Title	Roles of dominant understorySasabamboo in carbon and nitrogen dynamics following canopy tree removal in a cool-temperate forest in northern Japan
Author(s)	Fukuzawa, Karibu; Shibata, Hideaki; Takagi, Kentaro; Satoh, Fuyuki; Koike, Takayoshi; Sasa, Kaichiro
Citation	Plant Species Biology, 30(2), 104-115 https://doi.org/10.1111/1442-1984.12086
Issue Date	2015-04-09
Doc URL	http://hdl.handle.net/2115/61149
Rights	"This is the peer reviewed version of the following article: [Plant Species Biology, Volume 30, Issue 2, pages 104–115, April 2015], which has been published in final form at [doi: 10.1111/1442-1984.12086]. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Self-Archiving.
Type	article (author version)
File Information	Fukuzawa_psb.pdf

[Instructions for use](#)

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

Running title: Role of understory *Sasa* in forest

Authors: Karibu Fukuzawa, Hideaki Shibata, Kentaro Takagi, Fuyuki Satoh, Takayoshi Koike, Kaichiro Sasa

Corresponding author: Karibu Fukuzawa, Northern Forestry and Development Office, Field Science Center for Northern Biosphere, Hokkaido University, Nayoro 096-0071, Japan. E-mail: caribu@fsc.hokudai.ac.jp; Tel: +81-1654-2-4264; Fax: +81-1654-3-7522

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 NO_3^- and 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.

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

Introduction

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

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

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

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

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

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

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

Materials and Methods

Study site

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

We established a 0.25-ha plot for tree census (quadrat of 50m × 50m) in June 2001 prior to any measurements in a stand of our study forest, and numbered to the all trees with > 5cm diameter in this plot. In this plot, we measured the diameter at breast height (DBH) of the numbered trees. We also selected six trees of *Q. crispula* (the most dominant species) aged about 160 years whose DBH were ranged in 51–55 cm in order to establish the plots (ca. 5m × 5m, ~25 m²) to observe soil N and C dynamics and environment beneath the

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

Biomass of *S. senanensis* and trees

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

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

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

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

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

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

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

Plant area index

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

Soil temperature and soil moisture

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

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

Soil solution and chemical analysis

We established tension lysimeters with ceramic porous cups at 10, 20, 40, and 80 cm depths (DIK-8392, Daiki Rika Kogyo Co., Ltd., Konosu, Japan) in each plot. We collected the soil solutions by syringes from the tension lysimeters, by reducing the pressure (to -40 to -53 kPa) for 24 h. The solution was sampled once a month from July 2001 to October 2004 (but only in June, August, and October 2003), except during snow periods. The solutions were filtered through a $0.7\text{-}\mu\text{m}$ GF/F filter (Whatman Inc., Kent, UK) immediately after collection and kept below $4\text{ }^{\circ}\text{C}$ before chemical analysis. After further filtering solutions through a $0.2\text{-}\mu\text{m}$ -membrane filter (DISMIC-25; Advantec Inc., Tokyo, Japan), the concentrations of nitrate (NO_3^-) and ammonium (NH_4^+) were analyzed by ion chromatography (DX-500; Dionex Inc., Sunnyvale, CA, USA).

Soil respiration

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

CO₂ emission from the soil, each chamber was covered with a lid fitted with a non-dispersive infrared CO₂ analyzer (GMW22, Vaisala Inc., Vantaa, Finland), which took readings at 5-s intervals for about 10 min. The soil respiration rate, R_s ($\mu\text{mol CO}_2 / \text{m}^2 / \text{s}$), was calculated as the change of CO₂ concentration inside the chamber divided by the duration of measurement (s):

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

where C is the initial CO₂ concentration ($\mu\text{mol/mol}$), $\partial C / \partial t$ is the rate of change in CO₂ over time (s), 22.4 is the volume (L) of 1 mol of gas, T_s is the soil temperature measured just outside of the chamber at 5 cm ($^{\circ}\text{C}$), V is the chamber volume (m^3), and A is the area of the chamber (m^2). We measured the respirations in August and September 2001 and 2003 and once a month during the growing season in 2002 and 2004. There was no significant difference among the distances from the oak trees, so we used the average of three repetitions in each plot.

Statistical analysis

We used the t -test to analyze the differences in biomass, number of culms and leaves, dry weight of each leaf, and above- to below-ground ratio of *S. senanensis* between the canopy and the old gap patches, and in the inorganic N concentrations (NO_3^- and NH_4^+) in the soil 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

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

Results

Biomass of overstory trees and understory *Sasa* community

The biomasses of the *S. senanensis* leaves and culms and the above-ground total in the old gap were almost double those beneath the canopy ($P < 0.05$ except the leaves; Table 1). Both beneath the canopy and in the old gap, the culm biomass was the largest fraction in the biomass of *S. senanensis*, followed by the rhizomes, the fine roots, and the leaves. The ratio of above-ground biomass to below-ground biomass at both patches was about 1, with no significant difference ($P > 0.05$, t -test), indicating that light condition had no effect on the ratio. In addition, the number of culms (per m^2) and the dry weight of each leaf were significantly greater ($P < 0.05$) and the number of leaves (per m^2) was greater (n.s.) in the old gap than beneath the canopy. The canopy projected area in the stand was 59.8%, and the canopy-gaps accounted for the remaining 40.2% of the 0.25-ha plot for tree census (prior to gap creation by felling in this study). From these ratios, the stand *S. senanensis* biomass including all patches was calculated as 1682 g/m^2 above-ground, 1798 g/m^2 below-ground, and 3480 g/m^2 in total (Table 1). The trees comprised 8745 g/m^2 of trunk, 3173 g/m^2 of

branch, 312 g/m² of leaf (12230 g/m² of total above-ground), and 2617 g/m² of coarse root biomass in this stand. Therefore, *S. senanensis* equated to 12% and 41% of total (tree and *S. senanensis*) above-ground and below-ground biomass in the stand, respectively.

Temperature and moisture of soils

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

Fine-root dynamics

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

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

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

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 NO_3^- and NH_4^+ concentrations in the soil solution did not change significantly before and
 335 after the cutting ($P > 0.05$), except 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). 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 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

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

Discussion

Comparison of *Sasa* biomass with tree biomass

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

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

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

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

Effects of overstory opening on fine root dynamics

RLD as an indicator of fine-root density was greater at the gap-created patch by selective canopy-tree removal throughout the observation period (Table 2), accompanied with abundant cumulative fine-root production (Fig. 3), indicating that fine roots increased following the selective cutting. The same tendency was reported in the observations also made with the minirhizotron in canopy gaps in a slash pine (*Pinus elliottii*) forest in the southern USA (Schroeder et al. 1999). Such an increase has been attributed to the promotions of fine-root invasion from remained trees near the point of cut tree or growth of plants composing understory vegetation (Schroeder et al. 1999; McGuire et al. 2001). The threshold gap area above which fine-root biomass would decrease after the tree cutting has been reported to be 2000 m² (Jones et al. 2003) or 260 m² (Parsons et al. 1994). The canopy area

404 of cut trees in the present study was much smaller (42–89 m²). 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 C₄ 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 (Schroeder 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

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

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

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

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

counteracted by increased uptake by the remaining plants, preventing the detection of a
 cutting effect on the concentrations of inorganic N in the soil. Although it will be necessary
 to evaluate the root uptake capacity, we suspect that remaining and/or developed fine roots
 play a role as the major sink of the inorganic N in the soil of the gap patch (see Fukuzawa et
 al. 2006). We could not quantitatively evaluate the N uptake by plants at the present study
 site, while Fukuzawa (2007) estimated that N uptake by remaining above-ground *S.*
senanensis community at a clear-cut (whole above-grounds of canopy trees were removed)
 stand adjacent to the present study site was higher than at the uncut (intact) stand (12.0
 versus 7.1 gN/m²/yr), owing to the increased NPP of *S. senanensis* in the clear-cut stand,
 and the difference in N uptake between two stands nearly corresponded to the N uptake by
 canopy trees. Such observations indicated that *S. senanensis* community has a potential to
 compensate the decrease in N uptake by trees after the clear-cutting, supporting our views
 in the present study. Because the quantity of fine roots increased in the gap patch and so did
 PAI, which implied increased above-ground biomass of *S. senanensis* (Figs. 3, 4), any
 increased available N might have been taken up by *S. senanensis*, preventing increased N
 leaching from the soil even after the tree cutting.

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

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

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

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

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

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

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

Conclusion

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

Acknowledgements

This study was conducted in the Teshio Experimental Forest of Hokkaido University (Northern Hokkaido Forest), which is a JaLTER core site, as part of the CC-LaG (Carbon Cycle and Larch Growth) collaboration between the National Institute for Environmental Studies, Hokkaido Electric Power Co., Inc., and Hokkaido University. We are grateful to the staff at the forest for supporting our field work. This study was supported in part by JSPS KAKENHI (No. 22248016).

References

Bréda N. J. J. (2003) Ground-based measurements of leaf area index: a review of methods, instruments and current controversies. *Journal of Experimental Botany* **54**: 2403-2417.

- 522 Ewel K. C., Cropper W. P. & Gholz H. L. (1987) Soil CO₂ evolution in Florida slash pine
 523 plantations. I. Changes through time. *Canadian Journal of Forest Research* **17**: 325–
 524 329.
- 525 FAO (1988) Soil Map of the World. Revised Legend. Reprinted with corrections 1990.
 526 World Soil Resources Reports 60. FAO-UNESCO-ISRIC, Rome.
- 527 Fukushima K., Usui N., Ogawa R. & Tokuchi N. (2014) Impacts of moso bamboo
 528 (*Phyllostachys pubescens*) invasion on dry matter and carbon and nitrogen stocks in a
 529 broad-leaved secondary forest located in Kyoto, western Japan. *Plant Species Biology*
 530 (in press)
- 531 Fukuzawa K., Shibata H., Takagi K., Nomura M., Kurima N., Fukazawa T., Satoh F. &
 532 Sasa K. (2006) Effects of clear-cutting on nitrogen leaching and fine root dynamics in a
 533 cool-temperate forested watershed in northern Japan. *Forest Ecology and Management*
 534 **225**: 257–261.
- 535 Fukuzawa K., Shibata H., Takagi K., Satoh F., Koike T. & Sasa K. (2007) Vertical
 536 distribution and seasonal pattern of fine-root dynamics in a cool-temperate forest in
 537 northern Japan: implication of the understory vegetation, *Sasa* dwarf bamboo.
 538 *Ecological Research* **22**: 485–495.
- 539 Fukuzawa K. (2007) Role of fine roots in carbon and nitrogen dynamics in a cool-temperate
 540 forest covered with *Sasa* dwarf bamboo. Doctoral Thesis. Graduate School of
 541 Agriculture, Hokkaido University. (in Japanese)

- 542 Hendricks J. J., Nadelhoffer K. J. & Aber J. D. (1993) Assessing the role of fine roots in
543 carbon and nitrogen cycling. *Tree* **8**: 174–178.
- 544 Högberg P., Nordgren A., Buchmann N., Taylor A. F. S., Ekblad A., Hogberg M. N.,
545 Nyberg G., Ottosson-Lofvenius M. & Read J. D. (2001) Large-scale forest girdling
546 shows that current photosynthesis drives soil respiration. *Nature* 411: 789-792.
- 547 Jones R. H., Mitchell R.J., Stevens G.N. & Pecot S. D. (2003) Controls of fine root
548 dynamics across a gradient of gap sizes in a pine woodland. *Oecologia* **134**: 132–143.
- 549 Karizumi N. (1974) The mechanism and function of tree root in the process of forest
550 production II: Root biomass and distribution in stands. *Bulletin of the Government*
551 *Forest Experiment Station* **267**: 1–88.
- 552 Kobayashi T., Shimano K. & Muraoka H. (2004) Effect of light availability on the carbon
553 gain of beech (*Fagus crenata*) seedlings with reference to the density of dwarf bamboo
554 (*Sasa kurilensis*) in an understory of Japan Sea type beech forest. *Plant Species Biology*
555 **19**: 33-46.
- 556 Kobayashi T., Fukushima K., Hisamoto Y. & Inoue A. (2015) The species biology of
557 bamboos in Japan: from gene to landscape. *Plant Species Biology* **30**: 42-44
- 558 Likens G. E., Bormann F. H., Johnson N. M., Fisher D. W. & Pierce R. S. (1970) Effects of
559 forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook
560 watershed-ecosystem. *Ecological Monographs* **40**: 23–47.

- 561 Marks P. L. & Bormann F. H. (1972) Revegetation following forest cutting: mechanisms
562 for return to steady-state nutrient cycling, *Science* **176**: 914–915.
- 563 Mattson K. G. & Swank W. T. (1989) Soil and detrital carbon dynamics following forest
564 cutting in the southern Appalachians. *Biology and Fertility of Soils* **7**: 247–253.
- 565 McGuire J. P., Mitchell R. J., Moser E. B., Pecot S. D. & Gjerstad D. H. (2001) Gaps in a
566 gappy forest: plant resources, longleaf pine regeneration, and understory response to
567 tree removal in longleaf pine savannas. *Canadian Journal of Forest Research* **31**: 765–
568 778.
- 569 Moore P. T., Van Miegroet H. & Nicholas N. S. (2007) Relative role of understory and
570 overstory in carbon and nitrogen cycling in a southern Appalachian spruce–fir forest.
571 *Canadian Journal of Forest Research* **37**: 2689–2700.
- 572 Nakashizuka T. (1988) Regeneration of beech (*Fagus crenata*) after the simultaneous death
573 of undergrowing dwarf bamboo (*Sasa kurilensis*). *Ecological Research* **3**: 21–35.
- 574 Nishimura N., Matsui Y., Ueyama T., Mo W., Saijo Y., Tsuda S., Yamamoto S., Koizumi H.
575 (2004) Evaluation of carbon budgets of a forest floor *Sasa senanensis* community in a
576 cool–temperate forest ecosystem, central Japan (in Japanese with English summary).
577 *Japanese Journal of Ecology* **54**: 143–158.
- 578 Nilsson M. C. & Wardle D. A. (2005) Understory vegetation as a forest ecosystem driver:
579 evidence from the northern Swedish boreal forest. *Frontiers in Ecology and the*
580 *Environment* **3**: 421–428.

- 581 Noguchi M. & Yoshida T. (2004) Tree regeneration in partially cut conifer–hardwood
582 mixed forests in northern Japan: roles of establishment substrate and dwarf bamboo.
583 *Forest Ecology and Management* **190**: 335–344.
- 584 Ohtsuka T., Mo W. H., Satomura T., Inatomi M. & Koizumi H. (2007) Biometric based
585 carbon flux measurements and net ecosystem production (NEP) in a temperate
586 deciduous broad-leaved forest beneath a flux tower. *Ecosystems* **10**: 324–334.
- 587 Oshima Y. (1961) Ecological studies of *Sasa* communities II. Seasonal variations of
588 productive structure and annual net production in *Sasa* communities. *The Botanical*
589 *Magazine Tokyo* **74**: 280–290.
- 590 Parsons W. F. J., Miller S. L. & Knight D. H. (1994) Root-gap dynamics in lodgepole pine
591 forests: ectomycorrhizal and nonmycorrhizal fine root activity after experimental gap
592 formation. *Canadian Journal of Forest Research* **24**: 1531–1538.
- 593 Sakai T. & Akiyama T. (2005) Quantifying the spatio-temporal variability of net primary
594 production of the understory species, *Sasa senanensis*, using multipoint measuring
595 techniques. *Agricultural and Forest Meteorology* **134**: 60–69.
- 596 Sakai T., Akiyama T., Saigusa N., Yamamoto S. & Yasuoka Y. (2006) The contribution of
597 gross primary production of understory dwarf bamboo, *Sasa senanensis*, in a cool-
598 temperate deciduous broadleaf forest in central Japan. *Forest Ecology and Management*
599 **236**: 259–267.
- 600 Satomura T., Hashimoto Y., Koizumi H., Nakane K. & Horikoshi T. (2006) Seasonal

- 601 patterns of fine root demography in a cool-temperate deciduous forest in central Japan.
 602 *Ecological Research* **21**: 741-753.
- 603 Satomura T., Fukuzawa K. & Horikoshi T. (2007) Considerations in the study of tree fine-
 604 root turnover with minirhizotrons. *Plant Root* **1**: 34–45.
- 605 Schroeer A. E., Hendrick R. L. & Harrington T. B. (1999) Root, ground cover, and litterfall
 606 dynamics within canopy gaps in a slash pine (*Pinus elliottii* Engelm.) dominated forest.
 607 *Ecoscience* **6**: 548–555.
- 608 Shugart H. H., Saatchi S. & Hall F. G. (2010) Importance of structure and its measurement
 609 in quantifying function of forest ecosystems. *Journal of Geophysical Research—*
 610 *Biogeosciences* **115**: G00E13.
- 611 Stuefer J. F., Erschbamer B., Huber H. & Suzuki J.I. (2002) The ecology and evolutionary
 612 biology of clonal plants: an introduction to the proceedings of Clone-2000. In: Stuefer J.
 613 F., Erschbamer B., Huber H. & Suzuki J.I. (eds). *Ecology and Evolutionary Biology of*
 614 *Clonal Plants*. Kluwer Academic Publishers, Netherlands, pp. 223-230.
- 615 Takagi K., Fukuzawa K., Liang N., Kayama M., Nomura M., Hojyo H., Sugata S., Shibata
 616 H., Fukazawa T., Takahashi Y., et al. (2009) Change in CO₂ balance under a series of
 617 forestry activities in a cool-temperate mixed forest with dense undergrowth. *Global*
 618 *Change Biology* **15**: 1275–1288.
- 619 Takagi K., Kotsuka C., Fukuzawa K., Kayama M., Makoto K., Watanabe T., Nomura M.,
 620 Fukazawa T., Takahashi H., Hojyo H., et al. (2010) Allometric relationships and carbon

- 621 and nitrogen contents for three major tree species (*Quercus crispula*, *Betula ermanii*,
 622 and *Abies sachalinensis*) in northern Hokkaido, Japan. *Eurasian Journal of Forest*
 623 *Research* **13**: 1–7.
- 624 Takahashi K., Uemura S., Suzuki J.I. & Hara T. (2003) Effects of understory dwarf bamboo
 625 on soil water and the growth of overstory trees in a dense secondary *Betula ermanii*
 626 forest, northern Japan. *Ecological Research* **18**: 767–774.
- 627 Tripathi S.K., Sumida A., Shibata H., Uemura S., Ono K. & Hara T. (2005) Growth and
 628 substrate quality of fine root and soil nitrogen availability in a young *Betula ermanii*
 629 forest of northern Japan: Effects of the removal of understory dwarf bamboo (*Sasa*
 630 *kurilensis*). *Forest Ecology and Management* **212**: 278–290.
- 631 Tripathi S. K., Sumida A., Ono K., Shibata H., Uemura S., Takahashi K. & Hara T. (2006)
 632 The effects of understorey dwarf bamboo (*Sasa kurilensis*) removal on soil fertility in a
 633 *Betula ermanii* forest of northern Japan. *Ecological Research* **21**: 315–320.
- 634 Tripathi S. K., Sumida A., Shibata H., Ono K., Uemura S., Kodama Y. & Hara T. (2006)
 635 Leaf litterfall and decomposition of different above- and belowground parts of birch
 636 (*Betula ermanii*) trees and dwarf bamboo (*Sasa kurilensis*) shrubs in a young
 637 secondary forest in Northern Japan. *Biology and Fertility of Soils* **43**: 237–246.
- 638 Toyooka H, Ishizuka M, Kanbara S (1985) Dynamics of *Sasa senanensis* population after a
 639 clear cutting of upper trees. *Transactions of the Meeting in Hokkaido Branch of the*
 640 *Japanese Forest Society* **34**: 89–91 (in Japanese).

Vitousek P. M. & Melillo J. M. (1979) Nitrate losses from disturbed forests: patterns and mechanisms. *Forest Science* **25**: 615–619.

Yarie J. (1980) The role of understory vegetation in the nutrient cycle of forested ecosystems in the mountain hemlock biogeoclimatic zone. *Ecology* **61**: 1498–1514.

Figure legends

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

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

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

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

Figure 5 Concentrations of (a–d) NO_3^- and (e–h) NH_4^+ in soil solution. Arrow indicates period of cutting. Bars denote standard deviation ($n = 3$).

Figure 6 Soil respiration before and following selective cutting of trees (arrow). Bars represent standard deviation ($n = 9$). *Significant difference ($P < 0.05$) between treatments 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 ⁻²)		
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 ²)	37.3 (6.3)	56.7 (8.1) *	—
Number of leaves (per m ²)	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 2002	Aug 2002	May 2003	Aug 2003	Dec 2003	Apr 2004	Sep 2004	Nov 2004
			Root length density (mm cm ⁻²)							
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