



Title	Seasonal patterns of root production of Japanese oak seedlings and dwarf bamboo grown in rhizoboxes
Author(s)	Fukuzawa, K.; Dannoura, M.; Kanemitsu, S.; Kosugi, Y.
Citation	Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology, 144(2), 434-439 https://doi.org/10.1080/11263501003725971
Issue Date	2010-08-04
Doc URL	http://hdl.handle.net/2115/54047
Rights	This is an Author's Accepted Manuscript of an article published in Plant Biosystems Aug 2010 copyright Taylor & Francis, available online at: http://www.tandfonline.com/10.1080/11263501003725971
Type	article (author version)
File Information	Fukuzawa_2010_PlantBiosystems_144_434-439.pdf



[Instructions for use](#)

1 Running title: Root production of oak and bamboo

2

3 Corresponding author: Karibu Fukuzawa

4 Northern Forestry and Development Office, Field Science Center for Northern

5 Biosphere, Hokkaido University, 250 Tokuda, Nayoro, 096-0071, Japan, tel:

6 +81-1654-2-4264, fax: +81-1654-3-7522, E-mail: caribu@fsc.hokudai.ac.jp

7

8

9 Title: Seasonal patterns of root production of Japanese oak seedlings and dwarf
10 bamboo grown in the rhizoboxes

11

12 Authors: Karibu Fukuzawa, Masako Dannoura, Shuhei Kanemitsu, Yoshiko Kosugi

13

14 Abstract

15

16 We separately examined the temporal patterns of root production by Japanese oak
17 (*Quercus crispula*), and dwarf bamboo (*Sasa veitchii*) which is a major understory
18 species in cool-temperate forests. We grew Japanese oak seedlings and *Sasa* stocks (i.e.,
19 the rhizome and connected culms) in organic-free sand in rhizoboxes and then scanned
20 roots that were visible through the sides of the rhizoboxes to measure the length of each
21 root in images. Japanese oak root production peaked in July, but *Sasa* root production
22 peaked in both July and October. Soil temperature was highly correlated with root
23 production of Japanese oak, but less so with *Sasa* root. Leaves of *Sasa* expanded in late
24 summer, and the photosynthetic rate of *Sasa* was highest in September, suggesting that
25 aboveground phenology influences the extensive root production of *Sasa* in October due
26 to the supply of carbohydrate. These results demonstrate different temporal patterns of
27 root production by Japanese oak seedlings and understory species (*Sasa*), even under
28 similar environmental conditions.

29 Key words: root production, leaf phenology, Japanese oak, rhizobox, *Sasa*, understory
30 vegetation

31

32 Introduction

33

34 Understanding the seasonal pattern of fine-root dynamics is crucial for estimating
35 fine-root turnover, productivity and carbon cycling in forest ecosystems (Hendrick and
36 Pregitzer 1993; Gill and Jackson 2000). Previous studies, however, have revealed
37 contradictory results regarding these seasonal patterns and controlling factors due to
38 differences in climate and species between sites (Tierney et al. 2003). Root production
39 reached its maximum in mid – late summer in boreal and cool-temperate forests where
40 water did not limit production (Steele et al. 1997; Tierney et al. 2003; Fukuzawa et al.
41 2007), but it reached its maximum in spring or early summer and decreased during the
42 subsequent summer in temperate forests that experience intense drought during late
43 summer (Lyr and Hoffman 1967; Teskey and Hinckley 1981; Hendrick and Pregitzer
44 1997; Joslin et al. 2001). A number of exogenous and endogenous factors control the
45 seasonality of fine-root production. Exogenous factors include soil temperature, as
46 reported from a northern cool-temperate and boreal forest (Steele et al. 1997; Tierney et
47 al. 2003), and endogenous factors relate to carbohydrates from leaves, as reported from
48 a temperate forest (Reich et al. 1980; Joslin et al. 2001). Determining the factor
49 controlling fine-root dynamics (exogenous or endogenous) is difficult because
50 endogenous phenological cues would be expected to maximize root growth when
51 climate is normally favorable (Tierney et al. 2003). However, Kozłowski and Pallardy
52 (1997) reported the different pattern of fine-root production between species under

53 similar conditions, supporting the importance of endogenous factor (species-specific
54 phenology). In mixed forests, it is necessary to evaluate the root growth pattern of each
55 group (or species) for precise evaluation and prediction of fine-root production and
56 turnover.

57 Cool-temperate forests in Japan are characterized by dense understory vegetation,
58 such as dwarf bamboo (*Sasa* spp.) (Oshima, 1961). Fukuzawa et al. (2007) reported that
59 fine-root biomass (< 2mm in diameter) of *Sasa* is greater than that of tree species by
60 71% of the whole fine-roots in a cool-temperate forest in northern Japan. They also
61 reported that fine-root production was concentrated in the growing season, especially in
62 August, as reported in other boreal or cool-temperate forests without severe drought
63 (e.g., Tierney et al. 2003). However, they pointed out that not only soil temperature but
64 also leaf phenology of *Sasa* exerted a strong influence on the increases in fine-roots in
65 late summer because the temporal pattern of root production was synchronized with leaf
66 area index of *Sasa*. Lei and Koike (1998) reported that shade shoots of *Sasa* emerged
67 from August and the photosynthetic rate was high in autumn when tree leaf senescence
68 had occurred. However, the proportional contribution of this understory vegetation to
69 the whole fine-root dynamics according season in forest ecosystems is not well
70 understood. Identifying fine-roots of each species in the field study using minirhizotron
71 image analysis is difficult.

72 The objectives of this study were (1) to clarify whether the patterns of root production
73 of Japanese oak seedlings and *Sasa* differ, by observing roots planted separately in the
74 rhizoboxes under similar environmental conditions; and (2) to identify the relationship
75 of root production, soil temperature and leaf production in each species. Japanese oak
76 (*Quercus crispula*) is one of the major deciduous tree species in cool-temperate forests

77 in Japan. We hypothesized that temporal pattern of root production would be influenced
78 by seasonality of leaf production of each species, in addition to climatic factors such as
79 temperature.

80

81 Methods

82

83 Root dynamics

84 Root dynamics were studied at the Kitashirakawa Experimental Station of Field Science
85 Education and Research Center, Kyoto University, Japan (35°01'N, 135°47'E). Mean
86 annual air temperature and annual precipitation in 2008 were 15.7 C° and 1372 mm,
87 respectively (Kitashirakawa Experimental Station of FSERC, Kyoro University). Five
88 two-years-old Japanese oak (*Quercus crispula*) seedlings and 5 *Sasa* (*Sasa veitchii*)
89 stocks (i.e., the rhizome and connected culms) were grown in organic-free mountain
90 sand in transparent acrylic rhizoboxes under the shade from May 2008 (20 cm length ×
91 10 cm width × 30 cm depth for Japanese oak and 20 cm length × 20 cm width × 30 cm
92 depth for *Sasa*). Japanese oak seedlings were germinated and grown in the pot at the
93 commercial nursery in Shiga prefecture, central Japan. *Sasa* stocks grown under the
94 canopy in a forest-field in Kumamoto prefecture, western Japan were sampled and
95 grown in the pot at the other commercial nursery. *Sasa* species continue to be alive for
96 several decades, so it is difficult to identify the age of *Sasa*. However, leaf lifespan of
97 related species, *Sasa senanensis*, was reported to be only 1.98 years (Yajima and
98 Matsuda, 1997). Height and mean diameter of base of Japanese oak seedlings before
99 transplanting were ca. 50 cm and 7.5 mm, respectively. Similarly, height of *Sasa* stocks

100 was ca. 20 cm. One Japanese oak seedling died from insect damage during the
101 observation period. The rhizoboxes were wrapped with insulating materials to exclude
102 light and to prevent excessive increases in soil temperature. Plants were watered every a
103 few days to keep the soil water potential over -20 kPa.

104 Images of the Japanese oak and *Sasa* roots visible through one side of the rhizoboxes
105 were scanned every 2 weeks from June 2008 to April 2009 (Epson, GT-F670, Suwa,
106 Japan). During the dormant period (December to March), the interval of image capture
107 was 1 to 2 months. Root length and diameter were analyzed with image-analyzing
108 software (IMAGE MEASURE ver. 2.2, Imsoft Inc., Tokyo, Japan). Length and diameter
109 of all individual roots in the images were measured by tracing the computer mouse
110 separately; length data were then converted to the length per unit of image area (mm
111 cm^{-2}). We defined root production rate ($\text{mm cm}^{-2} \text{d}^{-1}$) of each period from the sum of
112 the new root lengths.

113 Root researches have until now chosen fine-root diameter classes varying from 0.1 to
114 10 mm to encompass what they called fine-roots (Vogt and Persson 1991). Most of the
115 roots were less than 1 mm in diameter (93 % and 97 % of the total length for Japanese
116 oak and *Sasa*, respectively). However, we did not fixate on the word “fine-roots” here,
117 because seedlings have thinner roots than mature trees.

118

119 Photosynthesis, soil temperature and leaf phenology

120 The total (aboveground + belowground) respiration and assimilation rate of *Sasa* was
121 measured every 1 to 3 weeks from July to December 2008 and in January and March
122 2009 in a closed dynamic chamber system consisting of an infrared CO_2 analyzer
123 (LI-820, LI-COR, Lincoln, NE, USA) without replication (Fig. 1). Net ecosystem CO_2

124 exchange (NEE) was measured under a transparent lid, and total ecosystem respiration
125 rate under a black lid (dark). Whole *Sasa* including canopy, rhizomes, and roots and
126 sand in rhizobox were considered as a small ecosystem. In this measurement, we
127 expressed respiration (CO₂ flow from vegetation to atmosphere) and assimilation (from
128 atmosphere to vegetation) as positive and negative values, respectively. When NEE is
129 negative value, gross canopy photosynthesis is larger than total respiration. Gross
130 canopy photosynthesis was calculated by adding total ecosystem respiration to minus
131 value of NEE at each measurement time. Microbial respiration in the rhizobox filled
132 with sand in a no-plant treatment was also measured to confirm that CO₂ efflux from
133 sand in the rhizobox is low. We used the database of hourly solar duration during 12:00
134 – 13:00 (h/h) measured at the point several kilo-meters far from our study point in
135 Kyoto city (Japan Meteorological Agency). <Fig. 1

136 Soil temperatures were measured hourly at 5 cm soil depth in the rhizoboxes of < Fig. 1, 2
137 Japanese oak and *Sasa* with a thermo recorder (TR-51S, T & D Corp., Matsumoto,
138 Japan). New leaves of Japanese oak and *Sasa* were counted and the lengths of every
139 new leaves were measured every 1 – 3 weeks from June to December 2008. Length and
140 area of Japanese oak and *Sasa* leaves that were sampled for calibration of length and
141 area were measured, using scale and scanner, respectively. Then all length data of
142 Japanese oak and *Sasa* measured above rhizoboxes were converted to the leaf area. The
143 relationship between root production and mean soil temperature at each observation
144 interval was analyzed by using Pearson's correlation.

145

146 Results

147

148 | Root production by Japanese oak showed a unimodal peak in July, whereas that of *Sasa*
149 | had a bimodal peak (July and October) (Fig. 2). Japanese oak roots were white-colored
150 | just at a time when they emerged and turned brown in a week, while *Sasa* roots were
151 | white at any time. Cumulative frequencies of root length less than 0.5 and 1.0 mm in
152 | diameter in Japanese oak and *Sasa* were 59 and 93%, 43 and 97%, respectively,
153 | indicating that most of roots were less than 1 mm in diameter. The minimum and
154 | maximum daily mean soil temperatures were 1.4 °C in January and 32.0 °C in July,
155 | respectively, and root production showed a significant relationship with soil temperature
156 | (Japanese oak $R = 0.81$, $P < 0.001$; *Sasa* $R = 0.73$, $P < 0.01$; Fig. 3).

<Figs. 3,4

157 | The pattern of leaf expansion was also different between the two species. *Sasa* leaves
158 | expanded mainly in August and September and continued until October, while the leaf
159 | area of Japanese oak remained constant from June to October (Japanese oak leaves
160 | senesce after October; Fig. 4). The gross canopy photosynthesis of *Sasa* was highest in
161 | September (Fig. 5). Hourly solar duration was high in 25 July, 13 November, 16 January
162 | (1.0 h/h), followed by 1 August, 11 September (0.8 h/h), 20 October, 12 December (0.7
163 | h/h), 5 September (0.6 h/h), 8 August (0.5 h/h).

< Fig. 3,4

164 | <Figs. 4,5

165 | Discussion

166

167 | Root production of Japanese oak seedlings was highest in July, corresponding to the
168 | seasonal pattern of soil temperature and had a significant positive relationship with soil
169 | temperature (Figs. 2, 3), indicating that soil temperature is a controlling factor in
170 | fine-root production, as reported in cool-temperate and boreal forests (Steele et al. 1997;

171 Tierney et al. 2003). Joslin et al. (2001), however, reported that fine-root production
172 peaked in early summer in a white oak-chestnut oak temperate forest that experienced a
173 severe drought by -2.5MPa in late summer, and they suggested ‘phenological
174 programming’ that is the strategy to maximize root growth under a favorable condition.
175 Our study area is in a temperate zone and temperatures in mid-summer are high;
176 however, the plants in our study received water throughout the year, which may be a
177 reason for the difference in peak times with Joslin et al. (2001).

178 Root production of *Sasa* also had a significant positive relationship with soil
179 temperature (Figs. 3), however, the bimodal pattern of root production of *Sasa* suggests
180 that endogenous factors control the pattern of root production (Fig. 2). Root production
181 of *Sasa* increased in October when soil temperature was below their maximum. Leaf
182 expansion in tree species delays the peak of root production, because the carbohydrate
183 supply is directed to the newly forming leaves rather than to the development of fine
184 roots, and then new carbohydrate that synthesized in new leaves is transferred to
185 below-ground for development of fine-roots (Lyr and Hoffman 1967). Reich et al.
186 (1980) reported that the timing of fine-root expansion and leaf expansion is
187 desynchronized because of competition between roots and shoots for carbohydrates.
188 Leaf expansion of *Sasa* increased after August (Fig. 4), corresponding to the results of
189 Lei and Koike (1998), who reported the active photosynthetic rate per leaf area in
190 autumn. Gross canopy photosynthesis of *Sasa* was highest in September despite
191 appropriate light condition in July and early August (Fig. 5). These phenological and/or
192 physiological patterns would have promoted the photosynthesis of whole *Sasa* in late
193 summer, although we did not measure active photosynthetic rate per leaf area. The
194 patterns of leaf expansion, photosynthesis and root production indicate that the

195 carbohydrate supply for root production is high during late summer (September),
196 enabling *Sasa* to produce new roots in October, when the climate is still mild.

197 Our results support the hypothesis by Fukuzawa et al. (2007) that suggested the
198 importance of understory *Sasa* spp. in the increase of root in late summer in
199 cool-temperate forests. However, there are several uncertainties in our study. An
200 analysis of annual variations in root production is not possible because our observations
201 were conducted for only 1 year. In addition, environmental conditions, such as light, soil
202 temperature and rhizosphere competition, might have differed from that in forest-fields,
203 especially cool-temperate forests in northern Japan. However, Japanese oak and *Sasa*
204 *veitchii* grow in forests near Kyoto where we conducted the study. We did identify the
205 different patterns of root production between Japanese oak seedlings and *Sasa* dwarf
206 bamboo under the same environmental conditions, and we clarified the linkage between
207 above-ground phenology and root phenology. These results suggest that the proportional
208 contribution of fine-root production from trees and *Sasa* differs in forest-fields
209 according to season. Our findings help clarify the processes involved in fine-root
210 dynamics in cool-temperate forests with dense understory vegetation.

211

212 Acknowledgements

213

214 We thank the staff of the Kitashirakawa Experimental Station of the Field Science
215 Education and Research Center, Kyoto University, for providing technical support and
216 meteorological data. We also thank Ms. Momoko Sakai, Dr. Keitaro Fukushima (Kyoto
217 University) for helping with the measurements, Dr. Naoko Tokuchi (Kyoto University),
218 Dr. Daniel Epron (Nancy University), members of Field Science Center for Northern

219 Biosphere, Hokkaido University for valuable comments, and Dr. Shozo Shibata (Kyoto
220 University) for helpful comments concerning cultivation of *Sasa* bamboo. This research
221 was supported in part by a Japanese Society for Root Research (Karizumi) Young
222 Researcher Travel Award and a Grant-in-Aid for Young Scientists (No. 20780116) from
223 Japan Society for the Promotion of Science.

224

225 References

226 Fukuzawa K, Shibata H, Takagi K, Satoh F, Koike T, Sasa K. 2007. Vertical distribution
227 and seasonal pattern of fine-root dynamics in a cool-temperate forest in northern
228 Japan: Implication of the understory vegetation, *Sasa* dwarf bamboo. *Ecol Res*
229 22:485-495

230 Gill RA, Jackson RB. 2000. Global patterns of fine root turnover for terrestrial
231 ecosystems. *New Phytol* 147:13-31

232 Hendrick RL, Pregitzer KS. 1993. The dynamics of fine root length, biomass, and
233 nitrogen content in two northern hardwood ecosystems. *Can J For Res* 23: 2507-2520

234 Hendrick RL, Pregitzer KS (1997) The relationship between fine root demography and
235 the soil environment in northern hardwood forests. *Ecoscience* 4:99–105

236 Joslin JD, Wolfe MH, Hanson PJ. 2001. Factors controlling the timing of root
237 elongation intensity in a mature upland oak stand. *Plant Soil* 228:201-212

238 Lei TT, Koike T. 1998. Functional leaf phenotypes for shaded and open environments of
239 a dominant dwarf bamboo (*Sasa senanensis*) in northern Japan. *Int J Plant Sci* 159:
240 812-820

241 Lyr H, Hoffmann G. 1967. Growth rate and growth periodicity of tree roots. *Int Rev For*
242 *Res* 2:181-236

243 Oshima Y. 1961. Ecological studies of *Sasa* communities II. Seasonal variations of
244 productive structure and annual net production in *Sasa* communities. *Bot Mag Tokyo*
245 74:280-290

246 Reich PB, Teskey RO, Johnson PS, Hinckley TM. 1980. Periodic root and shoot
247 growth in oak. *For Sci* 26:590-598

248 Steele SJ, Gower ST, Vogel JG, Morman JM. 1997. Root mass, net primary production
249 and turnover in aspen, jack pine and black spruce forests in Saskatchewan and
250 Manitoba, Canada. *Tree Physiol* 17:577-587

251 Teskey RO, Hinckley TM (1981) Influence of temperature and water potential on root
252 growth of white oak. *Physiol plant* 52:363–369

253 Tierney GL, Fahey TJ, Groffman PM, Hardy JP, Fitzhugh RD, Driscoll CT, Yavitt JB.
254 2003. Environmental control of fine root dynamics in a northern hardwood forest.
255 *Global Change Biol* 9:670-679

256 Vogt KA, Persson H (1991) Measuring growth and development of roots. – In: Lassoie
257 JP and Hinckley TM (eds) *Techniques and Approaches in Forest Tree Ecophysiology*.
258 Eds. CRS, Press, pp. 477-501

259 Yajima T, Watanabe N, Shibuya M (1997) Changes in biomass of above- and
260 under-ground parts in *Sasa kurilensis* and *Sasa senanensis* stands with culm height
261 (in Japanese with English summary). *J Jpn Forest Soc* 79:234–238

262

263 Legends to figures

264 Figure 1. Overview of the measurements on respiration and photosynthesis using
265 infrared gas analyzer (IRGA). Net ecosystem CO₂ exchange (NEE) was measured under
266 a transparent lid, and total ecosystem respiration rate under a black lid (dark). Sides of
267 the rhizoboxes were wrapped with insulating materials. Closed and open arrows denote
268 total ecosystem respiration and gross canopy photosynthesis, respectively.

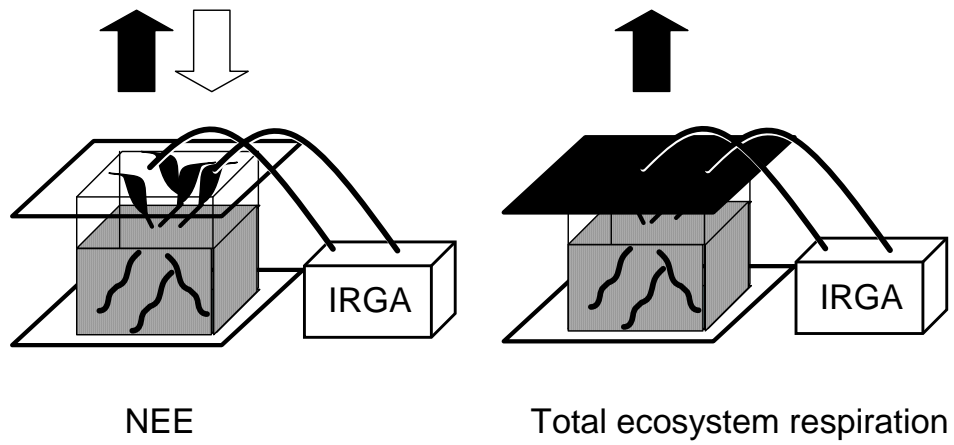
269 Figure 2. Temporal variation in root production of Japanese oak seedlings and *Sasa*
270 dwarf bamboo. Open square and closed circle symbols denote oak and *Sasa*,
271 respectively. Vertical bars represent SEM ($n = 4$ for oak, $n = 5$ for *Sasa*).

272 Figure 3. Relationship between root production and soil temperature of Japanese oak
273 seedlings and *Sasa*. Open square and closed circle symbols denote oak and *Sasa*,
274 respectively. Solid and dot lines represent the regression line of oak and *Sasa*,
275 respectively (Oak: $RP=0.0774e^{0.1678ST}$, *Sasa*: $RP=0.0324e^{0.238ST}$, where RP: Root
276 production; ST: Soil temperature).

277

278 Figure 4. Temporal variation in total leaf area of current leaves of Japanese oak
279 seedlings and *Sasa* dwarf bamboo. Open square and closed circle symbols denote oak
280 and *Sasa*, respectively. Vertical bars represent SEM ($n = 4$ for Japanese oak, $n = 5$ for
281 *Sasa*).

282 Figure 5. Temporal variation in gross canopy photosynthetic rate of *Sasa* dwarf bamboo
283 (solid line). The dashed line denotes the root production rate of *Sasa* shown in Fig. 2.

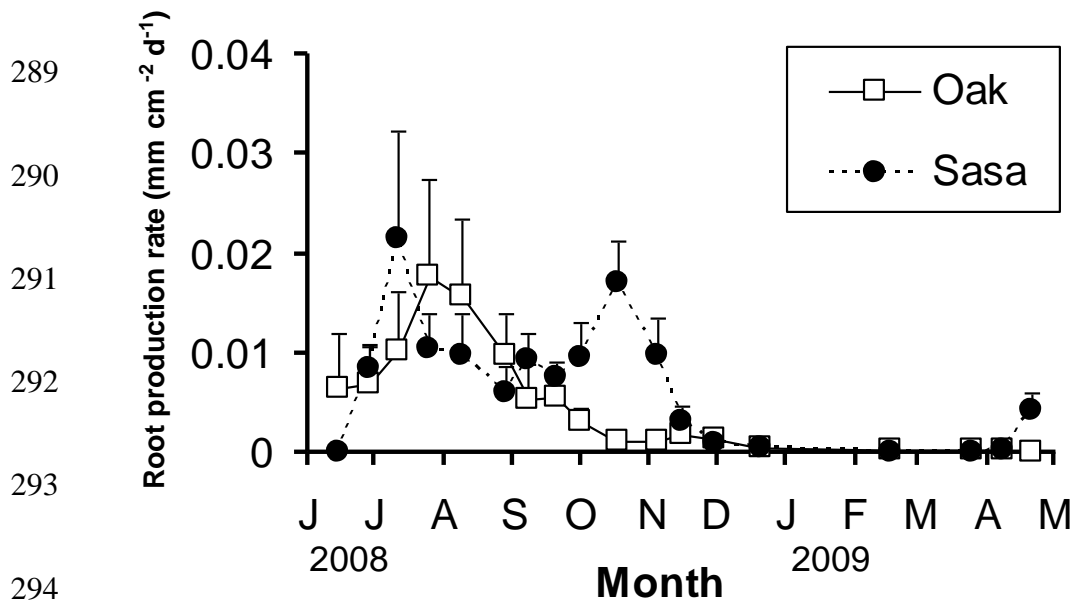


285

286 Figure 1

287

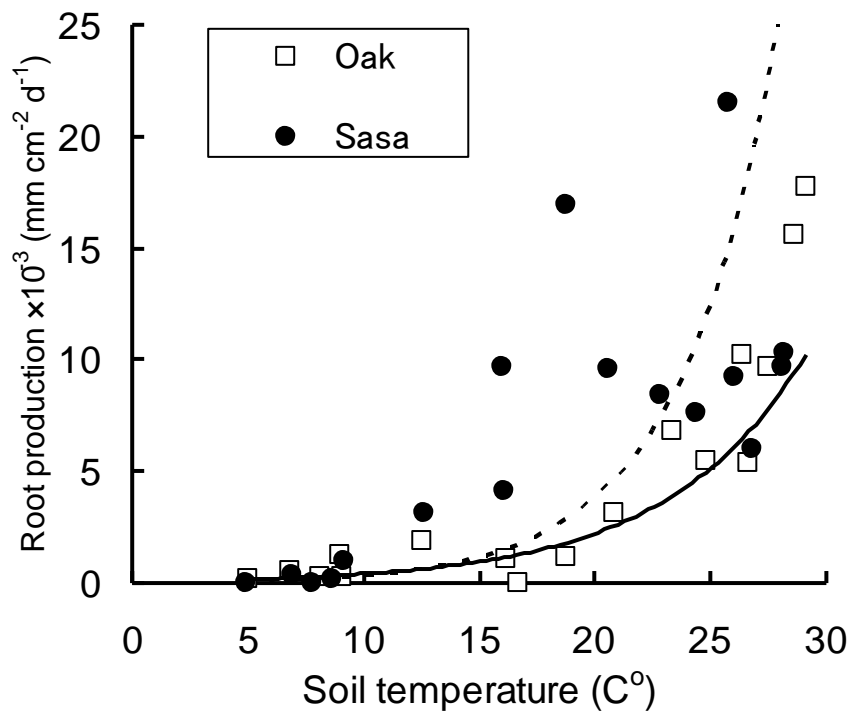
288



295 Figure 2

296

297

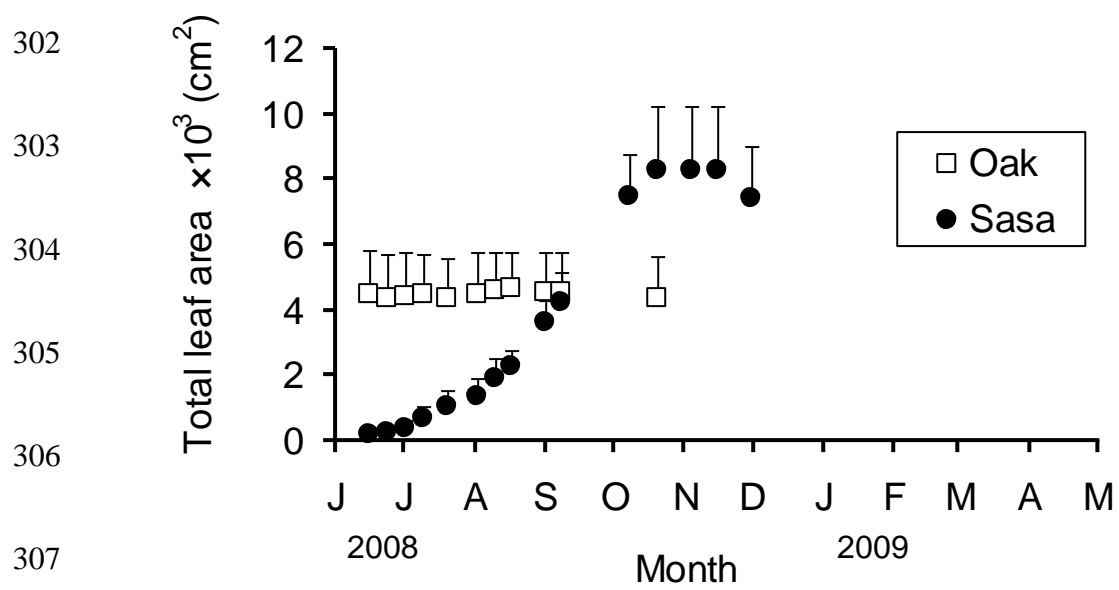


298

299 Figure 3

300

301



309 Figure 4

310

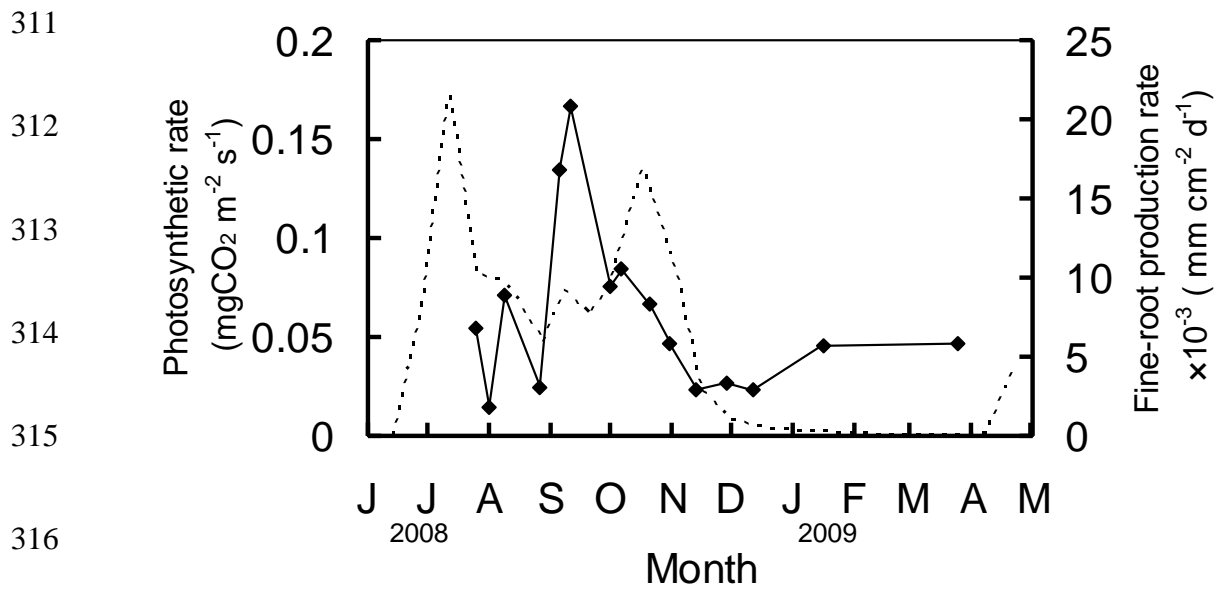


Figure 5

319 Complete addresses of the autor(s)

320

321 KARIBU FUKUZAWA 1,2:

322 1 NORTHERN FORESTRY AND DEVELOPMENT OFFICE, FIELD SCIENCE CENTER FOR
323 NORTHERN BIOSPHERE, HOKKAIDO UNIVERSITY, 250 TOKUDA, NAYORO 096-0071,
324 JAPAN

325 2 FIELD SCIENCE EDUCATION AND RESEARCH CENTER, KYOTO UNIVERSITY,
326 KITASHIRAKAWA-OIWAKECHO, KYOTO 606-8502, JAPAN

327 MASAKO DANNOURA, SHUHEI KANEMITSU, YOSHIKO KOSUGI:

328 Graduate School of Agriculture, Kyoto University, Kitashirakawa-Oiwakecho, Kyoto
329 606-8502, Japan