

## 37 **Introduction**

38 In the cool-temperate forests of Japan, the dense thickets of dwarf bamboo species (*Sasa*  
39 spp., an evergreen clonal rhizomatous species) are the dominant understory vegetation. In  
40 the semi-natural forests in northern Hokkaido, where the selective cuttings of canopy trees  
41 has been conducted for forest management for the past century, developed *Sasa* spp.  
42 understory inhibits the recruitment of tree seedlings in the gaps created by artificial felling  
43 (e.g. Nakashizuka 1988, Noguchi and Yoshida 2004), as with giant (Moso) bamboo  
44 (*Phyllostachys pubescens*) forests which replaced natural forests by invasion in central and  
45 western Japan (Kobayashi et al. 2015). The evaluations on ecosystem functions of such  
46 forests which have been subjected to human interferences (managements) with respect to  
47 the community structure and the life-history characteristics of composing species should  
48 also benefit from a better understanding of its role in C and nutrient cycling in the natural  
49 forests after disturbances (e.g. natural felling).

50 Although the vigor of *Sasa* thickets has been quantified along the overstory openness (e.g.  
51 Kobayashi et al. 2004), the responses of understory *Sasa* vegetation to overstory  
52 disturbances and the role of *Sasa* spp. in carbon (C) and nutrient cycling in the forest  
53 ecosystems are not well understood. The biomass production in *Sasa* thickets has been well

54 quantified in semi-natural grasslands (see Stuefer et al. 2002) and forest understory (e.g.  
55 Nishimura et al. 2004, Sakai et al. 2006), and the behaviors of overstory trees and the  
56 changes in microenvironments in response to the removal of *Sasa* understory have been  
57 well studied in the Japanese northern forests (e.g. Takahashi *et al.* 2003, Tripathi *et al.* 2005,  
58 2006a, 2006b), while the effects of canopy openings on C and nutrient cycling in the forest  
59 ecosystems with the understory *Sasa* behaviours are not well understood. In addition, both  
60 above-ground and below-ground biomass should be investigated, although a few studies  
61 have linked below-ground biomass to the carbon budgets in the forests with *Sasa* understory  
62 (e.g. Ohtsuka *et al.* 2007, Takagi et al. 2009).

63 The forest structure influences its ecosystem functions and C, water, and nutrient cycling  
64 (Shugart et al. 2010). The ecosystems of two layered forests are multiplied by a plant  
65 species assemble, consisting of both overstory trees and understory shrubs, but in often  
66 cases forest ecologists have ignored the roles of understory species, because dominance of  
67 these species are thought to be far less than that of overstory species. Some studies have  
68 focused on understory vegetation as a component of the forest ecosystems in temperate and  
69 boreal forests (Yarie 1980; Moore et al. 2007; Nilsson and Wardle 2005) and these studies  
70 reported that understory vegetation accounted for only a tiny fraction (few %) of total  
71 above-ground biomass in these forests. On the other hand, Sakai and Akiyama (2005) and  
72 Sakai et al. (2006) pointed out that understory *Sasa senanensis* community in a cool-  
73 temperate birch (*Betula ermanii*) forest of central Japan occupied a large fraction of

74 biomass and primary production in the forest ecosystem. In addition, Satomura et al. (2006)  
75 and Fukuzawa et al (2007) reported that the cases that fine roots dynamics of *S. senanensis*  
76 could be the main fraction of belowground plant behaviors in the cool-temperate forests in  
77 Japan. Therefore, *Sasa* spp. understory vegetation should play an important role in the  
78 ecosystem functions, such as C and nutrient dynamics in the forests of northern Japan.

79 In the natural forests, nitrogen (N), which is an essential nutrient in the biological  
80 productions, cycles internally within the plant–microbe–soil system, and N leaching from  
81 the forest ecosystem is generally small. However, artificial loggings and clear-cuttings or  
82 typhoon disturbances allow N to leach into stream waters by breaking the balance between  
83 N sources and N sinks, potentially leading to the eutrophications and the degradations of  
84 water quality in the downstream ecosystems (Likens et al. 1970, Fukuzawa et al. 2006). On  
85 the other hand, rapid recovery of vegetation after the disturbances minimizes the loss of N  
86 from the forest ecosystems, owing to N uptake by plant roots (Marks and Bormann 1972).  
87 Soil respiration is a major source of C loss to the atmosphere and is a significant component  
88 of the C balance in the forest ecosystems. However, the effects of forest cutting on the soil  
89 respiration vary among studies, from small decreases (Mattson and Swank 1989) to large  
90 increases (Ewel et al. 1987) following the clear-cutting. Therefore, identifying not only the  
91 forest structure, including below-ground roots, but also the responses of soil N and soil  
92 respiration following the management practices are necessary to evaluate N and C dynamics  
93 in the forests with bamboo understory.

94 The objectives of this study were (1) to quantify the biomass of *S. senanensis* understory  
95 in a cool-temperate forest in northern Japan, and (2) to reveal the effects of canopy openings  
96 (natural gaps and gaps created by selective cutting of canopy trees) on N and C dynamics in  
97 the soil, with a focus on the role of *S. senanensis* community. Firstly, we determined the  
98 above- and below-ground biomass of *S. senanensis* understory beneath the closed canopy  
99 and in the old canopy-gaps in order to evaluate the stand level *S. senanensis* biomass  
100 precisely, because many natural gaps have been created in the cool-temperate forests in  
101 northern Japan. Secondary, we measured N loss (leaching) from the soil, soil respiration  
102 rate at the soil surface, the leaf and root dynamics with respect to the remaining *S.*  
103 *senanensis* vegetation, and the soil environments in artificial gaps following the selective  
104 cutting of overstory trees and at the undisturbed (intact) patches of a deciduous *Quercus*  
105 *crispula* stand. We hypothesized that the biomass of *S. senanensis* is greater in the gap  
106 patches than closed canopy patches and *S. senanensis* is a significant component in this  
107 cool-temperate forest ecosystem that can buffer the effects of overstory heterogeneity and  
108 mitigate the effects of artificial disturbance (management) on N leaching and C loss from  
109 the forest soil owing to its substantial biomass.

110

## 111 **Materials and Methods**

112 Study site

113 We conducted our study in the natural, cool-temperate Teshio Experimental Forest of  
114 Hokkaido University, northern Japan (45°03'N, 142°06'E). The dominant tree species were  
115 mizunara oak (*Quercus crispula*), birch (*Betula ermanii* and *Betula platyphylla* var.  
116 *japonica*), and Sakhalin fir (*Abies sachalinensis*). The forest floor was covered with a dense  
117 understory of *Sasa senanensis*, an evergreen perennial rhizomatous dwarf-bamboo. The  
118 maximum height of the *S. senanensis* thicket was ca. 1.6 m. The annual mean air  
119 temperature ranged from 5.6 to 6.3 °C, and the maximum and minimum monthly mean  
120 temperatures were 16.1 to 18.3 °C and –8.4 to –6.4 °C, respectively in 2002 to 2004 (Takagi  
121 et al. 2009). The total annual precipitation ranged from 1135 to 1212 mm, of which 30%  
122 fell as snow during November to April (Takagi et al. 2009). Inorganic N deposition from  
123 the atmosphere was ca. 5 kg N/ha/year (Fukuzawa et al., unpublished data). The type of  
124 bedrock is Cretaceous sedimentary rock. The dominant soil is a gleyic Cambisol (FAO  
125 1988) with an O horizon of ca. 10 cm, an A horizon of ca. 20 cm, and a B horizon of ca. 30  
126 cm.

127 We established a 0.25-ha plot for tree census (quadrat of 50m × 50m) in June 2001 prior  
128 to any measurements in a stand of our study forest, and numbered to the all trees with >  
129 5cm diameter in this plot. In this plot, we measured the diameter at breast height (DBH) of  
130 the numbered trees. We also selected six trees of *Q. crispula* (the most dominant species)  
131 aged about 160 years whose DBH were ranged in 51–55 cm in order to establish the plots  
132 (ca. 5m × 5m, ~25 m<sup>2</sup>) to observe soil N and C dynamics and environment beneath the

133 canopy of these trees before creating canopy gaps by cutting. Three of these trees were cut  
134 down in March 2002 , when the foliage of these deciduous trees were shedding and the  
135 understory was packed by snow, without disturbing the understory vegetation or ground  
136 surface on account of the 1.5-m-deep snowpack. The logs and branches of the cut trees were  
137 removed from the studied stand (the trunk base and root systems of the cut trees were  
138 remained at the original point). This gave us three cut plots as the canopy-gap patches and  
139 three control plots as intact closed-canopy patches. Before the cutting, we determined the  
140 biomass of *S. senanensis* thickets beneath the canopy at the planned cut area and in an old  
141 gap area (see next section: survey1). Before and after the cutting, we investigated inorganic  
142 N concentration in the soil solution, soil respiration, soil temperature, and soil moisture, and  
143 after the cutting, fine-root dynamics and plant area index of *S. senanensis* (PAI) in the cut  
144 and control plots (survey2).

145

#### 146 Biomass of *S. senanensis* and trees

147 In October 2001, before the cutting of the targeted oak trees, we set a 2-m × 1-m strip in  
148 each plot beneath the canopy about 2 m apart from the trunk of the oak trees and in each  
149 plot in an old gap patch (ca. 25 m × 25 m) in the studied forest outside the plot for tree  
150 census. We set the strips in the old gap patch arbitrarily at the points over 5m away from  
151 any canopy trees. Although the time of the old gap creation was unclear, the old gap would

152 have created by past artificial felling or natural disturbance several decades ago (ca. 1940's).  
153 We counted the living *S. senanensis* culms within each strip, and then cut the culms at  
154 ground level and collected the culms. We separated the leaves from the culms and counted  
155 them. In a 0.5-m × 0.5-m area within each split, we dug out the soil to 40 cm depth,  
156 collected the living rhizomes and fine roots of *S. senanensis*, washed them with tap water,  
157 and oven-dried them at 80 °C for 48 h. We then weighed each part separately.

158 We measured the DBH and canopy width in the north–south and east–west directions of  
159 all trees (>5 cm DBH) in the 0.25-ha plot for tree census and calculated the total above- and  
160 below-ground woody biomass ( $Y$ , kg) as:

$$161 \qquad \qquad \qquad \ln Y = a \ln X + b \qquad \qquad \qquad (\text{Eq. 1})$$

162 where  $X$  is DBH (in cm). We calculated trunk, branch, and coarse root biomasses separately  
163 and summed the trunk and branch biomasses to give the above-ground biomass. The values  
164 of  $a$  and  $b$  were determined from dry-mass data of 22 broadleaved and coniferous trees  
165 within the Teshio Experimental Forest that ranged in DBH from 3.8 to 55 cm (Takagi et al.  
166 2010);  $a$  took the values 2.365 for trunks, 2.713 for branches, 2.224 for coarse roots, 1.974  
167 for broadleaves, and 2.192 for conifer leaves. The corresponding values of  $b$  were –2.596, –  
168 4.456, –2.918, –4.347, and –3.579, respectively. We calculated the canopy projected area  
169 within the 0.25-ha plot from the position of individual trees and the averaged canopy widths.  
170 Then we calculated the area ratios of closed canopy and the opened canopy (gap).

171

172 Fine root dynamics

173 We measured root-length density (RLD) and root production and mortality rate by using a  
174 minirhizotron (BTC-100X camera system and BTC I-CAP software, Bartz Technology Inc.,  
175 Santa Barbara, CA, USA). This semi non-destructive method allows individual roots to be  
176 followed from birth to death (e.g. Satomura et al. 2007). In June 2001, we installed  
177 transparent acrylic tubes (2 m long, 5.08 cm i.d.) in the ground 2 m from each tree trunk of  
178 the oaks in each plot at an angle of 45° to the ground surface to a depth of 50 cm. Three  
179 times a year (late April to early May, mid-August to early September, and mid-November to  
180 mid-December) from April 2002 to November 2004 (but only in May and August 2002), we  
181 inserted the minirhizotron camera into each tube and took color digital images (18 mm ×  
182 13.5 mm) of the soil and roots against the tube surface at 3-cm depth intervals within each  
183 tube to 45 cm depth.

184 We used the MSU ROOTs Tracer image analysis software (Michigan State University,  
185 East Lansing, MI, USA) to trace the length and diameter of individual roots in each image.  
186 All measurements were converted to root length density per unit image area (RLD, in mm  
187 /cm). We categorized each root into one of four types by color based on the visible color of  
188 individual roots in the images: “white” (white or cream), “woody” (dark brown), “brown”  
189 (between “white” and “woody”), and “black” (almost dead). We calculated the ratio of  
190 “white” roots length to the whole roots length in each tube at the end of observation. We  
191 calculated the rate of fine root production in each tube as the sum of the length of new roots

192 and the length growth of existing roots during each observation. Similarly, we calculated  
193 mortality as the sum of the length of roots that disappeared or shrank. Results are presented  
194 as averages for 0–15, 15–30, and 30–45 cm depths.

195

#### 196 Plant area index

197 We measured the PAI of *S. senanensis* once a month during the growing seasons of 2003  
198 and 2004 in each plot, using an LAI-2000 Plant Canopy Analyzer (Li-Cor, Lincoln, NE,  
199 USA). PAI is similar to leaf area index but includes light interception by all canopy  
200 elements, not only leaves but also trunks and branches (Bréda 2003; Takagi et al. 2009).  
201 Using the light value above the *S. senanensis* canopy as the reference, we measured light  
202 values near the soil surface beneath the *S. senanensis* canopy. For each subplot, we  
203 measured ten times in different positions and horizontal directions and averaged the  
204 readings.

205

#### 206 Soil temperature and soil moisture

207 We measured the soil temperature at 5 cm depth in each plot at 2 m from the trunk with a  
208 TR-71S thermo recorder (T&D Corp., Matsumoto, Japan) every 1 h from May 2001 to May  
209 2005. We measured the soil volumetric water content in the top 15 cm in each plot with  
210 three repetitions with a TRIME-FM time-domain reflectometer (IMKO GmbH, Ettlingen,

211 Germany) in August and September 2001 and once a month during the growing season in  
212 2002 and 2004.

213

214 Soil solution and chemical analysis

215 We established tension lysimeters with ceramic porous cups at 10, 20, 40, and 80 cm depths  
216 (DIK-8392, Daiki Rika Kogyo Co., Ltd., Konosu, Japan) in each plot. We collected the soil  
217 solutions by syringes from the tension lysimeters, by reducing the pressure (to -40 to -53  
218 kPa) for 24 h. The solution was sampled once a month from July 2001 to October 2004 (but  
219 only in June, August, and October 2003), except during snow periods. The solutions were  
220 filtered through a 0.7- $\mu\text{m}$  GF/F filter (Whatman Inc., Kent, UK) immediately after  
221 collection and kept below 4 °C before chemical analysis. After further filtering solutions  
222 through a 0.2- $\mu\text{m}$ -membrane filter (DISMIC-25; Advantec Inc., Tokyo, Japan), the  
223 concentrations of nitrate ( $\text{NO}_3^-$ ) and ammonium ( $\text{NH}_4^+$ ) were analyzed by ion  
224 chromatography (DX-500; Dionex Inc., Sunnyvale, CA, USA).

225

226 Soil respiration

227 Soil respiration was measured in closed chambers. Three stainless steel chambers (16 cm  
228 across, 18 cm high) were installed in the soil in each plot at 2, 3, and 4 m from the target  
229 tree at the timing of 1 month before the beginning of the measurements. When we measured

230 CO<sub>2</sub> emission from the soil, each chamber was covered with a lid fitted with a non-  
 231 dispersive infrared CO<sub>2</sub> analyzer (GMW22, Vaisala Inc., Vantaa, Finland), which took  
 232 readings at 5-s intervals for about 10 min. The soil respiration rate,  $R_s$  ( $\mu\text{mol CO}_2 / \text{m}^2 / \text{s}$ ),  
 233 was calculated as the change of CO<sub>2</sub> concentration inside the chamber divided by the  
 234 duration of measurement (s):

$$235 \quad R_s = \partial C / \partial t \times 10^3 / 22.4 \times 273 / (273 + T_s) \times V/A \quad (\text{Eq. 2})$$

236 where  $C$  is the initial CO<sub>2</sub> concentration ( $\mu\text{mol/mol}$ ),  $\partial C / \partial t$  is the rate of change in CO<sub>2</sub>  
 237 over time (s), 22.4 is the volume (L) of 1 mol of gas,  $T_s$  is the soil temperature measured  
 238 just outside of the chamber at 5 cm ( $^{\circ}\text{C}$ ),  $V$  is the chamber volume ( $\text{m}^3$ ), and  $A$  is the area of  
 239 the chamber ( $\text{m}^2$ ). We measured the respirations in August and September 2001 and 2003  
 240 and once a month during the growing season in 2002 and 2004. There was no significant  
 241 difference among the distances from the oak trees, so we used the average of three  
 242 repetitions in each plot.

243

#### 244 Statistical analysis

245 We used the  $t$ -test to analyze the differences in biomass, number of culms and leaves, dry  
 246 weight of each leaf, and above- to below-ground ratio of *S. senanensis* between the canopy  
 247 and the old gap patches, and in the inorganic N concentrations ( $\text{NO}_3^-$  and  $\text{NH}_4^+$ ) in the soil  
 248 solutions, the soil respiration rates, PAIs of *S. senanensis*, RLDs, soil temperatures, and the

249 soil volumetric water contents between the control plots (canopy patches) and the cut plots  
250 (gap patches) created by the artificial felling. We used two-way ANOVA to analyze the  
251 effects of the cutting treatment (or plots, in case prior to the cutting) and time (the timing of  
252 measure/sampling) on soil respiration rates during the periods before and after the tree-  
253 cutting separately. We also used two-way ANOVA for PAI of *S. senanensis* to analyze the  
254 effects of the cutting treatment and time using the data after the tree-cutting. We used  
255 repeated measures ANOVA to analyze the effects of the treatment and time on the soil  
256 temperature during the growing periods before (2001) and after the tree-cutting (2002,  
257 2003) separately, and the effects of the treatment, time, and soil depth on RLD during the  
258 period after the tree-cutting. We used two-way ANOVA to analyze the effects of treatment  
259 and soil depth on cumulative fine-root production and mortality using the maximum  
260 cumulative fine-root production and mortality (November 2004). In these analyses, the  
261 assumptions of the normality and homogeneity of variance were tested and log-  
262 transformation was conducted if these assumptions were violated. In the analysis of  
263 repeated-measures ANOVA, the sphericity assumption was tested and degrees of freedoms  
264 were Greenhouse–Geisser adjusted if the assumption was violated. We used Wilcoxon Rank  
265 sum test to analyze the difference of inorganic N concentrations in soil solution between the  
266 cut (gap patches) and control (intact canopy patches) plots using the pooled dataset  
267 including every observation time during the periods before and after the tree-cutting  
268 separately. Differences between before and after cutting in each plot (cut or control) were

269 also analyzed. We also used Wilcoxon Rank sum test to analyze the difference of soil water  
270 content between the cut and control plots as with inorganic N concentrations. We used  
271 Kruskal-Wallis Rank Sum test to analyze the difference in inorganic N concentrations  
272 among the soil depths.

## 273 **Results**

### 274 Biomass of overstory trees and understory *Sasa* community

275 The biomasses of the *S. senanensis* leaves and culms and the above-ground total in the old  
276 gap were almost double those beneath the canopy ( $P < 0.05$  except the leaves; Table 1).

277 Both beneath the canopy and in the old gap, the culm biomass was the largest fraction in the  
278 biomass of *S. senanensis*, followed by the rhizomes, the fine roots, and the leaves. The ratio

279 of above-ground biomass to below-ground biomass at both patches was about 1, with no  
280 significant difference ( $P > 0.05$ , *t*-test), indicating that light condition had no effect on the

281 ratio. In addition, the number of culms (per m<sup>2</sup>) and the dry weight of each leaf were  
282 significantly greater ( $P < 0.05$ ) and the number of leaves (per m<sup>2</sup>) was greater (n.s.) in the

283 old gap than beneath the canopy. The canopy projected area in the stand was 59.8%, and the  
284 canopy-gaps accounted for the remaining 40.2% of the 0.25-ha plot for tree census (prior to

285 gap creation by felling in this study). From these ratios, the stand *S. senanensis* biomass  
286 including all patches was calculated as 1682 g/m<sup>2</sup> above-ground, 1798 g/m<sup>2</sup> below-ground,

287 and 3480 g/m<sup>2</sup> in total (Table 1). The trees comprised 8745 g/m<sup>2</sup> of trunk, 3173 g/m<sup>2</sup> of

288 branch, 312 g/m<sup>2</sup> of leaf (12230 g/m<sup>2</sup> of total above-ground), and 2617 g/m<sup>2</sup> of coarse root  
289 biomass in this stand. Therefore, *S. senanensis* equated to 12% and 41% of total (tree and *S.*  
290 *senanensis*) above-ground and below-ground biomass in the stand, respectively.

291

292 Temperature and moisture of soils

293 The soil temperatures were comparable between the cut plots (gap patches) and the control  
294 plots (intact canopy patches), with no significant effect of the cutting treatment ( $P > 0.05$ ;  
295 Fig. 1). They fluctuated between 1 °C (December to March) and 16 °C (August) with a  
296 significant effect of time on soil temperature ( $P < 0.001$ ). The thick snowpack kept the  
297 temperature above 0 °C in winter. There were no significant differences in soil volumetric  
298 water contents between the plots ( $P > 0.05$ ; Fig. 2), although significantly lower value was  
299 observed in the cut than in the control plots in May 2004 ( $P < 0.05$ ). The minimum water  
300 content was 28% in every plots, in June 2004, indicating the absence of severe drought in  
301 the studied stand.

302

303 Fine-root dynamics

304 The RLDs were greater in the cut plots (gap patches) than control plots (intact patches)  
305 (Table 2), indicating that the quantity of fine roots increased after the tree-cutting in the cut  
306 plots. The values of RLD increased from the beginning of observations to the end of

307 observations with a maximum value in 2.5-years later. RLD was much lower at 30–45 cm  
308 depth than at 0–15 and 15–30 cm depth. There were significant effects of treatment, time,  
309 and soil depth on RLD with the interaction effects between treatment and time and between  
310 depth and time ( $P < 0.05$ ,  $P < 0.001$ ,  $P < 0.01$  for treatment, time, and soil depth,  
311 respectively, Table 3). In the cut plots, the white-root length averagely accounted for 67% at  
312 0–15 cm depth, 79% at 15–30 cm depth, and 95% at 30–45 cm depth of total root length at  
313 each depth. On the other hand, the corresponding values in the control plots were 57% at 0–  
314 15 cm depth, 54% at 15–30 cm depth, and 62% at 15–30 cm depth.

315 The cumulative production of fine roots during the 2.5 yr following gap creation was  
316 similar between the cut and the control plots at the depth of 0–15 cm, but that was greater in  
317 the cut plots below 15 cm depth (Fig. 3). The cumulative mortality of fine roots was higher  
318 in the control plots at 0–15 cm, but the value was extremely low ( $< 20 \text{ mm/cm}^2$ ) and similar  
319 in both plots below 15 cm depth. The cumulative production of fine roots 2.5 yr following  
320 gap creation was not affected by the cutting treatment but affected by soil depth ( $P > 0.05$ ,  
321  $P < 0.001$ , respectively; Fig. 3). There was no significant effect of treatment but there was  
322 significant effect of soil depth on the cumulative mortality of fine roots ( $P > 0.05$ ,  $P < 0.001$ ,  
323 respectively; Fig. 3). There were no interaction effects of treatment and soil depth in  
324 cumulative root production or mortality ( $P > 0.05$ ).

325

326 Plant area index

327 The PAI of *S. senanensis* was higher in the cut plots (gap patches) except in June 2004, with  
328 a significant difference in August and September 2003 ( $P < 0.05$ , Fig. 4). In both patches,  
329 PAI increased rapidly during June to August and reached the maximum during autumn. The  
330 cutting treatment, the time of observation and those interactions significantly affected on the  
331 PAIs of *S. senanensis* ( $P < 0.001$ ,  $P < 0.001$ ,  $P < 0.05$ , respectively, two-way ANOVA).

332

333 Inorganic N in soil solution and soil respiration

334  $\text{NO}_3^-$  and  $\text{NH}_4^+$  concentrations in the soil solution did not change significantly before and  
335 after the cutting ( $P > 0.05$ ), except  $\text{NH}_4^+$  concentration was significantly lower after the  
336 cutting than before the cutting ( $P < 0.01$ ). There was no significant difference between the  
337 cut plots (gap patches) and the control plots (intact canopy patches) during the periods both  
338 before and after the cutting ( $P > 0.05$ , Fig. 5).  $\text{NO}_3^-$  concentrations at 10 cm depth were  
339 greater in 2002 (after the cutting) than in 2001, but those trends were similar between the  
340 cut and control plots. These results show that the increases in  $\text{NO}_3^-$  concentrations after the  
341 cutting in the cut plots were not caused by the cutting. The concentrations were very small  
342 in both plots in subsequent years of cutting (2003 and 2004). The values were not  
343 significantly different among the soil depths over the examined years ( $P > 0.05$ ).

344 There were no significant differences in the soil respiration rate between the plots except  
345 in May 2002, just after cutting (Fig. 6). The respiration rates were smallest in May and

346 November and highest in August over the examined years. The cutting treatment did not  
347 affect but the time of observation affected the soil respiration rates during before and after  
348 the tree-cutting ( $P > 0.05$ ,  $P < 0.01$  or  $P < 0.001$ , respectively, two-way ANOVA) with no  
349 interaction effect ( $P > 0.05$ ).

350

## 351 **Discussion**

352 Comparison of *Sasa* biomass with tree biomass

353 Previous studies have been represented a small proportion of understory biomass in the  
354 forest ecosystems. For example, it accounted for <5% of total above-ground biomass in  
355 temperate coniferous forests in the southern USA and in western Canada (Yarie 1980;  
356 Moore et al. 2007). In the present study, however, *S. senanensis* understory equated to 12%  
357 of the total above-ground biomass and 41% of below-ground biomass in a stand. These  
358 stand-level proportions take into account both the gap patch and the closed-canopy patch  
359 (Table 1). In the above-ground parts, the trunks of trees have a huge biomass as reported  
360 that the ratio of the above-ground biomass to the below-ground biomass of some tree  
361 species is 3–4 (Karizumi 1974; Fukushima et al. 2014). In contrast, the above- and below-  
362 ground biomasses of *S. senanensis* were almost equal (Table 1). This should be caused by  
363 well-developed below-ground systems of dwarf-bamboo species, which accumulate a large  
364 fraction of photosynthates and perform active rhizomatous clonal growth (Oshima 1961).

365 Similarly, the ratio of above- to below-ground biomass of *S. senanensis* was reported to  
366 approximate 1 in cool-temperate forest in central Japan (Nishimura et al. 2004) and to be  
367 less than 1.5 in Moso bamboo (*P. pubescens*) invaded into a broad-leaved tree stand in  
368 western Japan (Fukushima et al. 2014). Thus, *S. senanensis* has a very large biomass  
369 relative to that of the overstory, making it a key component in cool-temperate forest,  
370 especially below ground.

371 The high proportion of *S. senanensis* biomass in the present stand should be caused by  
372 the following two reasons. First, *S. senanensis* grows densely, and its coverage can attain to  
373 100% (Noguchi and Yoshida 2004) and its seasonal maximum PAI attain to  $4.6 \text{ m}^2/\text{m}^2$   
374 (Takagi et al. 2009). Such dense and thick thickets of *S. senanensis* should have resulted in  
375 a high biomass per area. In contrast, the density and stand basal area of canopy trees in our  
376 forest were relatively low (470/ha and  $17.5 \text{ m}^2/\text{ha}$ , respectively), perhaps on account of  
377 selective cutting in the past century as well as the most of natural forests in northern  
378 Hokkaido, decreasing a biomass fraction of overstory trees. Nishimura et al. (2004) reported  
379 the smaller above- and below-ground biomasses of *S. senanensis* than the present study  
380 ( $640\text{--}670$  and  $590 \text{ g}/\text{m}^2$ , respectively), in a cool-temperate secondary forest in central Japan.  
381 The above-ground biomass of trees in the stand was comparable but the tree density of their  
382 stand was larger (690/ha) than that of the present study, suggesting that the difference of  
383 overstory canopy structure influences the understory light condition and the biomass of *S.*  
384 *senanensis*. Second, the canopy gaps enhance *S. senanensis* production, as shown by the

385 great difference in *S. senanensis* biomass between the closed-canopy area and the old gap  
386 area in the current study (Table 1). In supporting such view, Toyooka et al. (1985) and  
387 Kobayashi et al. (2004) also reported that overstory gaps made *Sasa* spp. understory denser  
388 and *Sasa* spp shoots greater in cool-temperate forests in Japan. The developed *Sasa* spp.  
389 understory also prevents the establishment and growth of canopy trees (Nakashizuka 1988,  
390 Noguchi and Yoshida 2004, Kobayashi et al. 2004). Based on such reasons, *S. senanensis*  
391 should have high proportion of biomass in the present study.

392

393 Effects of overstory opening on fine root dynamics

394 RLD as an indicator of fine-root density was greater at the gap-created patch by selective  
395 canopy-tree removal throughout the observation period (Table 2), accompanied with  
396 abundant cumulative fine-root production (Fig. 3), indicating that fine roots increased  
397 following the selective cutting. The same tendency was reported in the observations also  
398 made with the minirhizotron in canopy gaps in a slash pine (*Pinus elliottii*) forest in the  
399 southern USA (Schroerer et al. 1999). Such an increase has been attributed to the promotions  
400 of fine-root invasion from remained trees near the point of cut tree or growth of plants  
401 composing understory vegetation (Schroerer et al. 1999; McGuire et al. 2001). The threshold  
402 gap area above which fine-root biomass would decrease after the tree cutting has been  
403 reported to be 2000 m<sup>2</sup> (Jones et al. 2003) or 260 m<sup>2</sup> (Parsons et al. 1994). The canopy area

404 of cut trees in the present study was much smaller (42–89 m<sup>2</sup>). We could therefore expect  
405 that the invasion of roots from trees outside of the gap contributed the greater RLD in the  
406 gap patch. However, this may have been prevented by the high density of *S. senanensis*  
407 roots, as a large biomass of *S. senanensis* occupied the entire understory even before the  
408 selective tree cutting. Subsequently, the gap patch after the cutting should have favored the  
409 production of fine roots of *S. senanensis* rather than the remained and/or invaded trees. The  
410 previous studies conducted in the slash pine forests with woody or C<sub>4</sub> understory plants in  
411 the southern USA showed increases in fine-root biomass and fine-root length at canopy-gap  
412 sites following pine tree cuttings (Schroerer et al. 1999; McGuire et al. 2001; Jones et al.  
413 2003). They have been also emphasized a role of understory vegetation in the maintenance  
414 of fine roots in the overstory gaps of their stands. Water and nutrient competitions between  
415 the overstory and understory plants may be mitigated by the removal of overstory trees,  
416 encouraging fine-root growth of understory plants (McGuire et al. 2001; Jones et al. 2003).  
417 In addition, the increasing RLD during the observation period and the significant interaction  
418 of treatment and time in RLD (Tables 2, 3) indicate that the root biomass increased over  
419 several years after the canopy removal. Roots of *S. senanensis* are major component (71%)  
420 of the fine-root biomass in this forest (Fukuzawa et al. 2007) and white roots accounted for  
421 nearly 70% of total RLD at the end of observations in November 2004. The white roots are  
422 newly recruited roots in general, although those of *S. senanensis* may not turn to be distinct  
423 “woody” or “brown” roots with ageing. These observations support the view that the bulk

424 increase in roots of *S. senanensis* with RLD stimulated following the tree cutting in the gap  
425 patch.

426 The higher PAI (Fig. 4) and biomass (Table 1) of *S. senanensis* in the gap patch than  
427 beneath the canopy indicate the positive effects of increased light on the above-ground  
428 production (growth) of *S. senanensis* thickets. A study in central Hokkaido found a  
429 similar effect on PAI of *Sasa senanensis* over 4 years following the creation of gaps  
430 (Toyooka et al. 1985). McGuire et al. (2001) also found a positive relationship between  
431 light intensity and the above-ground biomass of understory vegetation. In the present study,  
432 because the above- and below-ground biomasses of *S. senanensis* increased simultaneously  
433 (Figs. 3, 5), the improved light regime promoted the leaf production by *S. senanensis*,  
434 supporting increased the fine-root production in the gap patch.

435

436 Relationship among C, N and fine root dynamics in the gap

437 The concentrations of inorganic N in the soil solution did not increase during the 3 years  
438 after the selective tree cutting in the cut plots (gap patches) (Fig. 5). The amount of  
439 inorganic N pool in the soil is thought to be mainly influenced by the balance of production  
440 of inorganic N in the physio-chemical/microbial processes and uptake by plant roots  
441 (Hendricks et al. 1993). Clear-cutting over the stand could induce N leaching from the soil  
442 by promoting N mineralization and decreasing or stopping N uptake by plants (Vitousek  
443 and Melillo 1979). On the other hand, the effects of our selective cutting may have been

444 counteracted by increased uptake by the remaining plants, preventing the detection of a  
445 cutting effect on the concentrations of inorganic N in the soil. Although it will be necessary  
446 to evaluate the root uptake capacity, we suspect that remaining and/or developed fine roots  
447 play a role as the major sink of the inorganic N in the soil of the gap patch (see Fukuzawa et  
448 al. 2006). We could not quantitatively evaluate the N uptake by plants at the present study  
449 site, while Fukuzawa (2007) estimated that N uptake by remaining above-ground *S.*  
450 *senanensis* community at a clear-cut (whole above-grounds of canopy trees were removed)  
451 stand adjacent to the present study site was higher than at the uncut (intact) stand (12.0  
452 versus 7.1 gN/m<sup>2</sup>/yr), owing to the increased NPP of *S. senanensis* in the clear-cut stand,  
453 and the difference in N uptake between two stands nearly corresponded to the N uptake by  
454 canopy trees. Such observations indicated that *S. senanensis* community has a potential to  
455 compensate the decrease in N uptake by trees after the clear-cutting, supporting our views  
456 in the present study. Because the quantity of fine roots increased in the gap patch and so did  
457 PAI, which implied increased above-ground biomass of *S. senanensis* (Figs. 3, 4), any  
458 increased available N might have been taken up by *S. senanensis*, preventing increased N  
459 leaching from the soil even after the tree cutting.

460 The quantity of fine roots increased following cutting owing to the promotion of *S.*  
461 *senanensis* root production, keeping the soil inorganic N pool low as a result of plant N  
462 uptake. This could explain why net N mineralization (ammonification and nitrification) in  
463 the soil did not increase at a clear-cut site where understory *S. senanensis* remained

464 (Fukuzawa et al. 2006). The low pool of inorganic N would imply that accelerated N  
465 mineralization would not occur even after the cutting. In addition, fine-root mortality and a  
466 limited supply of additional organic matter from logging residue, which may be a source of  
467 mineralized N, did not increase in the gap patch (Fig. 3). Such phenomena would result in a  
468 static change of N mineralization in the soil even after the gap creation.

469 *Sasa senanensis* understory kept not only the biological N uptake but also the soil  
470 physical environment stable. After the canopy tree cutting, the developed dense *S.*  
471 *senanensis* understory and the thick litter layer on the ground surface maintained the soil  
472 temperature and moisture content, which are key factors in N mineralization. Therefore, the  
473 stability of the soil environment would have maintained the N mineralization potential and  
474 soil respiration even when the canopy gaps were created.

475 Selective tree cutting did not affect on the rates of soil respiration (Fig. 6). Ewel et al.  
476 (1987) reported that the rate of soil respiration increased after forest cutting (whole  
477 aboveground removal) because of increased soil temperature and increased organic matter  
478 residues. On the other hand, Mattson and Swank (1989) reported that soil respiration  
479 decreased following forest cutting in the Coweeta Experimental Forest in the southern USA  
480 owing to the decrease in root respiration rate. Similarly, girdling treatment on the trunks of  
481 canopy trees, which blocks the current supply of photosynthates to belowground parts,  
482 reduced soil respiration by 54% within 1–2 months in boreal pine forest, owing to the  
483 decrease in root respiration (Högberg et al. 2001). Such conflicting responses may be due to

484 abiotic factors that promote microbial respiration, such as soil temperature and soil moisture,  
485 or to biotic factors that influence root respiration, such as fine-root production, all of which  
486 respond differently to forest cutting according to climate and vegetation. In a forest adjacent  
487 to the present study area, Takagi et al. (2009) attributed increased soil respiration following  
488 clear-cutting of canopy trees to increased root respiration of understory *Sasa senanensis*  
489 because dense *S. senanensis* prevented the change in soil temperature even after clear-  
490 cutting and temperature sensitivity of the soil respiration rate was increased and reached to  
491 the value in overstory gap after canopy-tree removal.

492         Although RLD increased during the 3 years following tree cutting in our study, the rate  
493 of increase in soil respiration rate would not have been as high as in the clear-cut stand of  
494 Takagi et al. (2009), so root respiration might have been relatively stable after the partial  
495 cutting alone. Increased root respiration by *S. senanensis* would have balanced the  
496 decreased root respiration of trees (loss of living root activity of canopy trees), and total root  
497 respiration would not have increased.

498         In addition, the stability of soil temperature, soil moisture, and fine-root mortality  
499 would have meant that microbial respiration, the dominant contributor to soil respiration,  
500 remained stable, although more detailed investigation would be required to clarify the  
501 mechanism of change in root and microbial respirations following the canopy tree removal.

502

## 503 **Conclusion**

504 Understory dwarf bamboo, *Sasa senanensis*, was found to be a key component of forest  
505 biomass, especially below-ground, in a cool-temperate forest. Partial canopy tree removal  
506 representative of selective cutting did not affect N leaching or C loss from the soil in the  
507 canopy gaps, on account of the stability of fine root biomass and soil temperature and  
508 moisture status. *S. senanensis* could play a significant role in the resistance of C and N  
509 dynamics to canopy disturbance by maintaining roots and the soil environment.

510

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518

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645

### 646 **Figure legends**

647 Figure 1 Monthly mean soil temperature (5 cm). Arrow shows period of tree cutting.

648 Figure 2 Soil volumetric water contents during 2001 (before tree cutting) and in 2002 and  
649 2004 (following cutting). Bars represent standard deviation ( $n = 9$ ). \*Significant difference  
650 ( $P < 0.05$ ) between treatments in single date.

651 Figure 3 Cumulative fine root (a–c) production and (d–f) mortality following selective  
652 cutting. Bars represent standard error ( $n = 3$ ).

653 Figure 4 Seasonal variation in *Sasa* plant area index. Bars show range ( $n = 3$ ). \*Significant  
654 difference ( $P < 0.05$ ) between treatments in single date.

655 Figure 5 Concentrations of (a–d)  $\text{NO}_3^-$  and (e–h)  $\text{NH}_4^+$  in soil solution. Arrow indicates  
656 period of cutting. Bars denote standard deviation ( $n = 3$ ).

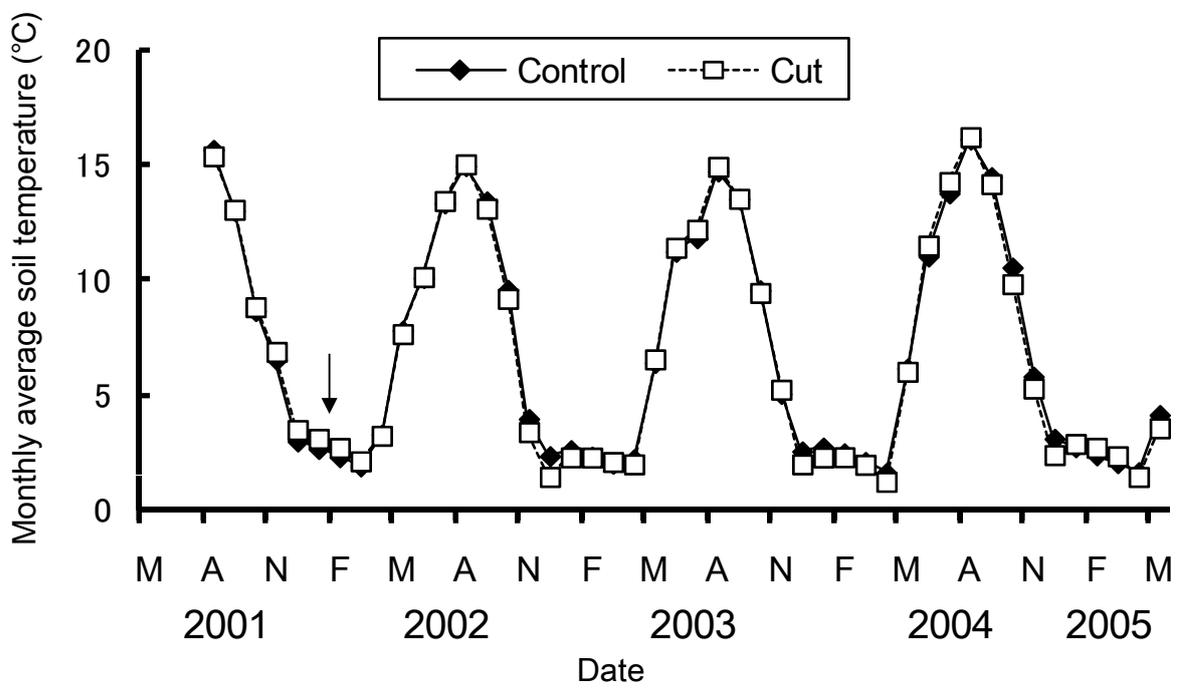
657 Figure 6 Soil respiration before and following selective cutting of trees (arrow). Bars  
658 represent standard deviation ( $n = 9$ ). \*Significant difference ( $P < 0.05$ ) between treatments  
659 in single date.

Table 1 Biomass of each part and number of culms and leaves of *Sasa senanensis* beneath the canopy and in the gap and weighted means. Values in parentheses denote standard deviation ( $n = 3$ ). Weighted means were calculated from area ratios.

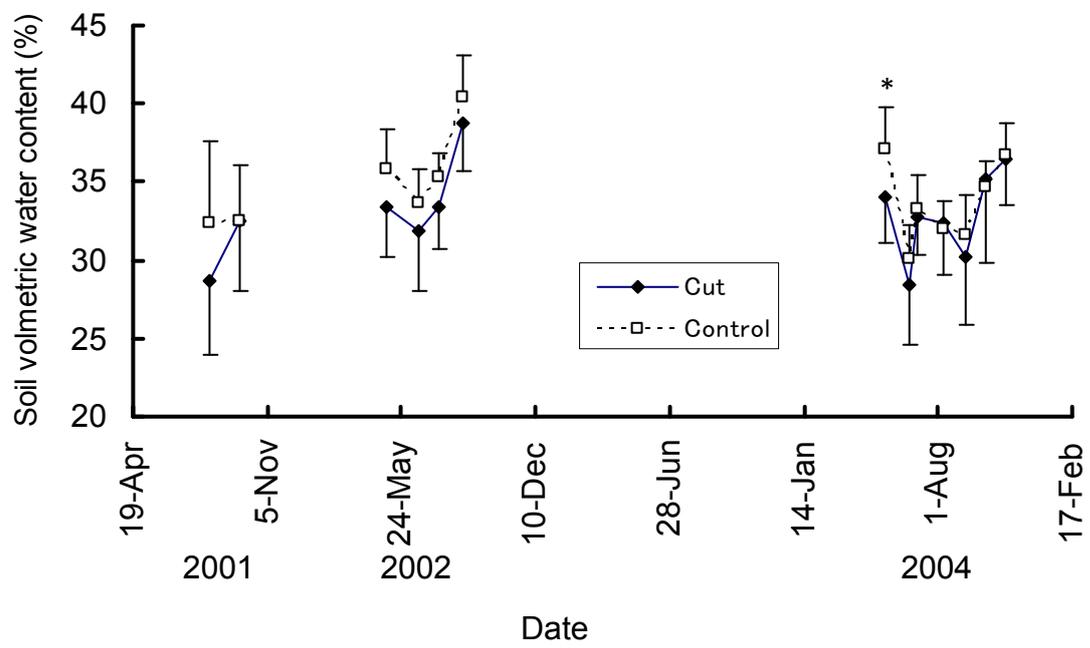
Parts	Beneath the canopy	Gap	Weighted mean
	Biomass (g m <sup>-2</sup> )		
Leaves	214 (8.4)	404 (81)	290
Culms	958 (7.0)	2035 (350) *	1392
Above-ground total (A)	1172 (115)	2439 (421) *	1682
Rhizomes	889 (164)	1912 (669)	1300
Fine roots	304 (142)	785 (271)	497
Below-ground total (B)	1193 (304)	2696 (938)	1798
Total (A + B)	2365 (406)	5135 (1289)	3480
A/B	1.02 (0.21)	0.95 (0.26)	–
Area ratio (%)	59.8	40.2	–
Number of culms (per m <sup>2</sup> )	37.3 (6.3)	56.7 (8.1) *	–
Number of leaves (per m <sup>2</sup> )	351 (16.2)	566 (135)	–
Dry weight of each leaf (g)	0.61 (0.03)	0.72 (0.03) *	–

\*significant difference ( $P < 0.05$ ) between sites.

## Fukuzawa et al. Table1



Fukuzawa et al. Fig. 1



Fukuzawa et al. Fig. 2

Table 2 Root length density at three soil depths over time following selective cutting in March 2002.

Depth (cm)	Treatment		Apr	Aug	May	Aug	Dec	Apr	Sep	Nov
			2002	2002	2003	2003	2003	2004	2004	2004
			Root length density (mm cm <sup>-2</sup> )							
0 - 15	Cut	mean	4.1	10.8	12.8	15.9	21.6	21.4	24.9	22.9
		SE ( <i>n</i> = 3)	1.1	2.1	2.6	5.6	6.6	6.5	7.0	5.4
	Control	mean	2.5	8.8	8.3	10.2	13.5	11.1	14.0	13.8
		SE ( <i>n</i> = 3)	0.9	1.4	1.3	1.7	1.6	2.2	2.9	2.9
15 - 30	Cut	mean	0.8	9.6	12.2	18.1	20.9	20.3	22.1	21.7
		SE ( <i>n</i> = 3)	0.2	1.9	1.5	1.7	4.0	3.7	4.1	3.7
	Control	mean	2.4	5.3	6.1	9.2	10.9	10.2	11.1	11.0
		SE ( <i>n</i> = 3)	1.3	2.4	2.7	2.6	1.9	1.9	1.5	1.8
30 - 45	Cut	mean	0.0	1.2	2.6	4.7	6.0	6.0	6.3	6.3
		SE ( <i>n</i> = 3)	0.0	0.6	1.3	1.9	2.6	2.6	2.7	2.7
	Control	mean	0.3	0.6	1.4	2.3	4.0	3.8	4.0	4.1
		SE ( <i>n</i> = 3)	0.3	0.3	0.8	0.8	1.2	1.2	1.0	0.8

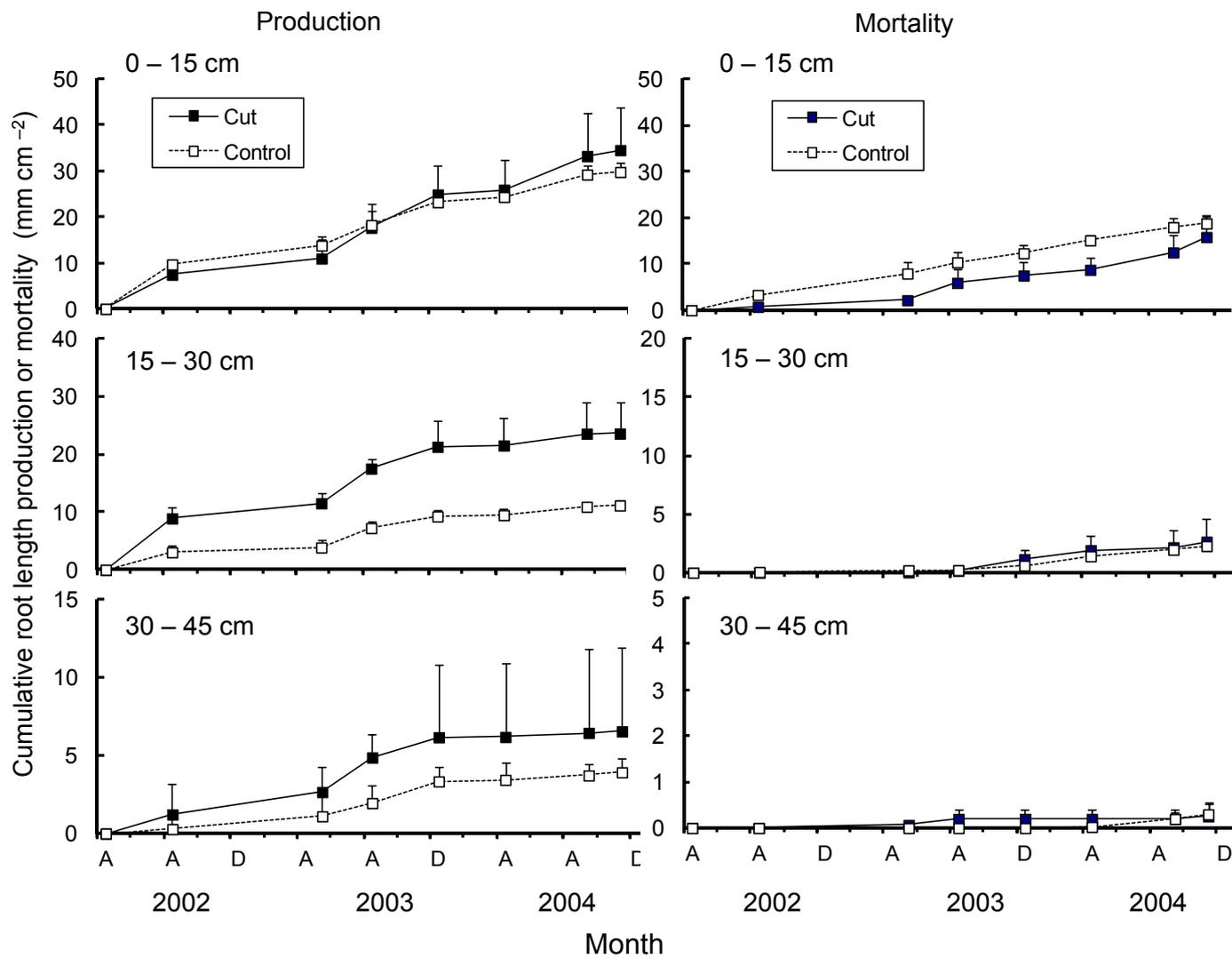
Fukuzawa et al. Table2

Table 3 Result of repeated measures ANOVA for the effects of treatment, time, and soil depth on root length density.

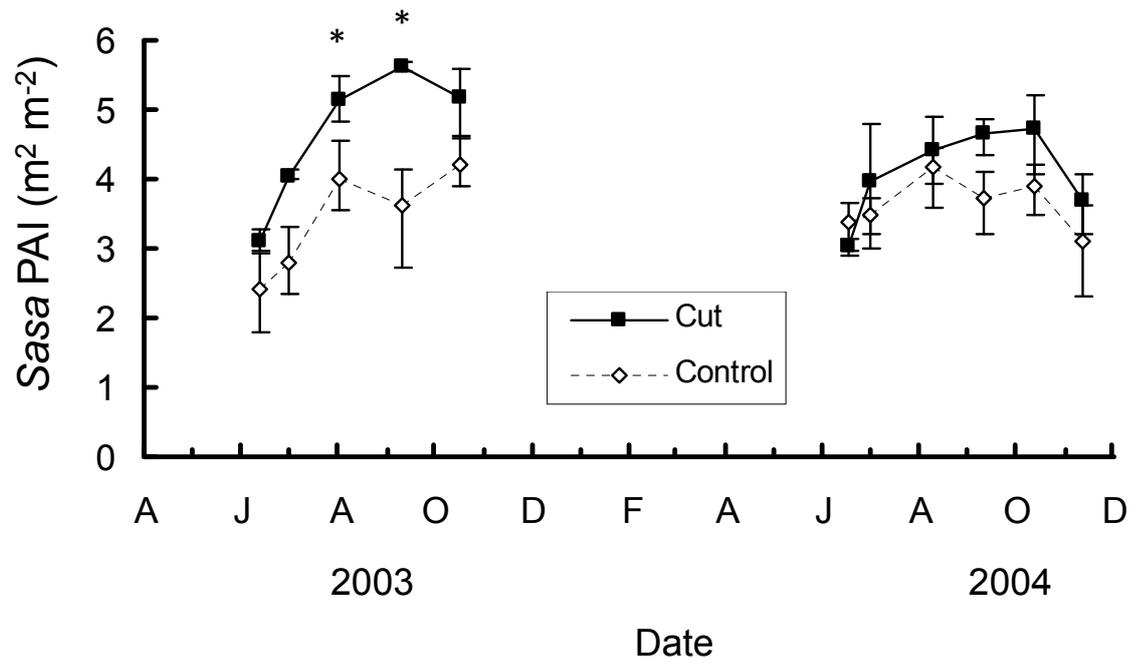
Source	<i>Df</i> †	<i>F</i>	<i>P</i>
Treatment	1	8.44	0.013
Time	7	30.3	< 0.0001
Treatment×Time	7	3.48	0.071
Depth	2	12.69	0.0011
Depth×Treatment	2	1.05	0.38
Depth×Time	14	2.35	0.12
Depth×Treatment×Time	14	0.54	0.64

† *Df*, degree of freedom.

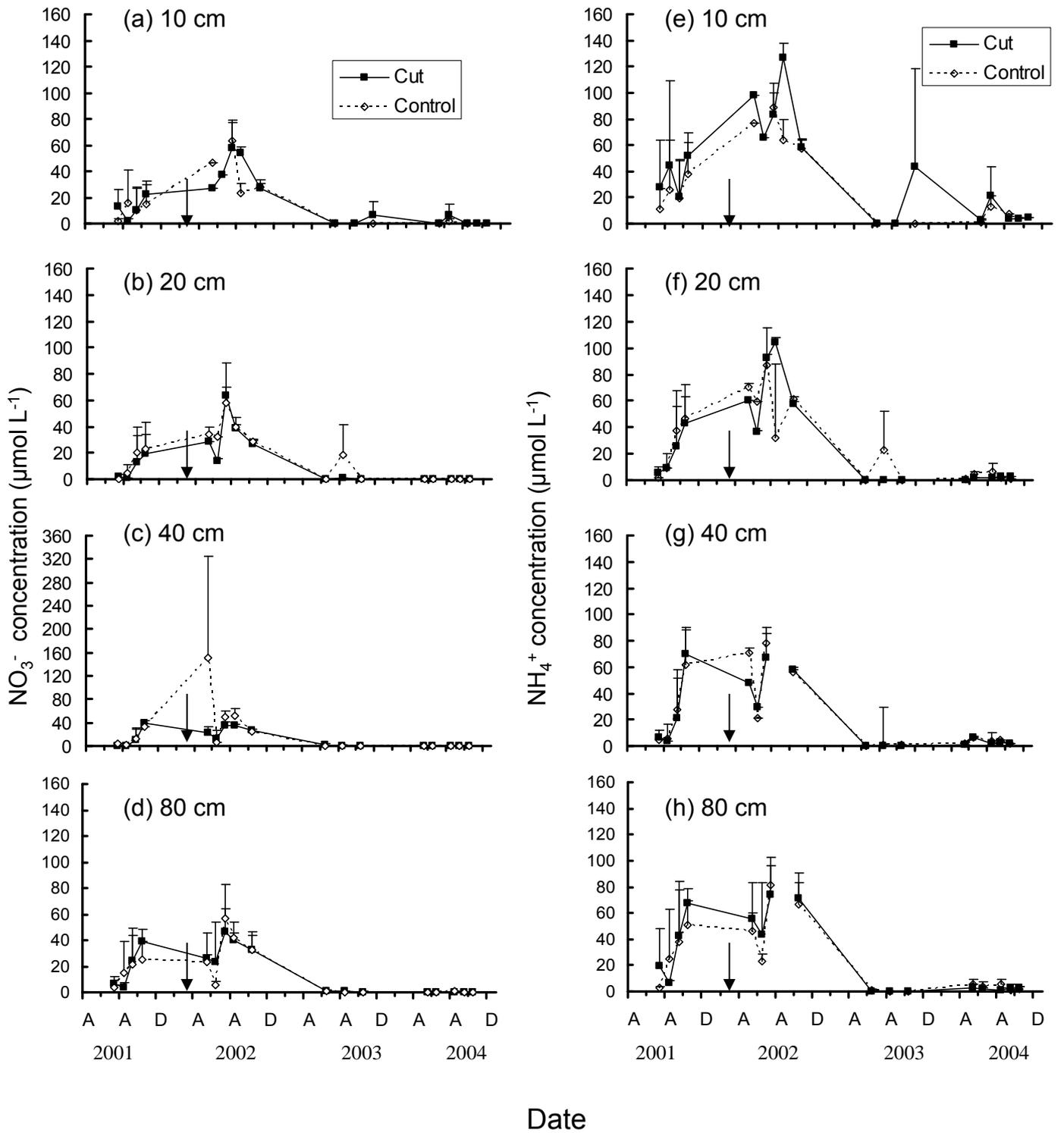
Fukuzawa et al. Table3



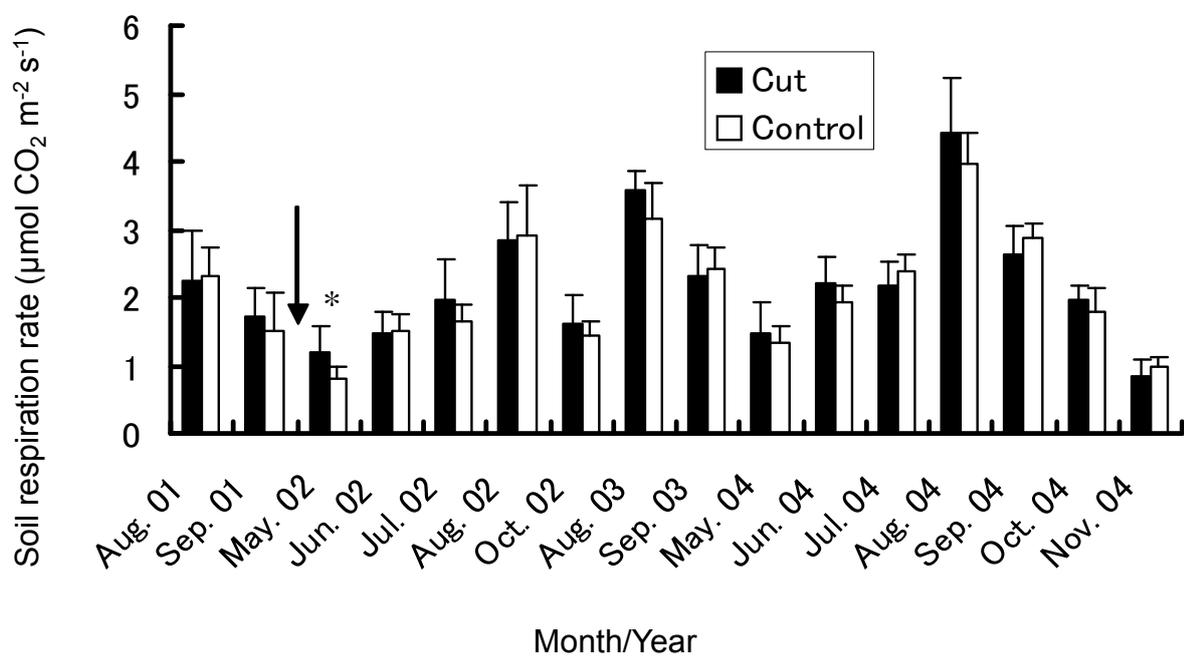
Fukuzawa et al. Fig. 3



Fukuzawa et al. Fig. 4



Fukuzawa et al. Fig. 5



Fukuzawa et al. Fig. 6