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1   Running title: Root production of oak and bamboo

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9   Title: Seasonal patterns of root production of Japanese oak seedlings and dwarf

10   bamboo grown in the rhizoboxes

11

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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

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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, Kozlowski 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^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

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 (mm cm^{-2} 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 (CO_2 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 CO_2 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

< Fig. 3,4

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).

<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

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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

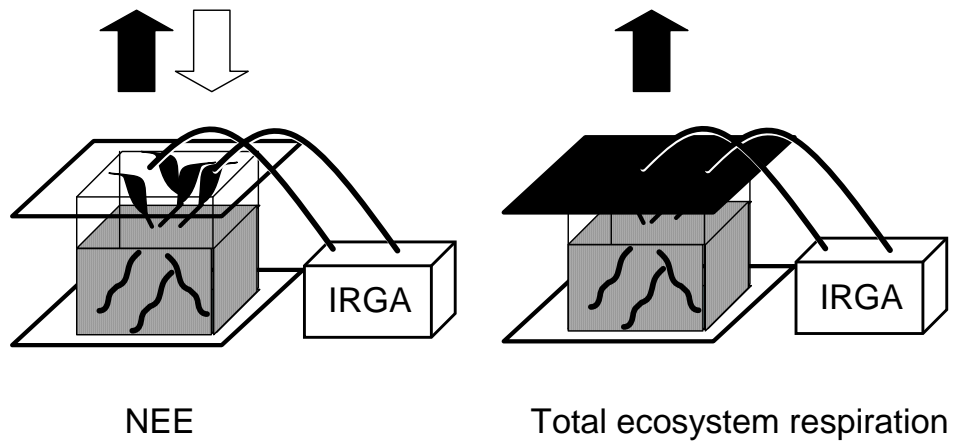268   total ecosystem respiration and gross canopy photosynthesis, respectively.

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

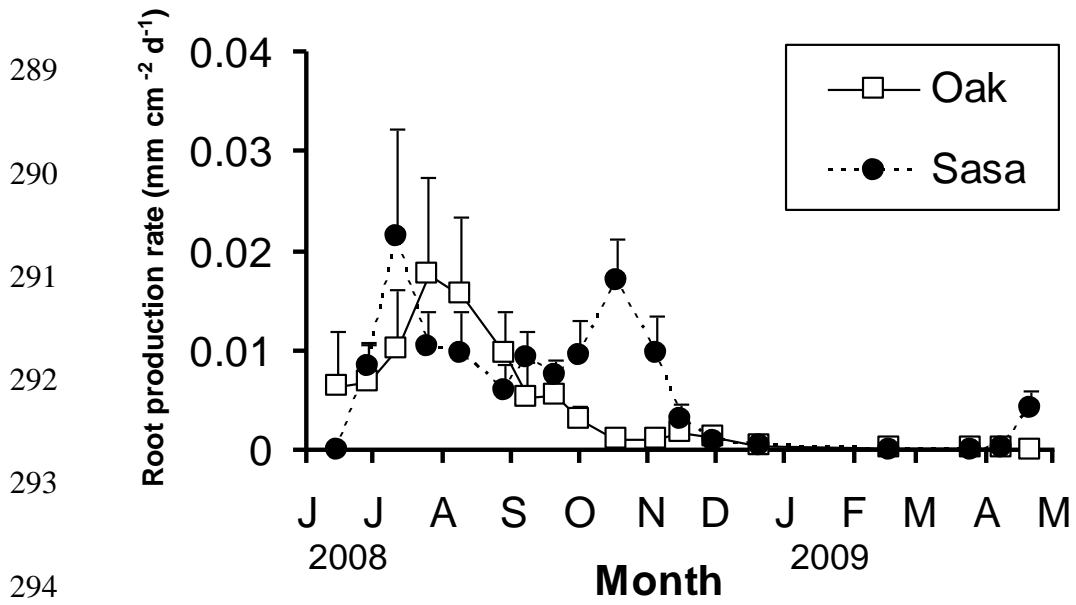283   (solid line). The dashed line denotes the root production rate of *Sasa* shown in Fig. 2.
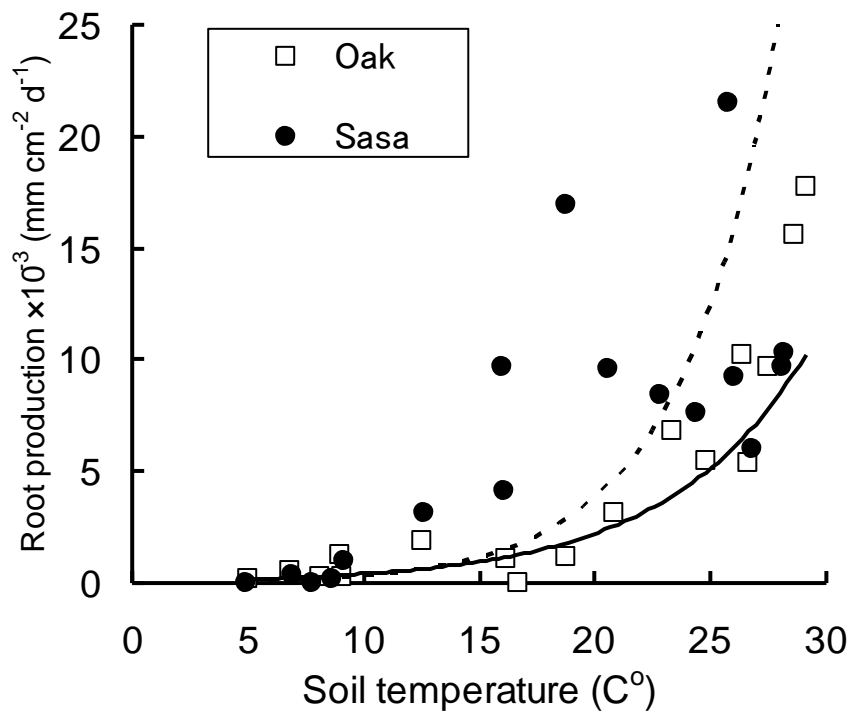
284   Figures

NEE   Total ecosystem respiration

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Figure 2

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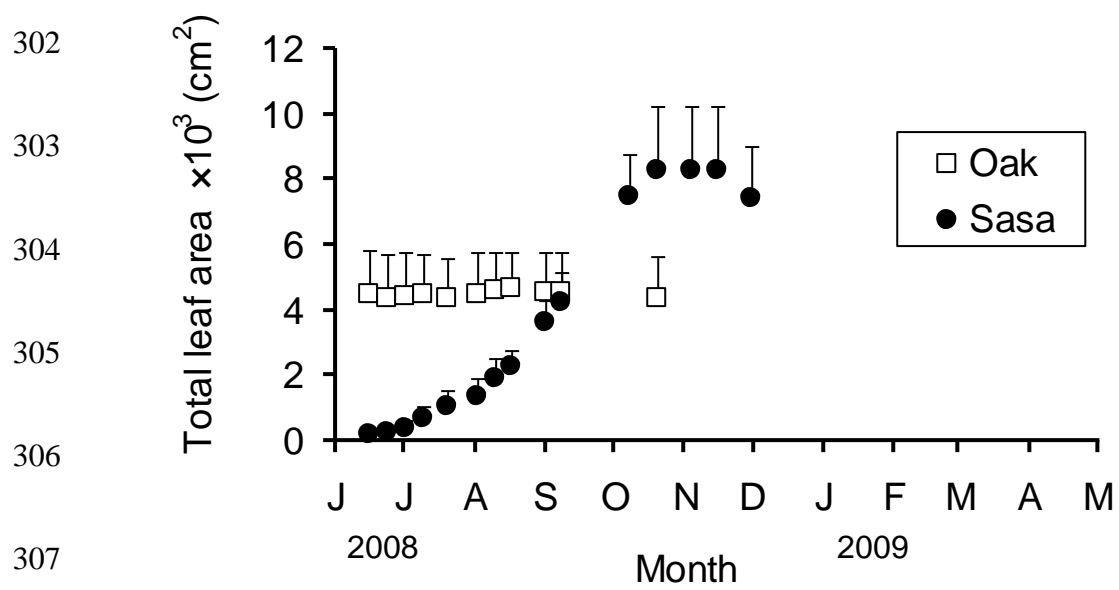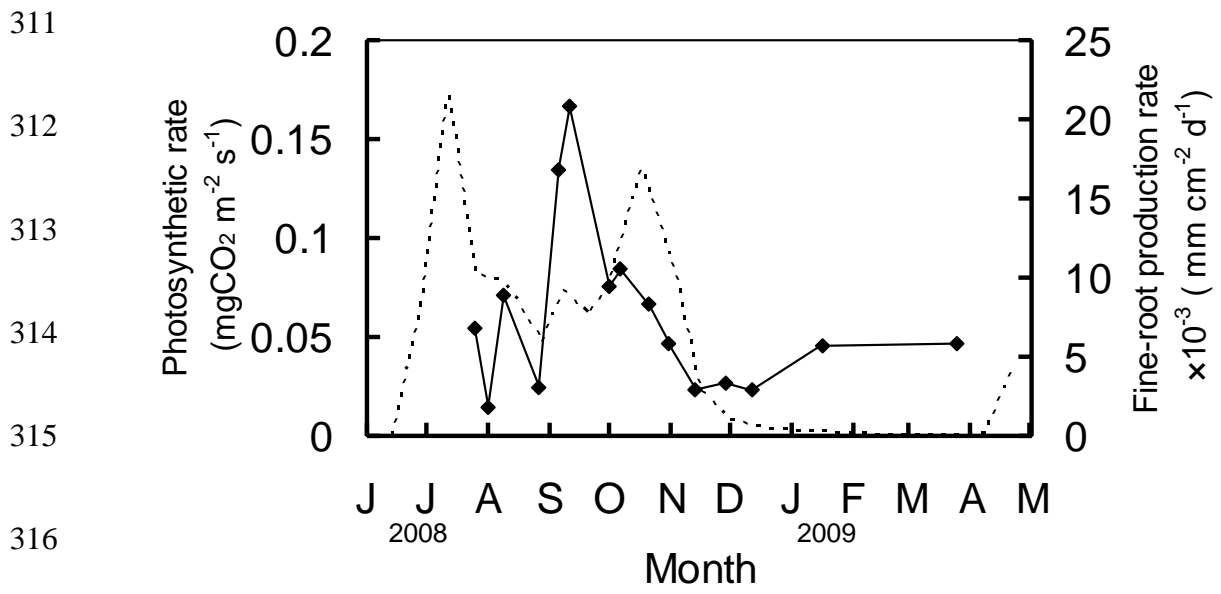
309   Figure 4

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Figure 5

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