

## Seasonal patterns of fine-root production and respiration of oak seedlings and dwarf bamboo

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### ABSTRACT

Understanding the temporal pattern of fine-root dynamics is important for evaluating fine-root turnover and production. We separately examined the temporal patterns of fine-root production by oak (*Quercus crispula*) and dwarf bamboo (*Sasa veitchii*), which is the major component of fine-root biomass in a cool-temperate forest. We grew 5 oak seedlings and 5 *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 the images. We defined the fine-root production rate as the total increase in root length measured during each observation interval. We also measured root respiration and whole-plant assimilation in a closed dynamic chamber system. Oak root production peaked in July, but *Sasa* root production peaked in both July and October. Soil temperature was highly correlated with oak root production, but less so with *Sasa* root production. Leaves of *Sasa* expanded in late summer, and the photosynthetic rate of *Sasa* was highest in September, suggesting that aboveground phenology influences the seasonality of fine-root production. The timing of oak root production was synchronized with root respiration, and the root respiration rate increased exponentially with increasing soil temperature. These results demonstrate different temporal patterns of fine-root production by oak seedlings and understory species (*Sasa*), even under similar environmental conditions.

KEYWORDS: oak, understory vegetation, *Sasa*, fine-root production, root respiration, rhizobox

### 1. INTRODUCTION

Understanding the seasonal pattern of fine-root (generally <2 mm in diameter) dynamics is crucial for estimating fine-root turnover, productivity and carbon cycling in forest ecosystems. A number of exogenous and endogenous factors control the seasonality of fine-root production. Exogenous factors include soil temperature, as reported from a northern boreal forest (Steele et

al., 1997), and endogenous factors relate to carbohydrates from leaves, as reported from a temperate forest (Reich et al., 1980, Joslin et al., 2001). Previous studies, however, have revealed contradictory results regarding these seasonal patterns (Tierney et al., 2003).

Root respiration is a major component of soil respiration and is important for carbon cycling in the plant–soil system. The ratio of root respiration to soil respiration ranges from 10% to 90%, based on studies from different parts of the world (Hanson et al., 2000). Soil respiration has been shown to increase exponentially with increasing soil temperatures, but the interaction between root respiration and root production remains unclear.

Cool-temperate forests in Japan are characterized by dense understory vegetation, such as dwarf bamboo (*Sasa* spp.). Fukuzawa et al. (2007) reported that fine-root biomass of *Sasa* is greater than that of tree species in cool-temperate forests in northern Japan. However, they were not able to distinguish the fine-root dynamic pattern between trees and *Sasa* in the analysis from images they obtained in the natural ecosystem, which contains roots of various species. Consequently, the role of understory vegetation in fine-root dynamics of forest ecosystems is not well understood.

The objectives of this study were (1) to clarify whether the patterns of fine-root production of oak seedlings and *Sasa* differ, by observing roots planted separately under similar environmental conditions; (2) to identify the relationship of fine-root production, soil temperature and leaf production in each species and the relationship between root respiration, fine-root production and soil temperature.

## 2. METHODS

### 2.1. Fine-root dynamics

Fine-root dynamics and root respiration were studied at the Kitashirakawa Experimental Station of FSERC, Kyoto University, Japan (35°01'N, 135°47'E). Five oak (*Quercus crispula*) seedlings and 5 *Sasa* (*Sasa veitchii*) stocks (i.e., the rhizome and connected culms) were grown in organic-free sand in transparent acrylic rhizoboxes from May 2008 (20 cm × 10 cm × 30 cm for oak and 20 cm × 20 cm × 30 cm for *Sasa*). One oak seedling died from insect damage during the observation period. The rhizoboxes were wrapped with insulating material to exclude light and to prevent excessive increases in soil temperature. Plants were watered every few days to keep the soil water potential over –20 kPa.

Images of the 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 v. 2.2 (Imsoft Inc., Tokyo, Japan)). Images of the individual roots were traced by computer mouse and then measured; length data were then converted to the length per unit of image area (mm cm<sup>-2</sup>). We defined root production rate (mm cm<sup>-2</sup> d<sup>-1</sup>) of each period from the sum of the new root lengths.

### 2.2. Respiration, soil temperature and leaf phenology

The soil respiration rate of the 4 oak seedlings was measured every 1 to 3 weeks from July to December 2008 in a closed dynamic chamber system consisting of an infrared CO<sub>2</sub> analyzer (LI-820, LI-COR, Lincoln, NE, USA). Measurements were also taken in January and March 2009.

Microbial respiration in the rhizobox filled with sand in a no-plant treatment was subtracted from soil respiration to calculate root respiration. The total (aboveground + belowground) respiration rate of *Sasa* was measured (without replication) with the same system. Net photosynthesis (gross photosynthesis – gross respiration) was measured under a transparent lid, and gross respiration under a black lid, and the gross photosynthetic rate was calculated as gross respiration rate – net respiration rate.

Soil temperature was measured hourly at a depth of 5 cm with a thermo recorder (TR-51S, T & D Corp., Matsumoto, Japan). New leaves were counted and the length of each leaf was measured. The relationship between fine-root production and mean soil temperature at each observation interval was analyzed by using Pearson's correlation.

### 3. RESULTS AND DISCUSSION

Fine-root production by oak showed a unimodal peak in July. However, that of *Sasa* had a bimodal peak (July and October), indicating different seasonal patterns between oak and *Sasa* (Fig. 1). The daily mean soil temperature was 1.4 °C in January and 32.0 °C in July. Root production and soil temperature showed a significant relationship (oak  $R = 0.81$ ,  $P < 0.001$ ; *Sasa*  $R = 0.73$ ,  $P < 0.01$ ). However, the bimodal production pattern suggests that endogenous factors are also important in the seasonality of fine-root production in *Sasa*. Lyr and Hoffman (1967) reported that leaf expansion in tree species delays the peak of fine-root production because of the importance of the carbohydrate supply from newly formed leaves in the development of fine roots. Reich et al. (1980) reported that the timing of fine-root expansion and leaf expansion is desynchronized because of competition between roots and shoots for carbohydrates. Here, *Sasa* leaves expanded mainly in August and continued until October, while the number and size of oak leaves remained constant (oak leaves grow in May and senesce after October; data not shown). Furthermore, the photosynthetic rate of *Sasa* was high in September, indicating that the carbohydrate supply for fine-root production is high then, enabling *Sasa* to produce new roots in the autumn when the climate is still mild.

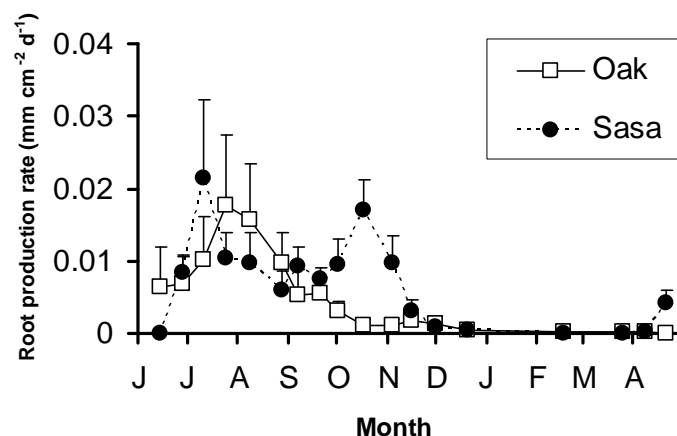


Figure 1. Temporal variation in fine-root production of oak seedlings and *Sasa* dwarf bamboo.

Vertical bars represent SEM ( $n = 4$  for oak,  $n = 5$  for *Sasa*).

Root respiration of oak seedlings was high in July and August, when root production rate was high, with  $0.042 \text{ mgCO}_2 \text{ m}^{-2} \text{ s}^{-1}$  in maximum, and increased exponentially with increasing soil temperature ( $Q_{10} = 1.8$ ). Microbial respiration in the sand was low because of the sand's low organic content.

#### 4. CONCLUSION

The seasonal pattern of fine-root production differed between oak seedlings and *Sasa* dwarf bamboo under the same environmental conditions, revealing the role of physiological factors in fine-root dynamics. These results will help clarify the processes involved in fine-root dynamics in cool-temperate forests with dense understory vegetation.

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