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Running title: Root production of oak and bamboo

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

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

Abstract

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

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

## Introduction

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

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

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

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

Photosynthesis, soil temperature and leaf phenology

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

exchange (NEE) was measured under a transparent lid, and total ecosystem respiration rate under a black lid (dark). Whole *Sasa* including canopy, rhizomes, and roots and sand in rhizobox were considered as a small ecosystem. In this measurement, we expressed respiration ($CO_2$ flow from vegetation to atmosphere) and assimilation (from atmosphere to vegetation) as positive and negative values, respectively. When NEE is negative value, gross canopy photosynthesis is larger than total respiration. Gross canopy photosynthesis was calculated by adding total ecosystem respiration to minus value of NEE at each measurement time. Microbial respiration in the rhizobox filled with sand in a no-plant treatment was also measured to confirm that $CO_2$ efflux from sand in the rhizobox is low. We used the database of hourly solar duration during 12:00 – 13:00 (h/h) measured at the point several kilo-meters far from our study point in Kyoto city (Japan Meteorological Agency). <Fig. 1

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

Results

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

<Figs. 3,4

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

< Fig. 3,4

<Figs. 4,5

## Discussion

Root production of Japanese oak seedlings was highest in July, corresponding to the seasonal pattern of soil temperature and had a significant positive relationship with soil temperature (Figs. 2, 3), indicating that soil temperature is a controlling factor in 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

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

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

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260 under-ground parts in *Sasa kurilensis* and *Sasa senanensis* stands with culm height
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262

263 Legends to figures

264 Figure 1. Overview of the measurements on respiration and photosynthesis using
265 infrared gas analyzer (IRGA). Net ecosystem $CO_2$ 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*).

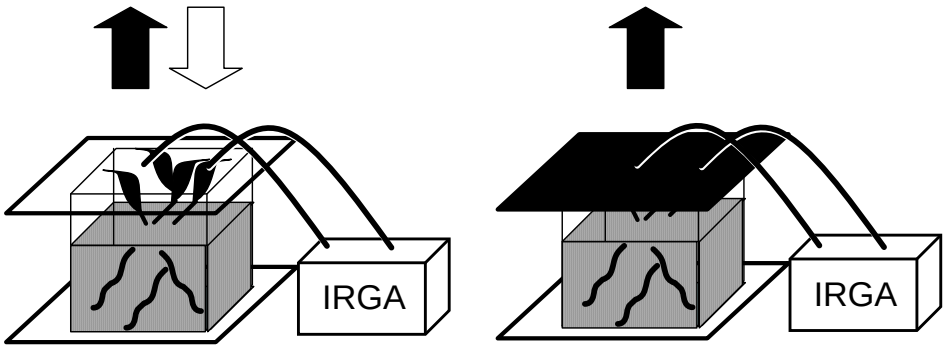
272 Figure 3. Relationship between root production and soil temperature of Japanese oak
273 seedlings and *Sasa*. Open square and closed circle symbols denote oak and *Sasa*,
274 respectively. Solid and dot lines represent the regression line of oak and *Sasa*,
275 respectively (Oak: $RP=0.0774e^{0.1678ST}$,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

284 Figures




285

286 Figure 1

287

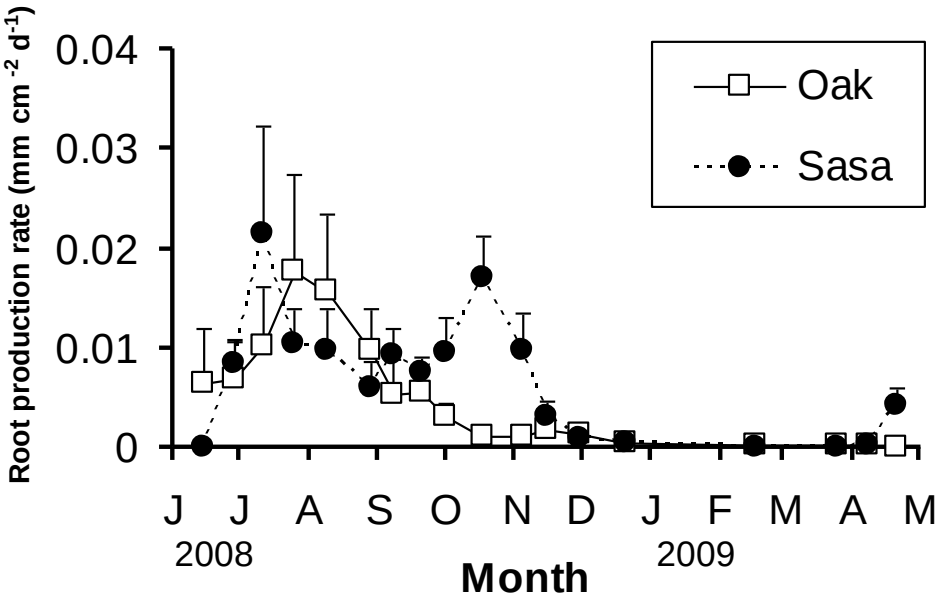
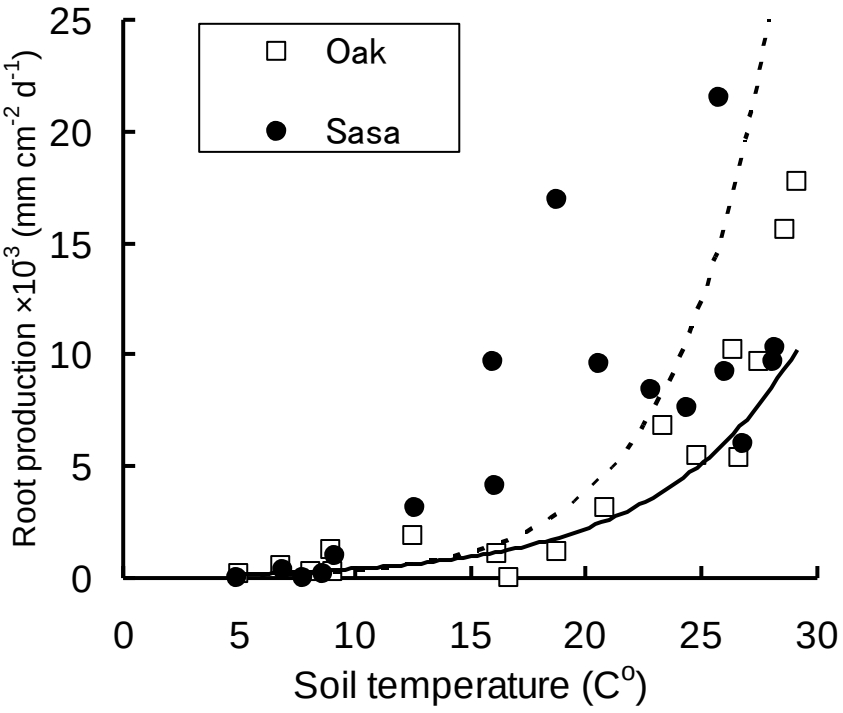

Root production rate (mm cm -2 d-1)
0.04
0.03
0.02
0.01
0
Oak
Sasa
J J A S O N D J F M A M
2008
2009
Month

Figure 2




298

299 Figure 3

300

301

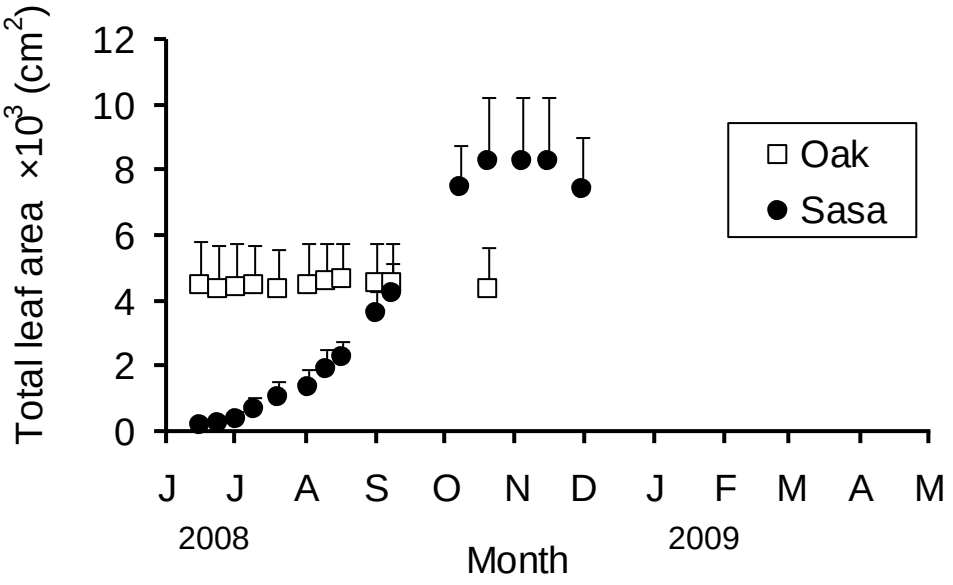

Total leaf area ×10$^3$ (cm$^2$)
12
10
8
6
4
2
0
J J A S O N D J F M A M
2008
2009
Month
Oak
Sasa

Figure 4

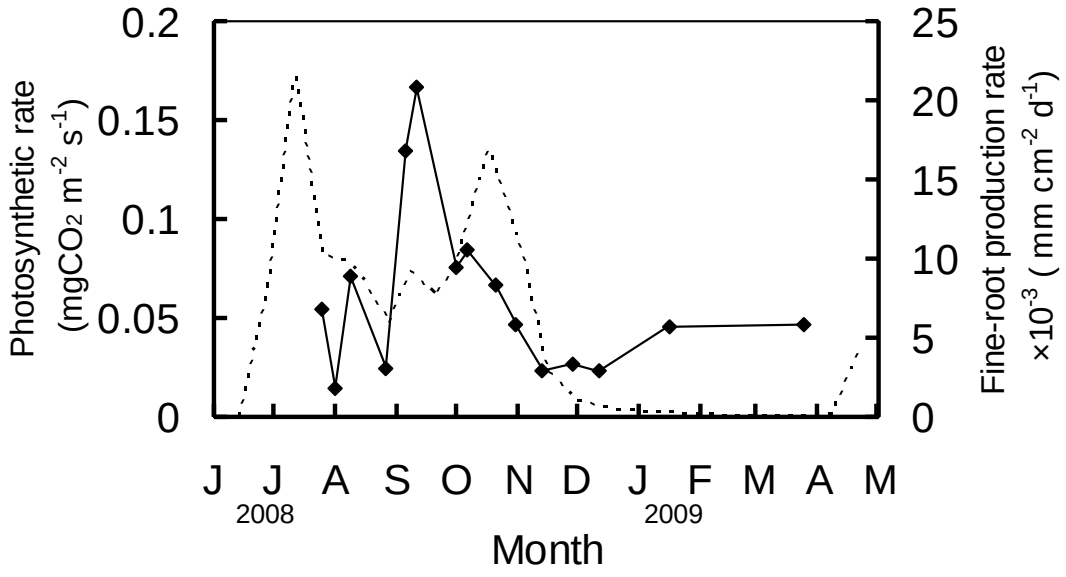

Photosynthetic rate
(mgCO2 m-2 s-1)
0.2
0.15
0.1
0.05
0
25
20
15
10
5
0
Fine-root production rate
×10-3 ( mm cm-2 d-1)
J J A S O N D J F M A M
2008
2009
Month

Figure 5

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