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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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This manuscript includes 37 pages of text, 5 tables and 6 figures.

Short running title: Temporal variation in fine root dynamics in a cool temperate forest

Abbreviations

FRP: Fine-root production, FRM: Fine-root mortality, FRB: Fine-root biomass

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 years 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 years 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⁻² yr⁻¹, 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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44 Keywords: fine roots, minirhizotron, oak forest, root biomass, root turnover, soil coring

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 (McClaugherty et al., 1982; Hendrick and Pregitzer, 1992, 1993; Nadelhoffer and Reich, 1992). After reviewing studies on a global scale, Gill and Jackson (2000) reported an average fine-root turnover of 0.56 yr^{-1} (maximum value: 2.6 yr^{-1}) 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^{-1} , respectively. Similarly, Yuan and Chen (2010) reported that the average fine-root turnover in boreal forests was 1.07 yr^{-1} . 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; Tatenó 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 two-fold, 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; (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⁻¹ 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 images. We traced the length and diameter of each individual root in each image and converted the values to length per imaged area (root length density (RLD): mm cm⁻²). For each tube, FRP was evaluated as the sum of the length of new roots and the increase in the length of existing roots during each observation interval. Similarly, we evaluated the FRM rate as the sum of the length of roots that disappeared (Tingey et al., 2000; Satomura et al., 2007). RLD, FRP, and FRM values obtained from five images were averaged for each 15 cm-thick soil layer for each tube. Coarse roots, i.e. roots thicker than 2.0 mm in diameter, were not evaluated in this study.

We calculated the turnover rate of FRP and FRM for each tube as the proportion of the cumulative annual length-based root production (ALRP) to maximum RLD (RLD_{max}) or mean RLD (RLD_{mean}) according to equation 1, and the annual length-based mortality (ALRM) to RLD_{max} or RLD_{mean} according to equation 2, respectively (Gill et al. 2002):

$$\text{Turnover rate of production (yr}^{-1}\text{)} = \text{ALRP/RLD}_{\text{max}} \quad \text{or} \quad \text{ALRP/RLD}_{\text{mean}} \quad (\text{Eq. 1})$$

$$\text{Turnover rate of mortality (yr}^{-1}\text{)} = \text{ALRM/RLD}_{\text{max}} \quad \text{or} \quad \text{ALRM/RLD}_{\text{mean}} \quad (\text{Eq. 2})$$

where ALRP and ALRM are expressed in mm cm⁻² yr⁻¹ and RLD_{max} and RLD_{mean} in mm cm⁻². We used RLD_{max} and RLD_{mean} for each year, based on the observed seasonal change in RLD. We also calculated the mean turnover rate as the ratio of mean ALRP or ALRM to mean RLD_{max} or RLD_{mean} for the three years.

2.3. Soil coring

We used a soil coring technique to measure FRB and necromass. We collected soil to a soil depth of 60

cm using a soil auger (inner diameter, 4.2 cm) in June, August, September, and October 2003, and May, July, September, and October 2004. Each soil sample was collected at a distance of 2 m from each oak tree, and the average of three points was used for further analyses. We divided the 60 cm soil core to four layers of 15 cm, washed them with water and then sieved them through a 0.25 mm mesh to collect the roots. We categorized the roots by state (living and dead), species (*Sasa* and trees) and diameter classes (<0.5 and 0.5 to 2.0 mm). We defined dead roots (necromass) as dark, inelastic roots. In measuring root necromass, classification by diameter was not conducted because of the fragility of the roots. We then oven-dried (70°C, 48 h) and weighed the samples. In all samples, herbaceous roots other than *Sasa* were so rare that we considered their contribution to be negligible because of the dense coverage by *Sasa*.

Mass-based fine-root productivity and mortality

Dry mass-based FRP and FRM were calculated according to Eq. 3 and Eq. 4, respectively, by assuming that the turnover rate of length-based values coincides with that of the dry mass-based value (Hendrick and Pregitzer, 1993). Turnover rates in Eq. 3 and Eq. 4 were obtained from Eq. 1 and Eq. 2, respectively. For the calculation using RLD_{max} , we used FRB data obtained within one month after the RLD_{max} was observed in December 2003 and September 2004. For the calculation of the turnover rate for 2002, we used the FRB data obtained at the beginning of the next growing season (May 2003) because of the lack of biomass data in 2002, even though RLD_{max} was observed in August 2002. However, this procedure was not considered to produce a large error as the RLD in May 2003 was similar to that in August 2002 (94% of that in August 2002). For estimating dry mass-based production or mortality in each year based

on the turnover rate in each year using RLD_{mean} , we used the respective mean FRB in 2003 and 2004. However, due to the lack of biomass data in 2002, we did not calculate mass-based FRP in 2002 using RLD_{mean} . We also evaluated the 3-year mean of mass-based FRP and FRM using mean turnover rates and mean FRB during the observation period using the following equations.

$$\text{Mass-based FRP (g m}^{-2} \text{ yr}^{-1}) = \text{FRB (g m}^{-2}) \times \text{Turnover rate of production (yr}^{-1}) \text{ (Eq. 3)}$$

$$\text{Mass-based FRM (g m}^{-2} \text{ yr}^{-1}) = \text{FRB (g m}^{-2}) \times \text{Turnover rate of mortality (yr}^{-1}) \text{ (Eq. 4)}$$

2.4. Temperature and soil moisture

We measured soil temperature hourly at a depth of 5 cm at a distance of 2 m from the observed trees, with three replications from January 2002 to December 2004, using a TR-71S thermo recorder (T & D Corp., Matsumoto, Japan). We measured air temperature at a height of 30 m and precipitation every 30 min from a meteorological tower 0.7 km away from the observation plot (Takagi et al., 2009). We measured soil volumetric water content at depths of 15 cm using a TRIME-FM device (IMKO GmbH Inc., Ettlingen, Germany) for time-domain reflectometry at monthly intervals during the growing season in 2002 and 2004. We measured the plant area indices (PAI) of overstory trees and *Sasa* once a month during the growing seasons in a representative area of the surrounding forest with three replications from 2002 to 2004 using an LAI-2000 Plant Canopy Analyzer (Li-Cor, Lincoln, NE, USA) (Takagi et al., 2009). For tree PAI, using the light value at an open site as a reference, we measured light values beneath the tree canopy. For *Sasa*-PAI, light values were measured beneath the *Sasa* canopy near the soil

surface, as well as above the *Sasa* canopy as a reference. For each of the three replicates, 10 measurements were taken at different positions in the horizontal direction before averaging the readings.

2.5. Above-ground productivity

We measured the DBH of all trees (>5 cm at DBH) in the 0.25 ha plot and calculated the above- and below-ground woody biomass from the allometric equation:

$$\ln Y = a \ln X + b \quad (\text{Eq. 5})$$

where X and Y represent DBH (in cm) and estimated biomass (in kg), respectively. We calculated the trunk, branch, and coarse root biomass separately and summed the trunk and branch biomass to estimate the above-ground biomass. Coefficients in this equation were determined using the dry mass data of 22 trees around the study site, ranging from 3.8 to 55 cm in DBH and including the three dominant tree species (Takagi et al., 2010). The values of the coefficients a and b for the trunk, branches, and coarse roots were 2.365, 2.713, 2.224, and -2.596 , -4.456 , and -2.918 , respectively.

To estimate the annual biomass increment of above-ground parts and coarse roots, we measured the radii of whole tree rings (half of DBH) and tree ring widths for the previous 5 years of three mature oak trees that were cut in 2001, with three replications per tree. We calculated the ratio of the mean annual increments in the radii (DBH) and the ratio of the annual increments in DBH as the radius at time t divided by the radius at time $t-1$. We then estimated the above-ground woody and coarse root biomass increments by multiplying each biomass by the ratio of the annual increment in DBH. We collected the litterfall of trees using a 0.5 m² litter trap below the canopy with nine replications in 2001.

Above-ground NPP of the trees was calculated as the sum of the annual above-ground woody biomass increment and litterfall. We measured the above-ground biomass of understory *S. senanensis* by harvesting a 1 m² area with four replications in October 2004, when biomass reached a maximum. Above-ground NPP of *Sasa* was measured as the biomass of culms and leaves of the current year.

2.6. Statistical analysis

We analyzed the relationships between the monthly FRP or FRM rate in each soil layer, and the air and soil temperatures, precipitation, soil water content, tree and *Sasa* PAI, and the increment of trees and *Sasa* PAI using regression analysis. In the analysis, we used the mean air and soil temperatures and mean daily precipitation during the minirhizotron observation interval, or the soil volumetric water content and PAI measured in each interval. Increments in the PAI were calculated as the difference between PAI_{time; t} and PAI_{time; t-1}. We used the FRP and FRM data obtained during the snow-free periods to analyze their relationship to PAI and soil moisture, because PAI and soil moisture were not measured during the snow period.

A repeated-measures ANOVA was used to examine the effects of depth, time of observation, and their interaction on the average values obtained for FRB, fine-root necromass, length-based production, and mortality for each year. Between-subject effect was evaluated as soil depth; within-subject effect was observation date (season). For FRB and fine-root necromass, additional analyses were also conducted by adding ‘year’ to the between-subject factor. In the repeated-measures ANOVA, the sphericity assumption

was tested and degrees of freedoms were Greenhouse-Geisser adjusted if the assumption was violated. The analyses were conducted with JMP software (SAS Institute, Cary, North Carolina, USA). Differences in ALRP, ALRM, and turnover rates for production and mortality between years were analyzed using one-way ANOVA followed by a Tukey HSD test. We used a Kruskal-Wallis Rank Sum test when there was nonhomogeneity, even after log transformation. The relationship between ALRP and ALRM was analyzed using Pearson's correlation.

3. Results

3.1. Temperatures, precipitation, and soil moisture

The annual mean air temperature in 2002, 2003, and 2004 was 5.5, 5.6, and 6.3°C, respectively, with maximum monthly mean temperatures of 16.1, 17.7, and 18.3°C in August and minimum monthly mean temperatures of -6.3, -8.4, and -6.4°C in January (February for 2003) (Fig. 1). The annual mean soil temperature at 5 cm soil depth in 2002, 2003, and 2004 was 7.2, 7.1, and 7.6°C, respectively, with maximum monthly temperatures of 15.0, 14.8, and 16.1°C in August and minimum monthly temperatures of 1.9, 2.0, and 1.6°C in March (April for 2004) (Fig. 1). Soil temperature in the dormant season from December to April was stable, ranging between 1 and 3°C due to the thick snowpack (about 1.5 m). Mean air temperature during the period of intensive FRP (May through August) in 2002, 2003, and 2004 was 13.4, 13.8, and 15.3°C, respectively, and the corresponding values for mean soil temperature were 11.6, 11.1, and 11.8°C, respectively.

Annual precipitation in 2002 was 1170 mm, of which snow accounted for 30% of the total. Total precipitation during May to August in 2002, 2003 and 2004 was 419, 311, and 363 mm, respectively. Soil volumetric water content was lowest in June, with values of 33.7% in 2002 and 30.1% in 2004, indicating that there was no severe drought throughout the year.

3.2. Fine-root biomass and necromass

Mean FRB at a surface soil depth of 60 cm was 891 g m⁻², ranging from 767 g m⁻² in October 2004 to 1,108 g m⁻² in June 2003, with no significant differences ($P > 0.05$) between sampling dates (Fig. 2, Table 1) or between years (data not shown). FRB, which was concentrated in the uppermost soil layer (0–15 cm depth) and accounted for 41–61% of the total biomass, decreased significantly between soil depths (Fig. 2, Table 1; $P < 0.001$). The amount of FRB finer than 0.5 mm in diameter was similar to that of roots 0.5–2 mm in diameter, and the proportion of roots thinner than 0.5 mm in the 0 – 15 cm soil layer was higher than in the other layers, with maximum and minimum values of 53 and 41% obtained in the 0–15 and 30–45 cm soil layers, respectively. The FRB of *Sasa* at each sampling date accounted for 59–88% of the total (trees plus *Sasa*) in each sampling date. The proportion of *Sasa* FRB was highest in the 15–30 cm soil layer, with maximum and minimum values of 78 and 61% obtained in the 15–30 and 45–60 cm soil layers, respectively.

Mean fine-root necromass was 76 g m⁻², ranging from 44 g m⁻² in May 2004 to 132 g m⁻² in June 2003 (Fig. 3, Table 1). There was no significant difference in fine-root necromass among sampling dates. The quantity of fine-root necromass was consistently less than FRB, with the biomass to necromass ratio

ranging from 8.4 to 20.1.

3.3. Root length density, production, mortality and turnover

In contrast to FRB, minirhizotron measurements revealed marked temporal variation in RLD (Fig. 4), which increased in the growing season. Measurements in 2003–2004, which we could observe through dormant season, revealed that RLD decreased during the dormant season. In addition, RLD in 2002 was lower than in 2003 and 2004. Although RLD could not be observed from August 2002 to May 2003, maximum RLD for 2002 was considered to have occurred in August 2002. Seasonal maximum RLD for 2003 and 2004 were observed in December and September, respectively. RLD_{max} of each year was used to calculate turnover. However, for the 15–30 and 30–45 cm soil layers in 2002, we used the values observed in May 2003 because of the slight increase in the RLD from August 2002 to May 2003. The extent of temporal variation was largest in the uppermost surface soil layer (0–15 cm), and decreased with increasing soil depth.

Length-based FRP rate was high in the growing season but low during the period from September to April (Fig. 5), and there was a significant difference between observation time and soil depth (Table 1). In 2002, FRP in August was significantly higher than in the other months, but it remained high from May through August of 2003 and 2004. The length-based production rate decreased in September and remained low during the dormant season until the next spring. The length-based FRM rate was high in July, but no clear temporal patterns or significant differences were observed among observation dates (Fig. 5, Table 1). FRP and FRM were high in surface soil and decreased with increasing soil depth (Fig.

5, Table 1).

ALRP in the surface soil layer (0–15 cm) was largest in 2002, with a significant difference observed between 2002 and 2004 (Table 2; $P < 0.05$). On the other hand, in the 30–45 cm soil layer, ALRP in 2003 was significantly higher than that in 2004. No significant difference was observed in ALRP among years in the 15–30 cm soil layer. ALRM did not differ significantly among years at any depth and ALRP was higher than ALRM for all years and depths (Table 2). The ratio of ALRP to ALRM increased with increasing soil depth, indicating that the mortality rate in particular decreased in deeper layers (Table 2). There was a significant positive relationship between ALRP and ALRM in each tube and in each soil layer (Fig. 6; $P < 0.0001$).

Turnover rates of both FRP and FRM were highest in 2002, with a significant difference ($P < 0.05$) observed in production turnover in the 0–15 cm layer between 2002 and 2004 (Table 3). In the case of using RLD_{mean} , significant differences ($P < 0.05$) were also observed in production turnover in layers deeper than 15 cm between 2002 and 2004; mean production turnover rates for the three years were 0.8, 0.4, and 0.5 yr^{-1} in the 0–15, 15–30, and 30–45 cm soil layers, respectively, and mortality turnover rates were 0.5, 0.08, and 0.03 yr^{-1} , respectively (Table 3). Production turnover was larger than mortality turnover for every year and depth.

3.4. Fine root production and above-ground NPP

Using the turnover rate calculated from RLD_{max} , mass-based FRP was estimated to be 1,287, 577, and 287 $g\ m^{-2}\ yr^{-1}$ in 2002, 2003, and 2004, respectively. Similarly, FRM estimated from RLD_{max} was 496, 273, and 180 $g\ m^{-2}\ yr^{-1}$ in 2002, 2003, and 2004, respectively. Using the turnover rate calculated from

RLD_{mean}, the corresponding FRP was estimated to be 846 and 273 g m⁻² yr⁻¹ in 2003 and 2004, respectively, and FRM from RLD_{mean} was estimated to be 373 and 164 g m⁻² yr⁻¹ in 2003 and 2004, respectively. During the three years, using the turnover calculated from RLD_{max}, mean FRP and FRM were 589 and 279 g m⁻² yr⁻¹, respectively, and the mean corresponding FRP and FRM calculated using RLD_{mean} were 726 and 342 g m⁻² yr⁻¹, respectively (Table 4).

Above-ground woody biomass of trees was 11,918 and coarse root biomass was 2,617 g m⁻²; the increments of above-ground woody biomass and coarse-root biomass were 72 and 16 g m⁻² yr⁻¹, respectively (Table 4). Stand density, mean DBH, and basal area were 470 trees ha⁻¹, 17.7 cm, and 17.5 m² ha⁻¹, respectively. Litterfall of trees was 267 g m⁻² yr⁻¹. Thus, above-ground NPP of trees was 339 g m⁻² yr⁻¹. On the other hand, the maximum height of *Sasa* culms was approximately 1.6 m, *Sasa* density was about 31 culms m⁻², and above-ground *Sasa* biomass was 1,509 g m⁻². Above-ground NPP of *Sasa*, that is, the biomass of culms and leaves that emerged during the growing season of the current year, was 689 g m⁻² yr⁻¹ (leaves, 230 g m⁻² yr⁻¹ and culms, 459 g m⁻² yr⁻¹, Table 4).

3.5. Relationships between fine-root dynamics and other factors

Length-based FRP rate in the 0–15 and 15–30 cm soil layers was significantly correlated with mean air and soil temperature at each observation interval (Table 5). No significant relationship between length-based FRP rate and precipitation was observed. There was a weak relationship between length-based FRP rate and volumetric soil water content ($r = 0.32$, $P = 0.19$) at each observation interval during the growing season in 2002 and 2004. No significant relationship was observed between

length-based FRP rate and *Sasa* PAI, except for the 30–45 cm layer. However, significant relationships were observed between length-based FRP rate and tree PAI in the 0–15 cm layer ($r = 0.60$, $P = 0.014$). A significant relationship was also observed between length-based FRP rate and increment of *Sasa* PAI during each observation interval for the 15–30 cm layer ($r = 0.57$, $P = 0.019$). The length-based FRM rate was not significantly correlated with any environmental factor, including soil or air temperature, precipitation, or volumetric soil water content ($P > 0.05$), while it showed a significant relationship with increment of *Sasa* PAI in the 0–15 cm layer ($r = 0.70$, $P = 0.003$).

4. Discussion

4.1. Seasonal variation in fine-root production and mortality with climatic factors

Although RLD exhibited seasonal variation and was highest in the growing season, no distinct temporal trend was observed in FRB (Figs. 2, 4). This seasonal pattern in RLD has also been observed in other studies using minirhizotrons (Hendrick and Pregitzer, 1993; Noguchi et al., 2005; Satomura et al., 2006). On the other hand, as in this study, FRB has been reported to exhibit relatively little, or no clear seasonal variation (Persson, 1978; Aber et al., 1985; Yuan and Chen, 2010), while other studies have recorded maximum biomass in autumn as a result of production during the growing period (McClaugherty et al., 1982; Brassard et al., 2009). It has been suggested that any spatial variation between sampling times due to destructive sampling during FRB measurements obscures temporal variation (Santantonio and Grace, 1987). It is also possible that the low sampling intensity employed in this study may have masked any

temporal variation in FRB. However, RLD, which was determined based on minirhizotron observations at the same locations used for those of FRB, exhibited a different temporal pattern. As a result, it is considered that RLD, rather than the FRB measured by sequential coring, would reveal the actual seasonal pattern of fine-root dynamics.

The root length-based production rate was high in the growing season, especially in mid- to late summer, and low in the dormant season (Fig. 5). Soil temperature was an important factor controlling FRP in this cool temperate forest (Table 5). This seasonal pattern of FRP is consistent with the observations of numerous studies that have been conducted in cool temperate and boreal forests in the absence of severe soil drought, and suggests that soil temperature is a controlling factor of fine-root growth (Tryon and Chapin, 1983; Burke and Raynal, 1994; Steele et al., 1997; Ruess et al., 1998; Tierney et al., 2003; Steinaker et al. 2010). Based on observations under controlled temperature conditions, Alvarez-Uria and Körner (2007) suggested that low soil temperature inhibited root growth in spring. However, in this study, the FRP rate was low in September and October despite still-favorable air and soil temperatures, indicating that the relationship between temperature and FRP rate may change between spring or early summer and late summer or autumn, as suggested by Tierney et al. (2003). Although new roots would be necessary to meet the demand for water and nutrients until midsummer, they would not be as necessary during the period before the dormant season, when the metabolic activity of the plants would be decreasing, as they would be during the middle period of growing season.

In contrast, as reported by Steinaker et al. (2010) in a boreal forest, the relationship between the FRP rate and precipitation or soil water content was weak in our study, indicating that soil moisture was not as important a factor as temperature at this moist site. The absence of a severe drought in late summer

would likely be associated with continuous FRP in mid- to late summer because the lowest volumetric soil water content at this site was 30%.

The FRP rate was also strongly related to air temperature, suggesting the importance of endogenous control via photosynthesis above ground, as air temperature would not control fine roots directly (Tierney et al. 2003). Joslin et al. (2001) reported that leaf phenology was also important in FRP; specifically, the increase in the supply of carbohydrates after leaf expansion in early summer facilitated FRP in a temperate forest in Tennessee in the USA. In cool temperate forests with dense understory vegetation in Japan, the influence of dense *Sasa*, which has more FRB than the surrounding trees, is considered to have a marked effect on the seasonal patterns of root production in these forests (Fukuzawa et al., 2007, 2010). The mean lifespan of *Sasa* leaves is 1.98 years (Yajima et al., 1997), and its new culms and leaves emerge most intensively in July. In this study, the FRP rate was more closely related to the increment in *Sasa* PAI than to *Sasa* PAI itself, while Fukuzawa et al. (2007) reported a significant relationship between *Sasa* PAI and FRP. This discrepancy in the relationship between *Sasa*-PAI and FRP in the two studies may arise from differences in observation period: the present results showed that FRP was low in autumn when *Sasa* PAI was high, which weakened the relationship, while Fukuzawa et al. (2007) related the PAI to FRP using data obtained up to late summer, during the increasing phase for both parameters. These results suggest that the increment in *Sasa* PAI may be a better indicator of FRP than *Sasa* PAI itself, because the increment in *Sasa* PAI reflects leaf production, although both the cumulative effect of emergence (production) and fall (mortality) of *Sasa* leaves are included in *Sasa* PAI (Fig. 1). On the other hand, the present study also showed that FRP was significantly related to tree PAI, which declined in autumn, in the topmost 15 cm soil layer. These results

imply that the timing of FRP is influenced by leaf phenology, as suggested by Joslin et al. (2001). Interestingly, Steinaker et al. (2010) proposed that root production lagged behind shoot production by 8 weeks in woody plants and 2–4 weeks in grasses. Thus, a high FRP rate in midsummer (July and August) is considered likely, in terms of tree roots and understory *Sasa* roots, in response to both environmental and endogenous factors.

There was no significant relationship between FRM and any environmental factor, including temperature, precipitation, or soil moisture, indicating that FRM was less affected by environmental factors. FRM tended to be high in July, but seasonal variation in FRM rate was not as clear as seasonal variation in FRP. In northern forests, FRM was reported to be highest in late summer to autumn (Tierney et al., 2003; Tingey et al., 2005; Brassard et al. 2009), after the peak period of growth, resulting in an inverse relationship between growth and mortality within a year. It has been suggested that defoliation promotes FRM in citrus and apple trees due to carbon limitation (Eissenstat and Duncan, 1992; Eissenstat and Yanai, 1997). In our study, carbon limitation in *Sasa* due to expansion of new leaves in midsummer may have stimulated FRM.

4.2. Interannual variation in fine-root production and mortality

Interannual variation was observed in ALRP, and it was significantly higher in 2002 than in 2004 in the surface 15 cm soil layer (Table 2). In 2003, ALRP was significantly higher than in 2004 in the 30–45 cm soil layer, although the value was quite low compared to the upper two layers. Several previous studies suggested that higher FRP in the first year of observation occurred due to compensation for trees having

fewer roots after tube installation, or due to increased nitrogen availability due to the promotion of mineralization immediately after tube installation (Joslin and Wolfe, 1999). However, in this study, since RLD observations were initiated in the year following tube installation, the disturbance effect would be minimized and would not be the main cause of the high fine-root productivity observed in 2002.

Ruess et al. (1998) suggested that FRP is high in warmer and drier years in boreal forests. Joslin et al. (2000) reported higher FRP and FRM at a wet experimental site. In our study, the mean soil temperature during the growing season (May to August) of 2002 was near the average of the observed values, while the mean air temperature was the lowest; however, the mean air temperature during the spring (March and April) was 1.2°C higher than the mean value for 2002–2004. Higher air temperatures in spring caused leaf expansion to occur earlier and promoted net ecosystem production in the early growing period of 2002 on a broad scale in East Asia (Saigusa et al., 2008). Since FRP is considered to be positively correlated with above-ground production (Vogt et al., 1986), it is probable that this higher net ecosystem production promoted FRP in 2002, although no data for production at this site is available.

ALRM was lower than ALRP in each year by up to 60% (Table 2 and Fig. 6). This imbalance caused an increase in RLD, especially during 2002 to 2003 (Fig. 4), although the maximum value for RLD in 2003 and 2004 was similar. Conflicting results have been obtained regarding the relationship between production and mortality rates in previous studies, for example, similar production and mortality in a temperate conifer plantation (Noguchi et al., 2005), and lower mortality in a cool temperate hardwood forest and shortgrass steppe (Hendrick and Pregitzer, 1993; Gill et al., 2002). Gill et al. (2002) attributed this imbalance between production and mortality to an underestimation of mortality due to the existence of only young roots after tube installation. Production due to tube installation was also considered, as

described above. In our study, the ratio of production to mortality (P/M) did not change much over time in the surface 15 cm layer, implying that tube installation did not affect FRP or FRM; however, P/M was high in the 15–30 cm layer in 2002 (Table 2) owing to the low mortality in that year. Since production was higher than mortality in each year, the definition used for mortality may have been a factor in the imbalance (Tingey et al., 2000; Satomura et al., 2007). We defined FRM as indicating roots that disappeared; consequently, this definition of mortality may have led to mortalities always being lower than production.

4.3. Estimation of turnover rate in fine-roots and mass-based fine root production

Turnover rates of FRP ranged between 0.2 and 2.7 yr⁻¹ and mortality ranged between 0 and 1.6 yr⁻¹ (Table 3); both production and mortality turnover decreased with increasing soil depth, indicating a shorter root lifespan and rapid decomposition in the surface soil layer. The present study revealed that the proportion of roots thinner than 0.5 mm in FRB was highest in the topmost soil layer and it decreased with increasing soil depths. However, Fukuzawa et al. (2007) quantified the proportion of the corresponding diameter class in the image analysis of minirhizotron and showed that roots thinner than 0.5 mm accounted for 80% in the topmost soil layer (0 – 15 cm), but only for 16% in 30 – 45 cm layer, therefore, the diameter of the observed roots may also be an important factor affecting the turnover of fine roots (Joslin et al., 2006). High interannual variation in production and mortality turnover might have been caused by high variation in FRP and FRM, and in RLD, which was influenced by climate each year as described above. Therefore, here we discuss the range or the mean value of the turnover

rather than the interannual variation of turnover.

The uppermost value of 1.7 yr^{-1} obtained in our study was near the higher end of those described in Gill and Jackson (2000) (0.1 and $\text{ca. } 2.6 \text{ yr}^{-1}$), and within the range of $1.4\text{--}3.3 \text{ yr}^{-1}$ as reported by Steele et al. (1997). In contrast, the average production turnover values in the surface 15 cm soil layer that we observed, i.e. 0.8 or 1.0 yr^{-1} , were consistent with numerous previous studies: $0.7\text{--}0.8 \text{ yr}^{-1}$ ($0\text{--}10 \text{ cm}$; Burton et al., 2000), $1.0\text{--}1.1 \text{ yr}^{-1}$ ($0\text{--}30 \text{ cm}$; Hendrick and Pregitzer, 1993) in temperate or cool temperate forests in the USA, $0.9\text{--}1.2 \text{ yr}^{-1}$ in a cool temperate deciduous forest in Japan ($0\text{--}20 \text{ cm}$, Satomura et al., 2006), $0.9\text{--}1.1 \text{ yr}^{-1}$ in European beech and spruce forests (Brunner et al., 2013), and 0.9 yr^{-1} , which is the average turnover of minirhizotron studies conducted around the world (Finér et al., 2011).

Reports on FRM turnover rate are more limited than on production. Mean turnover of mortality in our study (i.e. 0.5 or 0.7 yr^{-1} calculated using RLD_{max} or RLD_{mean} , respectively, in the surface 15 cm layer, Table 3) was a little lower than the $\text{ca. } 0.5\text{--}1.1 \text{ yr}^{-1}$ for every 5 cm in a $0\text{--}15 \text{ cm}$ layer in a cool temperate forest reported by Satomura et al. (2006), but a little higher than the value of $0.4\text{--}0.5 \text{ yr}^{-1}$ in a $0\text{--}10 \text{ cm}$ layer in a northern cool temperate hardwood forest reported by Burton et al. (2000), and higher than the $\text{ca. } 0.3 \text{ yr}^{-1}$ in the $0\text{--}20 \text{ cm}$ layer of a shortgrass steppe reported by Gill et al. (2002).

In our study, the mean FRP calculated from RLD_{max} and RLD_{mean} (589 and $726 \text{ g m}^{-2} \text{ yr}^{-1}$, respectively) over three years was higher than that of other studies using minirhizotrons. For example, FRP was $58\text{--}235 \text{ g m}^{-2} \text{ yr}^{-1}$ in jack pine, aspen and black spruce forests in Canada (Steele et al., 1997) and $320 \text{ g m}^{-2} \text{ yr}^{-1}$ in a cedar plantation in central Japan (Noguchi et al., 2005). In contrast, our data were more consistent with those of Hendrick and Pregitzer (1993) who obtained values in the range $730\text{--}808 \text{ g m}^{-2} \text{ yr}^{-1}$ in cool temperate forests in Michigan, USA, especially when we calculated FRP from RLD_{mean} .

Our estimates of FRP were also higher than the average values of 311 and 428 g m⁻² yr⁻¹ obtained for boreal and temperate forests, respectively, or the average value of 420 g m⁻² yr⁻¹ obtained using a minirhizotron (Finér et al. 2011), or the 201 g m⁻² yr⁻¹ average obtained for broad-leaved species in boreal forests (Yuan and Chen 2010). Thus, the FRP recorded in the present study is considered to be very high, even on global scale. Finér et al. (2011) showed that the factor contributing the most to FRP was FRB, as opposed to temperature or precipitation, implying that the observed variation in FRB was larger than that in fine-root turnover. At our experimental site, fine-root turnover was close to the global average value, thus, the high FRP in this study might have been attributed to the high FRB.

However, the ratio of FRP (NPP_{fr}) to total NPP (NPP_{fr}/NPP_{total}, %) would be a more useful indicator for understanding the role of fine roots in forest productivity, because NPP_{fr} and above-ground NPP both change between sites, although few studies have measured both fine-root and above-ground production. In our study, NPP_{fr}/NPP_{total} was 36 or 41% (Table 4) depending on whether RLD_{max} and RLD_{mean} were used to calculate turnover, respectively. These findings indicate that methods for calculating turnover rate did not markedly affect the inferred contribution of FRP to total NPP, and that a significant portion of forest net primary production was allocated to below-ground root systems. Vogt et al. (1996) reported that below-ground production accounted for 3–54 % of forest NPP, which means that the value in our study was in the uppermost range of those in Vogt’s review. Using a minirhizotron, Hendrick and Pregitzer (1993) reported that NPP_{fr}/NPP_{total} was 58–60% in a cool temperate forest in Michigan, USA, but Lopez et al. (2001) reported that NPP_{fr}/NPP_{total} was only 11% in a Mediterranean oak forest in Spain. On the other hand, Aber et al. (1985) reported that NPP_{fr}/NPP_{total} was 24–41% or 4–35% in broad-leaved forests and 18–30% or 10–38% in conifer forests, in the northern USA using a nitrogen budget method

and a sequential coring (max-min) method, respectively. Tateno et al. (2004) reported that NPP_{fr}/NPP_{total} was 16–56% in a cool temperate forest in western Japan using an ingrowth-core method. The values in our study were similar to the upper ranges reported by these studies and confirmed the significance of FRP in forest NPP in our study area.

One of the imitations of our study could be the low spatial sampling intensity and the location of observations; i.e. we only investigated FRB and root dynamics beneath the canopy of the dominant oak trees using three replications. Consequently, our results can only be applied to the narrow area surrounding dominant oak trees. Further efforts are therefore required to extend the application of the methods described here to a larger stand-scale and to consider a mixture of species, although this may be complicated by the marked variation that would expected from such an analysis. For example, the FRB of *Sasa* below canopy gaps was twice that beneath the canopy (Fukuzawa et al., unpublished data). Despite being unable to separately evaluate the fine-root turnover or FRP of *Sasa* and the trees, we expect that *Sasa* contributes considerably to the FRP in this stand, particularly since *Sasa* accounted for considerable proportion of FRB and above-ground NPP, and because *Sasa* PAI was larger than that of the trees. Relatively few studies have clarified the importance of understory vegetation (e.g. shrubs and herbaceous species) on forest structure and biogeochemical cycling in boreal or temperate forests (Yarie, 1980; Nilsson and Wardle, 2005; Kolari and Pumpanen, 2006; Koike et al., 2010; Moore et al., 2007; Cavard et al. 2011; Finér et al., 2011). Makkonen and Helmisaari (2001) reported that the FRB of understory vegetation was equal to or larger than that of overstory trees in Finnish boreal Scots pine forests. Finér et al. (2011) proposed that FRP could be clarified more precisely if tree roots were separated from the roots of the understory vegetation. Consequently, evaluating the fine-root turnover of

tree and *Sasa* roots will be necessary to precisely estimate fine-root dynamics in this stand in the future. On the other hand, this study has illustrated the important contribution that understory *Sasa*, which is distributed throughout East Asia, makes to biomass and productivity both below- and above-ground. Consequently, the contribution of understory vegetation to C cycling should be considered on a global scale. Indeed, we have shown that FRP is a major component of NPP in this stand of cool temperate forest.

5. Conclusions

We clarified the probable range of fine-root turnover in a cool temperate forest over a three-year. We estimated that the mean fine-root turnover was 0.8 and 1.0 yr⁻¹ in surface 15 cm soil layer and that mass-based FRP was 589 and 726 g m⁻² yr⁻¹ using two different calculation methods. Using each of these methods, the contribution of FRP to total NPP was estimated to be 36 or 41%, depending on the method used, indicating that significant portion of assimilated carbon was allocated to below-ground root systems in a cool temperate forests stand covered by dense a understory of *Sasa*.

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Figure captions

Fig. 1 Monthly average air and soil temperatures and the increments in plant area indices (PAI) of *Sasa* and trees from 2002 to 2004.

Fig. 2 Temporal variation in fine-root biomass classified by (a) soil depth layer, (b) root diameter, and (c) plant type. Vertical bars represent ± 1 S.E. for total and each component, respectively (n=3).

Fig. 3 Temporal variation in fine-root necromass. Vertical bars represent ± 1 S.E. for total (n=3).

Fig. 4 Temporal variation in root length density (RLD) of fine roots in three soil layers for three years. Vertical bars represent ± 1 S.E. (n=3).

Fig. 5 Fine-root production and mortality rate for three years at depths of (a) 0–15 cm, (b) 15–30 cm, and (c) 30–45 cm. Vertical bars represent ± 1 S.E. (n=3).

Fig. 6 Relationship between annual length-based root production (ALRP) and annual length-based root mortality (ALRM) in each tube and soil layer.

Table 1. *F* values of a repeated measures ANOVA of the effects of depth, time of the observation (season), and their interaction on fine-root biomass, necromass, and length-based production and mortality rates for each year.

	Year	Depth	Time	Depth×Time
Biomass	2003	27 ***	1.07	0.79
	2004	38.6 ***	0.28	0.92
Necromass	2003	1.44	1.10	0.97
	2004	11.3 **	0.65	0.34
Production	2002	29.3 ***	7.64 *	2.54
	2003	7.86 *	7.44 *	1.14
	2004	24.3 **	5.95 *	2.66
Mortality	2002	28.5 ***	0.39	0.39
	2003	18.8 **	2.29	3.23
	2004	2.94	1.06	0.83

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Fukuzawa et al. Table 1

Table 2. Changes in annual length-based root production (ALRP), annual length-based root mortality (ALRM), and the ratio of production to mortality (P/M) over time.

Soil depth (cm)	Year	ALRP (mm cm ⁻² yr ⁻¹)	ALRM (mm cm ⁻² yr ⁻¹)	P/M
0-15	2002	13.8 (1.94) ^a	7.96 (2.36) ^a	1.91
	2003	10.8 (1.82) ^{ab}	7.19 (1.52) ^a	1.58
	2004	5.85 (0.87) ^b	3.70 (1.56) ^a	2.27
15-30	2002	3.86 (1.39) ^a	0.21 (0.14) ^a	25.3
	2003	5.59 (0.72) ^a	1.19 (0.57) ^a	7.16
	2004	1.68 (0.72) ^a	0.88 (0.57) ^a	12.2
30-45	2002	1.11 (0.56) ^{ab}	0 ^a	-
	2003	2.44 (0.43) ^a	0.02 (0.02) ^a	34.3
	2004	0.57 (0.14) ^b	0.27 (0.26) ^a	10.2

Mean values are shown with +1 SE in parentheses (n=3). Different superscript letters indicate significant difference between years at each soil depth.

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Table 3. Mean fine-root turnover, or ratio of the mean annual length-based root production (ALRP) or mean annual length-based root mortality (ALRM) to the mean root length density in different years of the study.

Depth (cm)	Year	Turnover (yr ⁻¹)							
		Production				Mortality			
		ALRP/RLD _{max}		ALRP/RLD _{mean}		ALRM/RLD _{max}		ALRM/RLD _{mean}	
0-15	2002	1.65 (0.33)	^a	2.65 (0.64)	^a	0.95 (0.27)	^a	1.57 (0.54)	^a
	2003	0.79 (0.05)	^{ab}	1.00 (0.02)	^{ab}	0.53 (0.08)	^a	0.67 (0.11)	^a
	2004	0.43 (0.03)	^b	0.44 (0.01)	^b	0.30 (0.15)	^a	0.30 (0.13)	^a
	3 years	0.84 (0.05)		1.04 (0.11)		0.53 (0.08)		0.66 (0.13)	
15-30	2002	0.73 (0.14)	^a	1.66 (0.80)	^a	0.03 (0.03)	^a	0.05 (0.04)	^a
	2003	0.56 (0.15)	^a	0.72 (0.26)	^{ab}	0.10 (0.03)	^a	0.12 (0.04)	^a
	2004	0.16 (0.06)	^a	0.17 (0.06)	^b	0.09 (0.08)	^a	0.09 (0.08)	^a
	3 years	0.42 (0.08)		0.52 (0.12)		0.08 (0.03)		0.10 (0.03)	
30-45	2002	0.81 (0.15)	^a	2.76 (1.23)	^a	0	^a	0	^a
	2003	0.69 (0.15)	^a	1.01 (0.28)	^{ab}	0.01 (0.01)	^a	0.01 (0.01)	^a
	2004	0.19 (0.10)	^a	0.20 (0.11)	^b	0.05 (0.05)	^a	0.05 (0.05)	^a
	3 years	0.49 (0.09)		0.62 (0.10)		0.03 (0.02)		0.03 (0.02)	

Values are means +1 SE in parentheses (n=3). Results of two calculations using root length density (RLD_{max} or RLD_{mean}) are shown. Different superscript letters denote a significant difference among years at each soil depth.

Table 4. Estimated forest net primary production (NPP) showing each component (above-ground NPP for each species and parts, and coarse and fine-root production).

Parts	NPP (g m ⁻² yr ⁻¹)
<i>Above-ground</i>	
Tree litterfall	267 (75)
Woody biomass increment	72 (19)
Above-ground tree total	339
<i>Sasa</i> leaves	230 (37)
<i>Sasa</i> culms	459 (105)
Above-ground <i>Sasa</i> total	689
<i>Below-ground</i>	
Woody coarse root increment	16 (4)
Fine root production (NPP _{fr}) ^b	589 (107), 726 (132)
Total	1632, 1769
NPP _{fr} /NPP _{total} (%)	36, 41

Values are means +1 SD in parentheses.

^an=3 for above-ground woody and woody coarse-root biomass increments, n=4 for above-ground *Sasa* NPP, n=6 for NPP_{fr}, and n=9 for tree litterfall.

^bNPP_{fr} calculated from RLD_{max} are shown, followed by that calculated from RLD_{mean}.

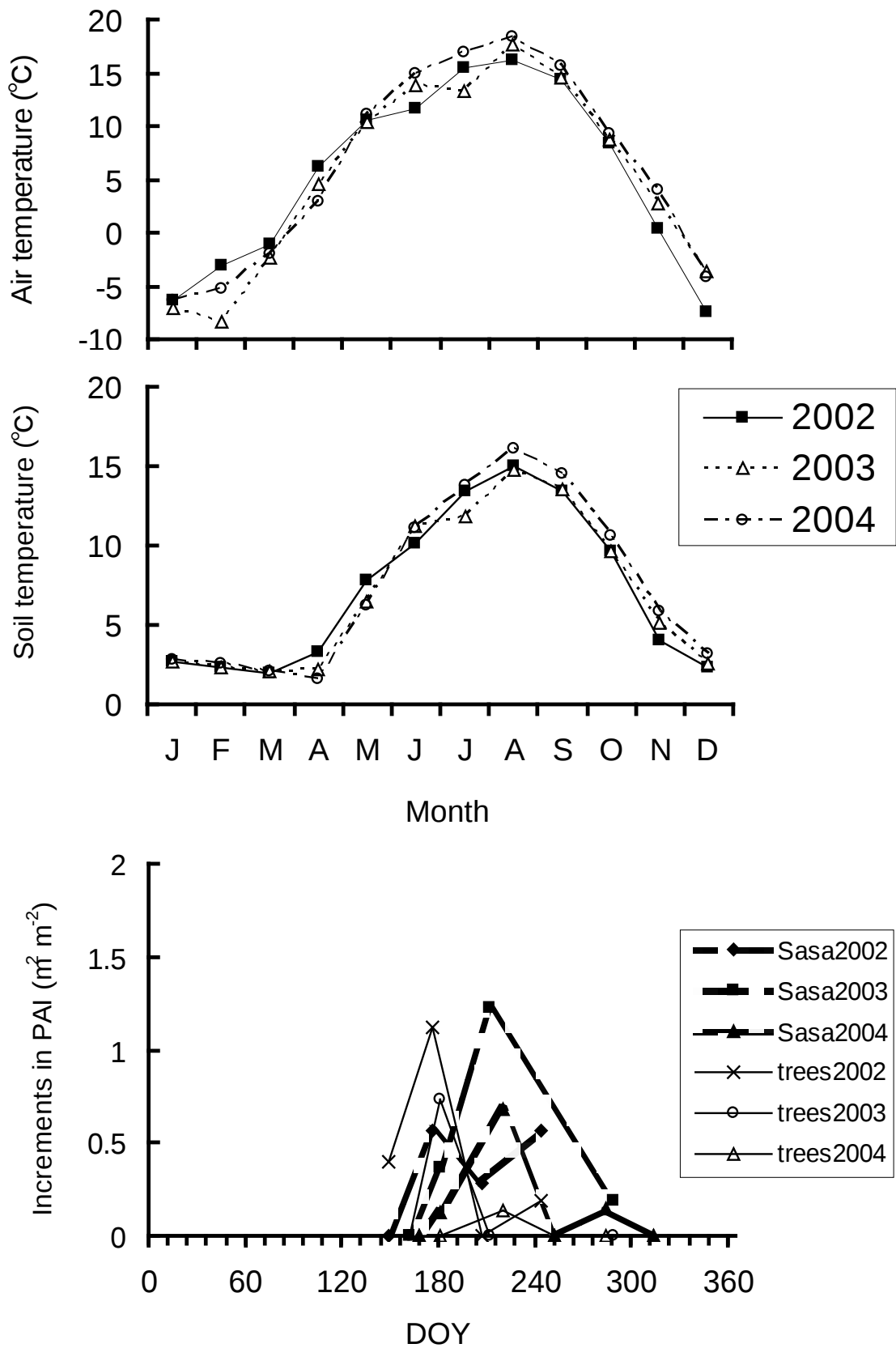
Table 5. Regression analysis of fine root production (FRP), fine root mortality (FRM), and environmental and endogenous factors.

Depth (cm)	Regression equation	N	Adj. R ²	P value
Fine root production (mm cm ⁻² d ⁻¹)				
0 - 15	Ln(FRP) = 0.107(ST) - 4.51	18	0.24	*
	Ln(FRP) = 0.0921(AT) - 4.45	18	0.42	**
	Ln(FRP) = 0.789(treePAI)-4.845	14	0.36	*
15 - 30	Ln(FRP) = 0.260(ST) - 7.50	18	0.50	***
	Ln(FRP) = 0.143(AT) - 6.53	18	0.30	*
	Ln(FRP) = 2.39(Δ SasaPAI) - 5.30	14	0.33	*
30 - 45	Ln(FRP)=5.69(SasaPAI) - 27.7	14	0.65	***
Fine root mortality (mm cm ⁻² d ⁻¹)				
0 - 15	Ln(FRM) = 1.17(Δ SasaPAI)-4.32	14	0.50	**

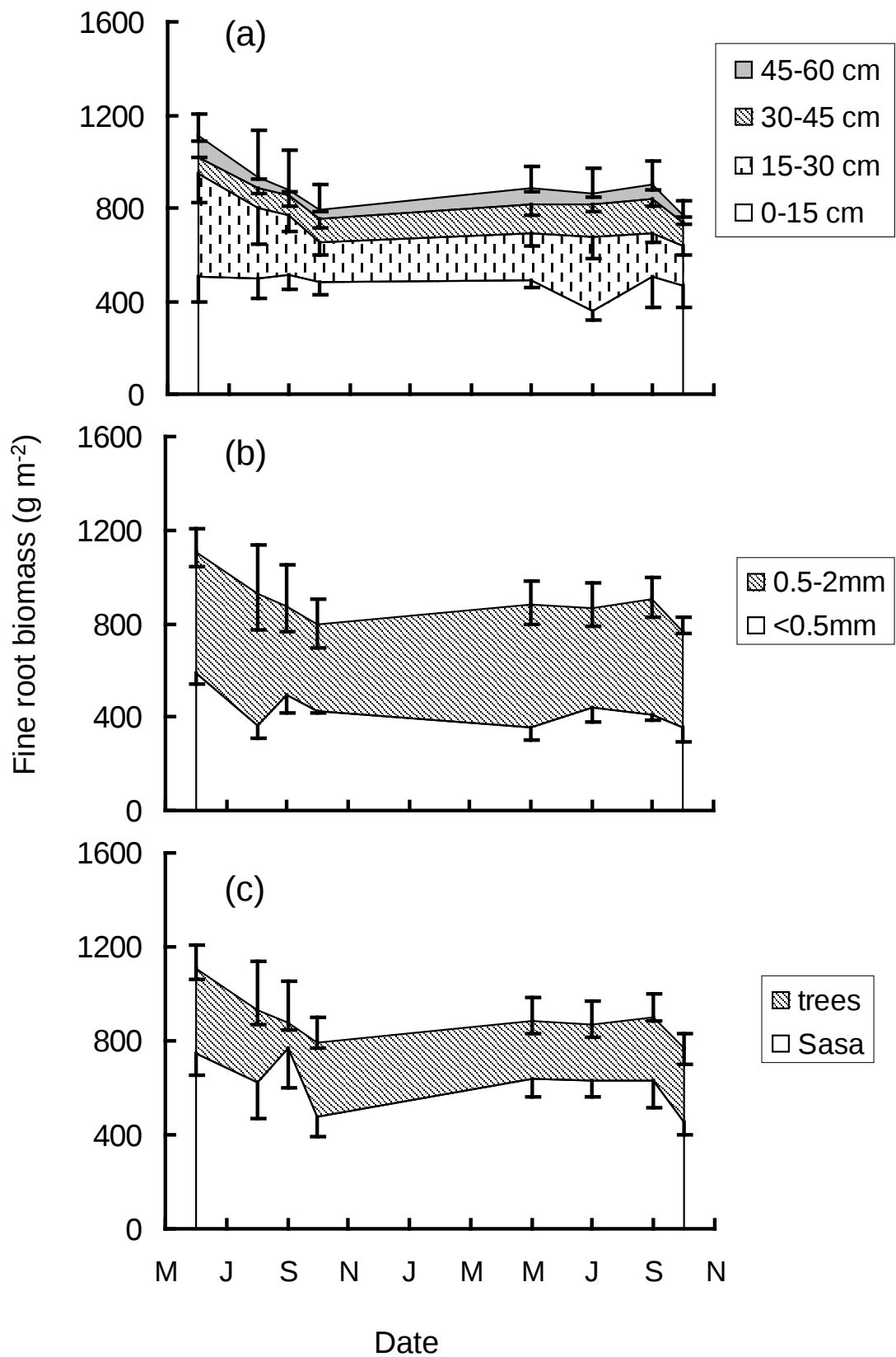
N: Number of observation for each regression.

ST: mean soil temperature, AT: mean air temperature, Δ Sasa PAI: increment in *Sasa* PAI. FRP and FRM were log-transformed. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

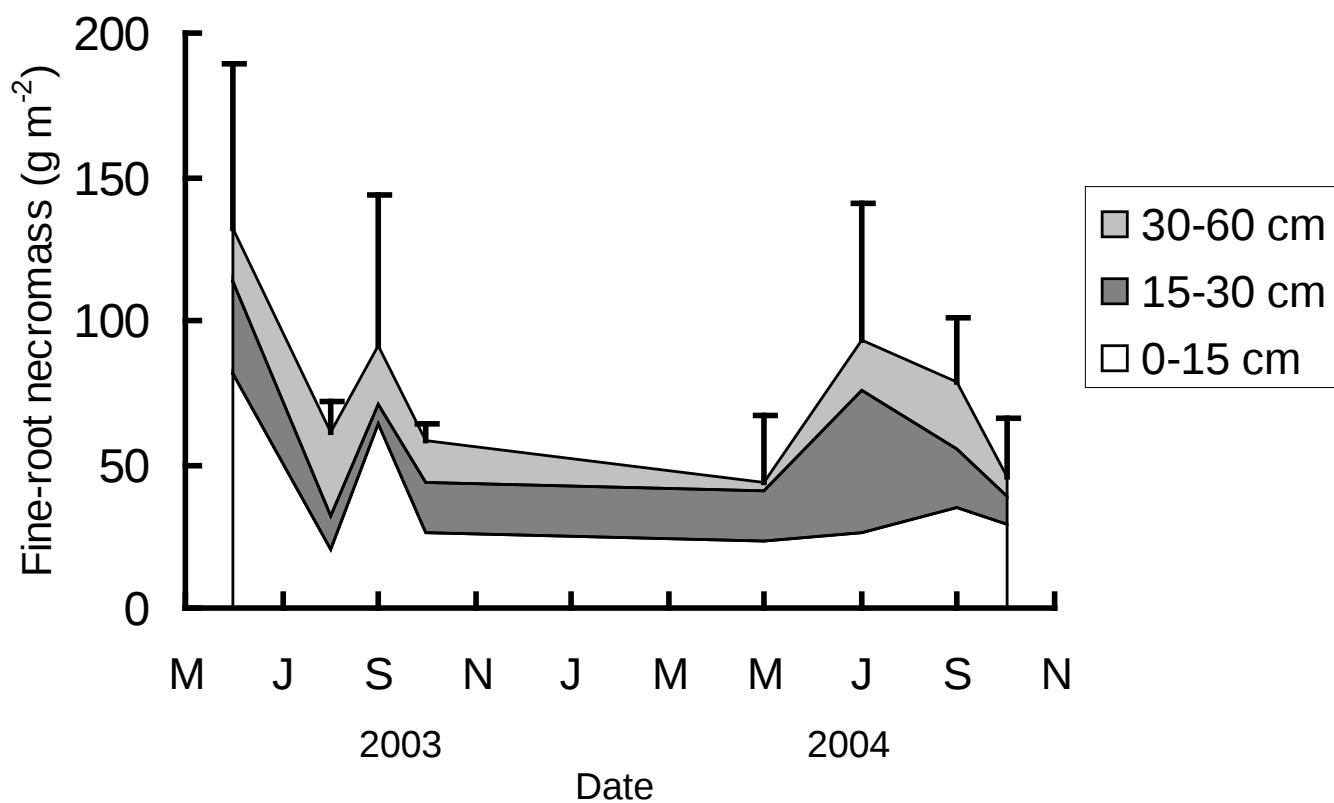
Fukuzawa et al. Table 5



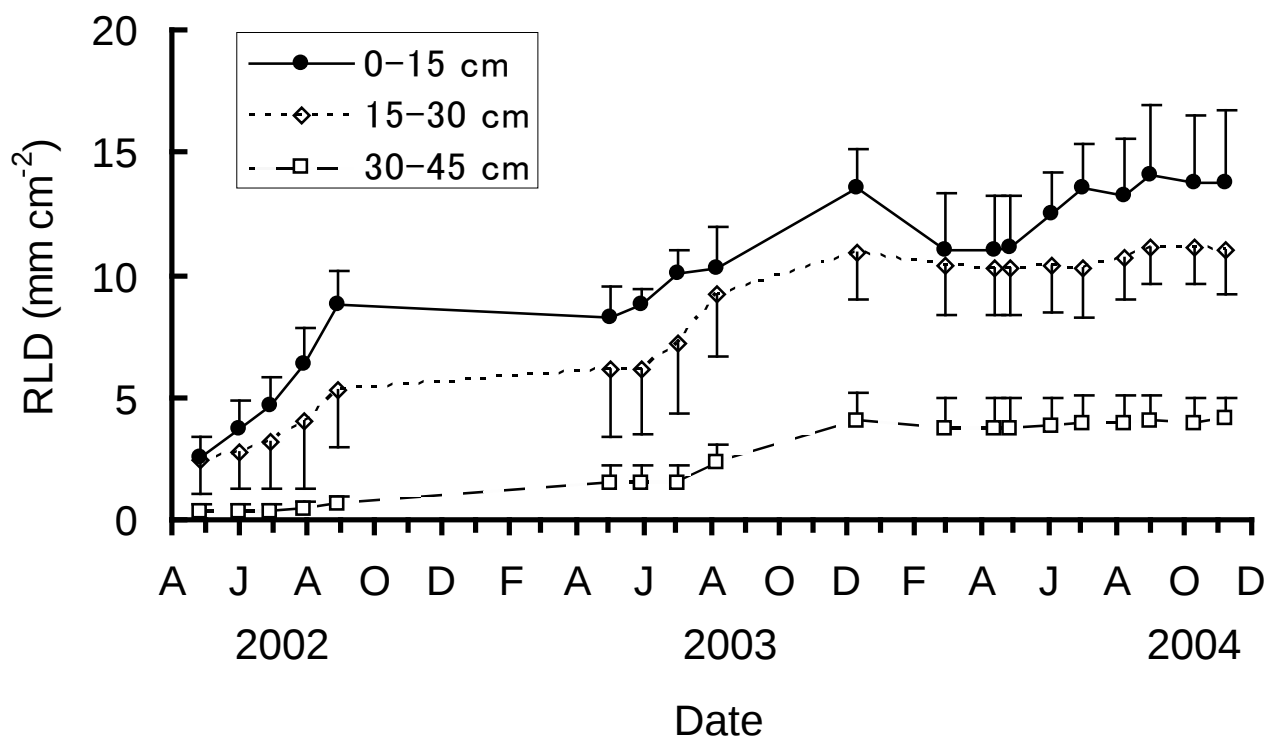
Fukuzawa et al. Fig. 1



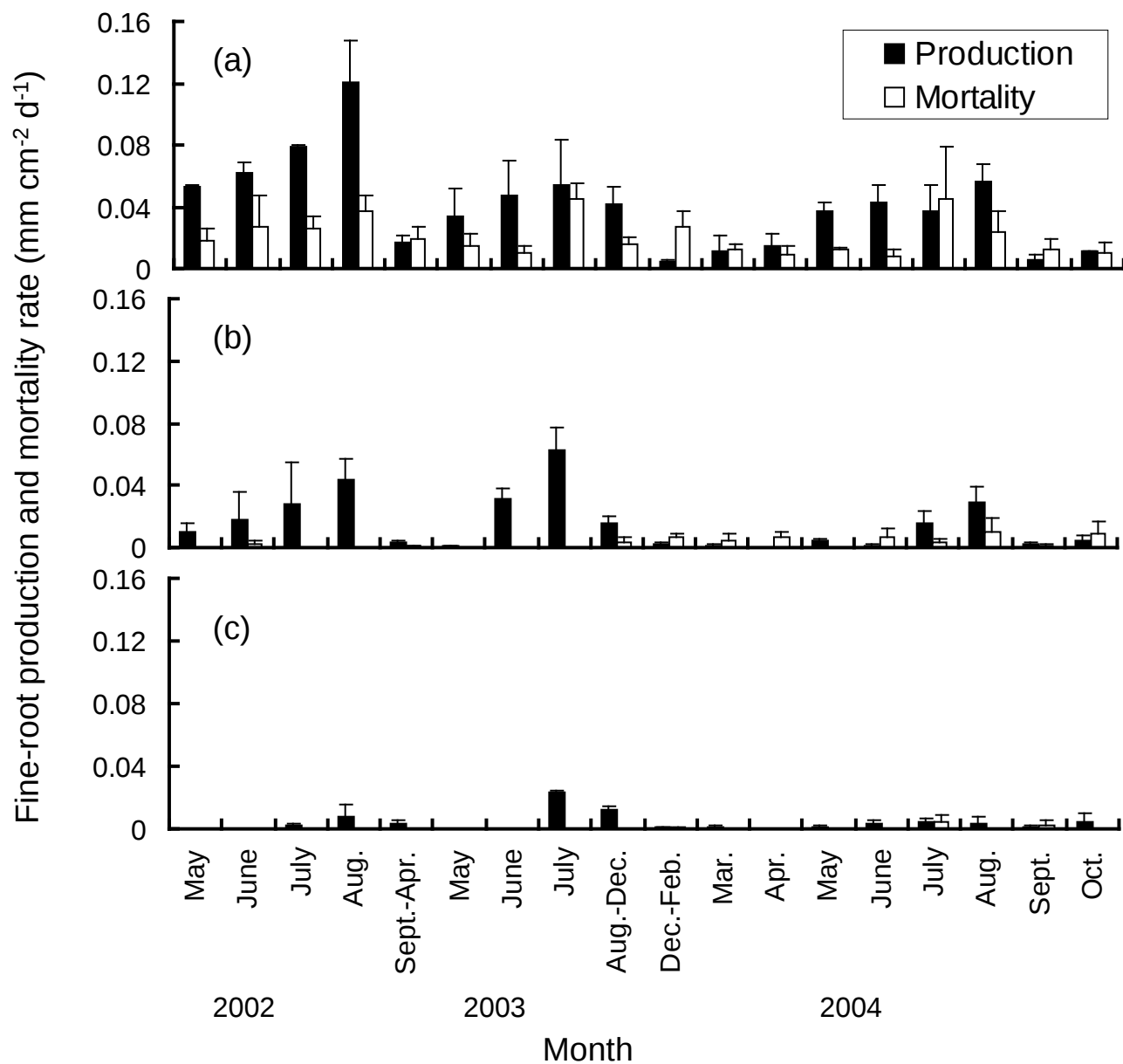
Fukuzawa et al. Fig. 2



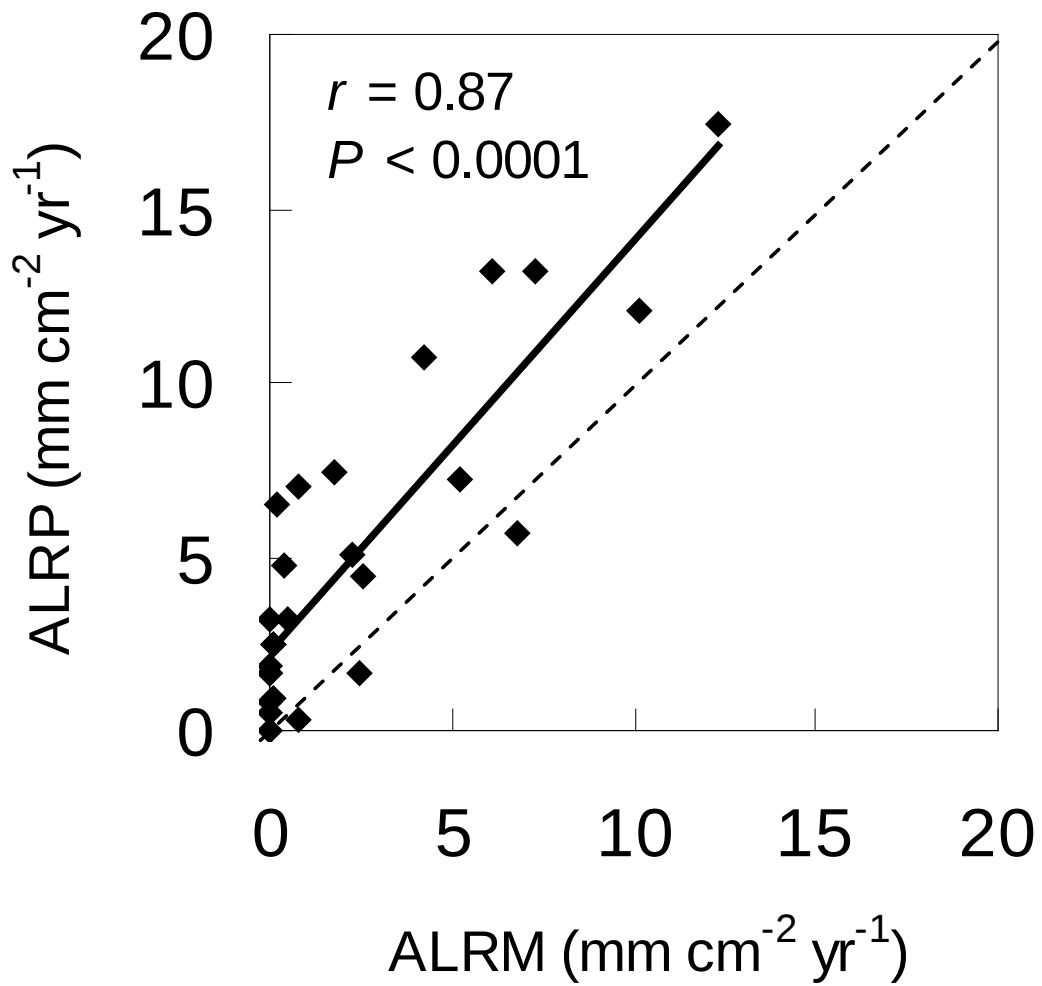
Fukuzawa et al. Fig. 3



Fukuzawa et al. Fig. 4



Fukuzawa et al. Fig. 5



Fukuzawa et al. Fig. 6