



# Temporal variation in fine-root biomass, production and mortality in a cool temperate forest covered with dense understory vegetation in northern Japan



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## ABSTRACT

To understand the temporal pattern of fine-root dynamics and the factors that affect it, we investigated the seasonal and interannual variation in fine-root production (FRP) and fine-root mortality (FRM) rates, as well as fine-root biomass (FRB) and necromass in a cool temperate forest in northern Japan that was covered with dense understory vegetation of *Sasa senanensis*. We measured the root length density (RLD) and the rate of root production and mortality over 3 yr using minirhizotrons, and compared these rates with temperature, precipitation, soil moisture, and plant area indices (PAI). We also measured the FRB and the necromass of fine roots four times per year for 2 yr using soil cores and calculated dry weight-based FRP and FRM. FRB in the uppermost 15 cm of the surface-soil layer accounted for 41–61% of the biomass up to 60 cm soil depth, and decreased with increasing soil depth. The biomass of fine roots with root diameters <0.5 mm was almost equivalent to that of roots measuring 0.5–2 mm in diameter. *Sasa* roots accounted for 59–88% of the total FRB. FRB did not fluctuate seasonally, whereas RLD did. The FRP rate was high in mid- to late summer and correlated significantly with air and soil temperatures, indicating that temperature affects FRP. However, the relationship between FRP and soil moisture was weak. FRP was significantly correlated with the PAI of oak trees and the increment in the PAI of *Sasa*, suggesting that endogenous factors also affect FRP. Depending on the method used to calculate turnover, mean FRP for the 3-year study period was 589 or 726 g m<sup>-2</sup> yr<sup>-1</sup>, accounting for 36% or 41% of forest net primary production, respectively. The results of this study illustrate the substantial seasonal and interannual fluctuations in FRP, and indicate that a significant proportion of assimilated carbon was allocated to below-ground root systems in an oak-*Sasa* stand.

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## 1. Introduction

Despite making up only a small percentage of total tree biomass (Karizumi, 1977; Vogt et al., 1996; Scarascia-Mugnozza et al., 2000; Helmisaari et al., 2002; Hertel et al., 2009), the rapid turnover of fine-root biomass (FRB) means that fine roots (<2 mm in diameter) are an important component of carbon and nutrient cycling in forest ecosystems (McClougherty et al., 1982; Hendrick and Pregitzer, 1992, 1993; Nadelhoffer and Raich, 1992). After reviewing studies on a global scale, Gill and Jackson (2000) reported an average fine-root turnover of 0.56 yr<sup>-1</sup> (maximum value:

*Abbreviations:* FRP, fine-root production; FRM, fine-root mortality; FRB, fine-root biomass.

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2.6 yr<sup>-1</sup>) in forest ecosystems and showed that it increased with an increase in annual mean temperature. Finér et al. (2011) also summarized global datasets and calculated the mean fine-root turnover of boreal, temperate, and tropical forests to be 0.77, 1.21, and 1.44 yr<sup>-1</sup>, respectively. Similarly, Yuan and Chen (2010) reported that the average fine-root turnover in boreal forests was 1.07 yr<sup>-1</sup>. These studies showed that fine-root production (FRP) is an important component of total net primary production (NPP) in forest ecosystems; indeed, several studies have reported that FRP contributes 40–60% of total NPP (Aber et al., 1985; Hendrick and Pregitzer, 1993; Vogt et al., 1996; Tateno et al., 2004). However, considerable uncertainty remains regarding the extent to which fine-root turnover and FRP can be generalized as both of these factors can vary considerably, even under the same environmental conditions. In addition, since our current knowledge of below-ground fine root dynamics and productivity is considerably

more limited than it is for above-ground biomass, further studies need to be conducted in this area.

Information on the temporal variation in FRB, FRP and fine-root mortality (FRM) is essential for estimating fine-root turnover and FRP. Although seasonal variation in FRB has been reported to be a small part of variation compared to spatial variation (Yuan and Chen, 2012), relating the temporal patterns of fine-root dynamics to climatic factors at a local scale is necessary for generalizing FRP characteristics and for anticipating fine-root dynamics under a changing climate (Tierney et al., 2003). Minirhizotron-based techniques are useful for detecting temporal changes in fine-root dynamics because they can pursue the fate of an individual root continuously under conditions in which FRP and FRM occur simultaneously (Hendrick and Pregitzer, 1992; Fukuzawa et al., 2007; Satomura et al., 2007).

Several studies have shown that substantial FRP occurs during the growing season in forests ranging from temperate to boreal (Tryon and Chapin, 1983; Joslin et al., 2001; Steinaker et al., 2010), although there is a discrepancy in the peak period of root production. Of the factors that have been shown to affect fine-root dynamics, soil temperature was considered to be the factor most closely correlated with FRP in forests not experiencing soil drought (Tryon and Chapin, 1983; Steele et al., 1997; Steinaker et al., 2010). On the other hand, soil moisture was correlated with FRP rate in temperate forests experiencing severe drought in late summer (Joslin et al., 2001), illustrating the importance of endogenous controls, such as timing of carbohydrate supply from leaves (Joslin et al., 2001; Tierney et al., 2003). However, few studies relating seasonal patterns of FRP to shoot phenology have been reported, limiting our understanding of the interactions between above- and below-ground environments in areas with marked differences in seasonality (Steinaker et al., 2010). It is therefore still necessary to measure fine-root dynamics and relate them to changes in environmental and endogenous factors in forests with a diversity of vegetation types and climate conditions. In addition, since the pattern of fine-root dynamics has been reported to differ among species (Kozłowski and Pallardy, 1997; Steinaker et al., 2010; Fukuzawa et al., 2010), considering the species composition of the forest would be necessary, unless the stand is in a plantation of a single species.

The role of understory vegetation in carbon and nutrient cycling in forests is not fully understood, although some studies have suggested that it is important, especially in temperate or boreal forests (Nilsson and Wardle, 2005; Moore et al., 2007; Koike et al., 2010; Cavard et al., 2011; Finér et al., 2011). In northern Japan, *Sasa* dwarf bamboo grows very densely as understory vegetation in forest ecosystems. Fukuzawa et al. (2007) showed that the FRB of *Sasa* spp. is larger than that of the trees in such ecosystems and suggested the possibility that the leaf phenology of *Sasa* determines the pattern of FRP. Their study focused on the role of *Sasa* in carbon and nutrient cycling in cool temperate forests. However, because their study was based on observations from a single year with no observations from autumn to winter, the resulting data had uncertainties regarding seasonal and interannual variations in the pattern of fine-root dynamics. Ruess et al. (1998) reported that FRP is large in Alaskan boreal forests mainly dominated by willow species, with interannual variation exceeding twofold, and suggested that this interannual variation is affected by annual differences in climatic conditions. Furthermore, even under the same temperature conditions, the endogenous situation can differ between spring and autumn (Tierney et al., 2003). Thus, in order to more accurately clarify the dominant factors affecting fine-root dynamics and to predict their effects, examining fine-root dynamics throughout the year over multiple years, and relating these observations to environmental and endogenous factors, is considered necessary. Secondly, it is also necessary to evaluate mass-based

FRP per unit area and compare it with above-ground production in order to clarify the role of fine roots in carbon and nutrient cycling (Vogt et al., 1986).

We hypothesized that the seasonal and interannual patterns of FRP and FRM are influenced by environmental factors, such as temperature and soil moisture, and that above-ground phenological fluctuations, particularly those of understory *Sasa*, also affect temporal changes in fine-root dynamics and productivity of forest ecosystems.

The objectives of this study were as follows: (1) to determine the seasonal and interannual variation in FRB, FRP and FRM in a cool temperate forest in northern Japan, and relate these fine-root parameters to climatic factors, such as air and soil temperatures, precipitation, and soil moisture, as well as to above-ground phenology, which is related to endogenous controls and (2) to evaluate fine-root turnover and mass-based FRP and FRM in the forest, including *Sasa*, and to elucidate the contribution of fine-root productivity to forest NPP.

## 2. Materials and methods

### 2.1. Study site

We conducted the study in a mature cool temperate forest in the Teshio Experimental Forest of Hokkaido University in northern Japan (45°03'N, 142°06'E, 70 m a.s.l.). The dominant tree species, which constituted 84.5 Mg ha<sup>-1</sup> of above-ground tree biomass, consisted of Mongolian oak (*Quercus crispula*), followed by birches (*Betula ermanii* and *B. platyphylla* var. *japonica*) and Sakhalin fir (*Abies sachalinensis*) (Koike et al., 2001). The forest floor was covered with a dense understory of evergreen dwarf bamboo, *Sasa senanensis*. There is continuous snowpack from November to late April or early May, with maximum snow depth (about 1.5 m) occurring in March. The bedrock is Cretaceous sedimentary rock and the dominant soil is a Gleyic Cambisol (FAO, 1990) with about 10 cm of O horizon with a mor humus type, 20 cm of A horizon, and 30 cm of B horizon.

To investigate fine-root dynamics and the environmental parameters described in the following section, we established a 0.25 ha plot at the study site and selected three oak trees within the plot aged approximately 160 yr and 50–60 cm in diameter at breast height (DBH). We set the observation points under the tree canopy to cover both trees and *Sasa* vegetation. Observations were conducted over three growing seasons, from late April 2002 to November 2004.

### 2.2. Minirhizotrons

We observed fine-root length-based production and mortality using minirhizotrons (BTC-100X camera system and BTC I-CAP software, Bartz Technology Corp., Santa Barbara, CA, USA). In June 2001, we installed transparent acrylic tubes (2 m long with a 5.08 cm inside diameter) 2 m from the three observed oak trees at an angle of 45° to the soil surface, slanting toward the observed trees. We captured digital images of the soil, including fine roots in contact with one side of each tube, and stored the digital images on a personal computer. Each image (18 × 13.5 mm) was obtained at 3 cm depth intervals within each tube to a depth of 45 cm. Minirhizotron measurements were conducted from April 2002 to November 2004 at monthly intervals during the growing season. We also obtained images three times during the dormant season (December, February, and early April of 2003–2004). Accordingly, we analyzed 836 images over the three-year period.

We used MSU ROOTs Tracer software (Michigan State University, East Lansing, MI, USA) to analyze the roots in the captured

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