



Seasonal patterns of fine root dynamics and their contribution to net primary production in hinoki cypress (*Chamaecyparis obtusa*) and konara oak (*Quercus serrata*) forests

Ji Young An^{1,2,3} · Akira Osawa^{1,4}

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Abstract

Key message Fine root and litterfall are major contributor of NPP and fine root production may reflect forest productivity in a warm-temperate forest in Japan.

Abstract Forest ecosystems play an important role as the major carbon sink on land, with fine root dynamics and litterfall representing major carbon fluxes. The objectives of this research were to estimate NPP including annual fine root production values, to investigate fine root dynamics and the relationships between above- and belowground organs in konara oak (*Quercus serrata*) and hinoki cypress (*Chamaecyparis obtusa*) forests. Litterfall was collected seasonally for 1 year from June 2013. The ingrowth core method and the sequential soil core method were applied with a root litterbag experiment to estimate fine root (< 2 mm) production (FRP), mortality (FRM), and decomposition (FRD) for 1 year (from 2013 to 2014), using the continuous inflow estimate method and the simplified decision matrix. The total NPP ranged from 8.2 to 13.9 (t ha⁻¹ yr⁻¹), and the sum of aboveground litterfall and FRP accounted for 60% of the total NPP on average, confirming the significance of above- and belowground litter for the forest NPP as a source of detritus for the decomposer system. In hinoki cypress stand, fine root biomass peaked in the end of winter while fine root necromass showed the highest peak in late summer. In konara oak stand, only very fine root (< 0.05 mm) biomass and necromass demonstrated significant seasonal patterns. The seasonal patterns of fine root production did not differ between forest types and root diameter classes. We found a possible relationship between above- and belowground production and fine root production tended to be high in productive forests. This study improves our understanding of different patterns of carbon dynamics between temperate broadleaved and coniferous forest ecosystems.

Keywords Fine root biomass · Fine root necromass · Fine root production · Ingrowth core method · Sequential soil core method · Continuous inflow estimate method

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✉ Ji Young An
ajy2656@cnu.ac.kr

- ¹ Division of Forest and Biomaterials Science, Graduate School of Agriculture, Kyoto University, Kyoto 606-8502, Japan
- ² Institute of Agricultural Science, Chungnam National University, 99 Daehak-ro, Yuseong-gu, Daejeon 34134, Republic of Korea
- ³ Department of Environment and Forest Resources, College of Agriculture and Life Sciences, Chungnam National University, Daejeon 34134, Republic of Korea
- ⁴ Department of Natural Resources, Graduate School of Global Environmental Studies, Kyoto University, Kyoto 606-8502, Japan

Introduction

Understanding patterns of carbon dynamics in terrestrial forest ecosystems is important in the matter of climate change, because carbon fluxes between forest ecosystems and the atmosphere are closely related to changing concentration of carbon dioxide in the atmosphere (Dixon et al. 1994; Fang et al. 2014; Xu et al. 2014). The amount of carbon fixed by forests is indicated by an important index describing carbon budget of ecosystems, which is called net primary production (NPP). NPP can be used to evaluate the processes of carbon cycling in forest ecosystems (Luo et al. 2002). In most studies on forest productivity such as estimating NPP, belowground fine root (traditionally defined for roots with diameter of less than 2 mm) production has been ignored because of difficulty in its estimation; however, it

may account for up to 70% of total NPP (Keyes and Grier 1981; Santantonio 1989; Jackson et al. 1997; Gill and Jackson 2000; Janssens et al. 2002; McCormack et al. 2015). Moreover, variations in belowground fine root productivity have not been fully quantified across forest types while aboveground productivity has been widely compared along with an understanding of responses to changing environmental conditions (Gower et al. 2001; Xiao et al. 2003; Girardin and Malhi 2010; Yuan and Chen 2010a, b).

Fine roots primarily have an important role of resource acquisition such as soil nutrient and water (Bardgett et al. 2014). Moreover, fine roots provide organic matter into a soil as a plant litter with rapid turnover rate (Ruess et al. 2003; Yuan and Chen 2010a, b; McCormack et al. 2013; Leppälampi-Kujansuu et al. 2014), and thus influence soil biogeochemical cycles (Sun et al. 2013; Vesterdal et al. 2013). Fine roots show seasonal patterns of production similar to aboveground leaf phenology, seasonal patterns of growth and senescence. It is critical to identify temporal and spatial dynamics of fine roots for understanding how plants respond to changing environment and evaluating productivity of ecosystems. Despite the recognized important role of fine roots and increasing researches on root dynamics, patterns and amount of fine root production have not been fully identified yet, resulting in highly simplified descriptions of belowground processes in models (Ostle et al. 2009; Iversen 2010). McCormack et al. (2014) reported that there was wide variation in the timing of root production among 12 temperate tree species, with some species showing a single root flush in early summer and other species presenting either a uniform pattern or multiple peaks of root production. Also, large inter-annual differences of root production were found even within species. Similarly, we can assume that seasonal patterns of fine root production vary between forest types because of internal (e.g., genotype of plant species and species composition of forests) and external (e.g., climatic conditions, soil properties, and nutrient availability) factors (Steele et al. 1997; Pregitzer et al. 2000; Tierney et al. 2003; Majdi et al. 2005; Brassard et al. 2009).

While fine root production constitutes a large proportion of annual NPP, only a few studies reported on both below- and aboveground production simultaneously or the relationship between compartments of NPP (Helmisaari et al. 2002). Understanding the relationships between above- and belowground production patterns is also important for improving our knowledge about forest production processes (Zak and Pregitzer 1998; Trumbore and Gaudinski 2003; Litton et al. 2007), because belowground fine root dynamics are closely related with aboveground physiological processes and production (Satomura et al. 2006). Although several studies reported the positive relationship between fine root production and aboveground production/or NPP (Nadelhoffer et al. 1985; O'Grady et al. 2006; Van Do et al. 2015a; Do

et al. 2015b), there is still no general consensus about this relationship in forests.

Fine root production and turnover rates vary considerably depending on many endogenous and exogenous factors such as forest type, soil properties, and climatic conditions (Nadelhoffer and Raich 1992; Eissenstat and Yanai 1997). The estimates of fine root production and turnover also depend on measurement and calculation methods, even though several methods have been developed and used to estimate fine root production, such as the sequential soil core (Persson 1980; Ostonen et al. 2005), ingrowth core (Finér et al. 1997; Ostonen et al. 2005) minirhizotron (Hendrick and Pregitzer 1996; Majdi 1996), nitrogen budget (Nadelhoffer et al. 1985), and carbon balance (Ågren et al. 1980) methods. Several calculation methods for fine root dynamics are also available, such as decision matrix (Fairley and Alexander 1985; Hertel et al. 2009), maximum-minimum (Keyes and Grier 1981; Hertel and Leuschner 2002) the compartment flow model (Santantonio and Grace 1987), and others. The decision matrix has been widely used for sequential soil coring and ingrowth coring. However, the decision matrix is limited, as this method provides underestimates of the variable of interest, because some terms of production, mortality, and decomposition must be neglected in specific calculations. Recently, the continuous inflow estimate method was suggested by Osawa and Aizawa (2012), with the addition of a simple root litter bag experiment. This approach provided more reliable estimates of fine root production, mortality, and decomposition.

The objectives of this study were to investigate fine root dynamics with seasonal patterns of fine root mass, production, mortality, and to relate belowground growth parameters to aboveground organs in hinoki cypress and konara oak forest of Japan. We used both the sequential soil core and ingrowth core methods to estimate fine root dynamics and to allow a comparison between the two methods. We hypothesized that aboveground and belowground production are positively related and that seasonal patterns of fine root production vary between different forest types.

Materials and methods

Study site and stand descriptions

This study was conducted in hinoki cypress (*C. obtusa*) and konara oak (*Q. serrata*) stands in the Ryukoku Forest in Shiga, Japan (34°58'N, 135°56'E, 130 m a.s.l.). The Ryukoku Forest is a secondary forest composed primarily of *Q. serrata* Thunb. and *Pinus densiflora* Sieb. et Zucc. The soil of the study area is characterized by sand and small round gravels and is classified as yellowish brown forest soil of the Kobiwako group derived from lacustrine sediments of

Cenozoic origin (Osawa and Aizawa 2012; Ministry of Land Infrastructure Transportation and Tourism 1982). Soil bulk density is 1.23 g cm⁻³ in cypress stand and 1.26 g cm⁻³ in oak stand with a texture of sandy clay loam (Nakahata and Osawa 2017). To estimate NPP and investigate fine root dynamics, we established four study plots (Table 1) in ca. 80-year-old hinoki cypress plantations (CO1 and CO2) and broadleaved secondary forests composed primarily of konara oak as canopy trees (QS2 and QS3). The plots also contain some canopy and subcanopy trees of *Clethra barbinervis*, *Ilex pedunculosa*, *Juniperus rigida*, *Eurya japonica*, and *Cleyera japonica*. In QS2 plot, the relative basal area was 12% for *C. barbinervis*, 5% for *I. pedunculosa*, and 5% for *C. obtusa*. In QS3 plot, *I. pedunculosa*, *J. rigida*, *E.*

japonica, and *C. japonica* accounted for 24, 7, 6, and 6% of total basal area, respectively.

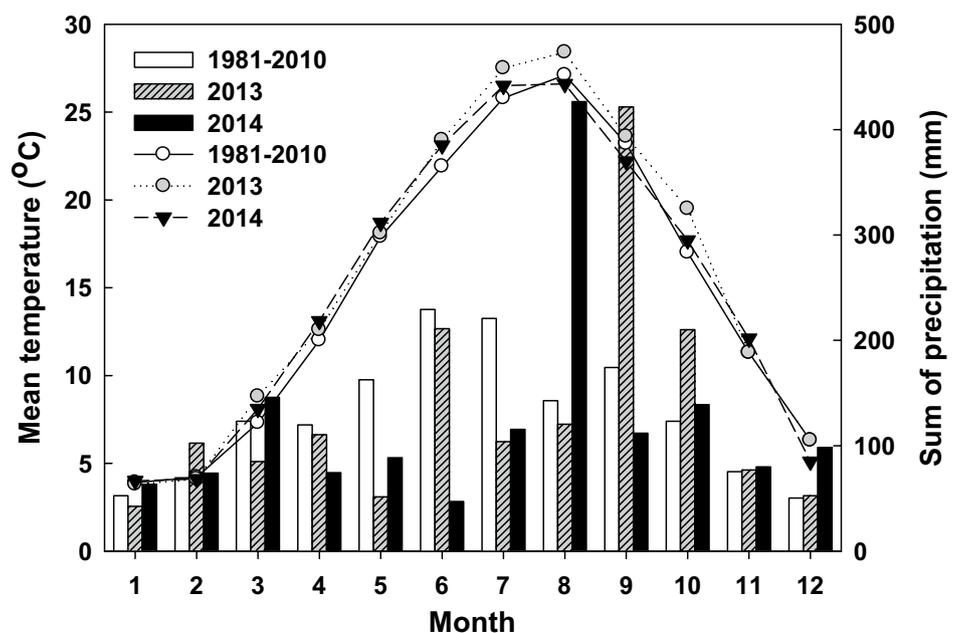
The mean annual precipitation from 1981 to 2010 was 1530 mm, and the temperature was 14.9 °C. The annual mean temperatures were 15.6 in 2013 and 15.1 °C in 2014. The annual precipitation was 1589 mm in 2013 and 1465 mm in 2014. The mean monthly temperatures in 2013 were higher than the long-term averages for April to October (Fig. 1). The precipitation in September 2013 was approximately 2.4 times greater than expected based on the long-term average, while the lowest precipitation was observed in July 2013, which was 47% of the usual level (Fig. 1). The total amounts of precipitation for April to June 2014 were less than the long-term values

Table 1 Stand descriptions of the hinoki cypress (CO1 and CO2) and konara oak (QS2 and QS3) stands in the Ryukoku Forest of Japan

Stand	Dominant species	Mean DBH (cm)	Mean tree height (m)	Stem density (stems ha ⁻¹)	Basal area (m ² ha ⁻¹)
Hinoki cypress stands					
CO1	<i>Chamaecyparis obtusa</i>	24.4 (24.9)	20.2 (20.6)	1033 (983)	53.4 (52.0)
CO2	<i>Chamaecyparis obtusa</i>	10.3 (27.8)	8.8 (19.7)	1864 (478)	37.1 (32.2)
Konara oak stands					
QS2	<i>Quercus serrata</i> , <i>Clethra barbinervis</i> , <i>Ilex pedunculosa</i> , <i>Chamaecyparis obtusa</i>	6.5 (22.0)	6.8 (17.8)	3717 (392)	24.1 (15.6)
QS3	<i>Quercus serrata</i> , <i>Ilex pedunculosa</i> , <i>Juniperus rigida</i> , <i>Eurya japonica</i> , <i>Cleyera japonica</i>	6.1 (21.0)	6.8 (15.9)	4225 (238)	20.7 (8.6)

Values presented in parentheses indicate those obtained for canopy tree species (*Chamaecyparis obtusa* in hinoki cypress stands of CO1 and CO2; *Quercus serrata* in konara oak stands of QS2 and QS3). Understory vegetation with a diameter at breast height of less than 2 cm was ignored. Dead trees were excluded

Fig. 1 Mean monthly temperatures and monthly precipitation sums (data from the Japan Meteorological Agency)



for those months; in addition, the precipitation in June 2014 was remarkably low, at 21% of the normal amount.

Vegetation censuses and biomass estimation

At the beginning and end of the 2013 and 2014 growing seasons, the tree diameter at breast height (DBH, in cm) was measured for all trees larger than 2 cm in DBH. Because measuring tree height in fully closed forest stands is not always easy and accurate, the tree height (H , in m) was estimated using the following hyperbolic equation (Ogawa and Kira 1977):

$$\frac{1}{H} = \frac{1}{(a \times DBH^b)} + \frac{1}{H_{max}}$$

where a and b are plot-specific constants and H_{max} is another constant representing the asymptotic tree height. The parameters of the equation were determined by non-linear regression analysis, based on subsamples of trees for which both tree height and DBH were measured in each plot ($r^2 = 0.96$ – 0.99 for each parameter, $p < 0.0001$).

The biomass of stems, branches and coarse roots of all trees in each plot were estimated from DBH (cm) and tree height (m) using the allometric equations presented below. The following allometric equations were used for hinoki cypress trees (Hagihara et al. 1993):

$$W_s(kg) = 0.01652(D_{0.1}^2 H)^{0.9983}$$

$$W_b(kg) = 0.001669(D_{0.1}^2 H)^{1.0145}$$

$$W_r(kg) = 0.006001(D_{0.1}^2 H)^{0.9843}$$

where $D_{0.1}$ is stem diameter at a height of $H/10$ and W_s , W_b and W_r are the biomass (based on dry weight) of stems, branches and coarse roots of hinoki cypress trees, respectively. We did not measure $D_{0.1}$ in 2013 and 2014 so $D_{0.1}$ was estimated using the equation $D_{0.1} = 0.9322D + 0.9222$ developed from hinoki cypress trees for which both D and $D_{0.1}$ were measured in November 2012.

We used the following allometric equations developed in the Ryukoku Forest (Miyaura et al., personal communication) to estimate aboveground biomass of deciduous and evergreen broadleaved trees and conifers other than hinoki cypress.

For deciduous broadleaved trees:

$$W_s(kg) = 0.122D^{2.14}$$

$$W_b(kg) = 0.0298D^{2.26}$$

where W_s and W_b are the biomass (based on dry weight) of stems and branches of deciduous broadleaved trees, respectively.

For evergreen broadleaved trees:

$$W_s(kg) = 0.177D^{1.96}$$

$$W_b(kg) = 0.0862D^{1.88}$$

where W_s and W_b are the biomass (based on dry weight) of stems and branches of evergreen broadleaved trees, respectively.

For conifers other than hinoki cypress:

$$W_s(kg) = 0.157D^{2.02}$$

$$W_b(kg) = 0.00210D^{3.05}$$

where W_s and W_b are the biomass (based on dry weight) of stems and branches of conifers, respectively.

Because the allometric equation for coarse roots was not developed in the Ryukoku Forest, we used the equation, $W_r(kg) = 0.0093D_0^{2.5015}$ (Cheng 2017) developed using the data from the Yamashiro Experimental Forest (Dannoura et al. 2006), where W_r is the biomass of coarse roots of broadleaved and coniferous trees, and D_0 (cm) is the diameter at basal portion of stem. We did not measure D_0 in 2013 and 2014 so D_0 was estimated using the equation $D_0 = 1.527D^{0.962}$ developed from trees for which both D and D_0 were measured in 2007 in the Ryukoku Forest (Naruse 2008).

Litterfall collection and sample processing

Seven square-shaped litter traps with a collection area of 1 m² at a height of 1 m above the forest floor were randomly deployed in CO1 in March 2010. The traps were emptied monthly starting in April 2010 (Ishii 2014). In CO1, litterfall samples collected from June 2013 to June 2014 were used for the present study and they were processed in the same manner as the others. We established twelve litter traps with a circular opening and a collection area of 0.283 m² at a height of 1 m above the forest floor, with three traps on each of four transects, in each of the remaining plots (CO2, QS2, and QS3) to estimate annual litterfall production. The litter traps were set out in March 2013 and emptied in June and August 2013 and in January, March and June 2014. The collected litterfall was stored under shade and cool condition in the laboratory before processing. Six litter traps were randomly selected from each plot and processed for this study. The samples were sorted into leaves, twigs (diameter < 1 cm), and others which is the remaining fraction including bark, seeds, and miscellaneous items. Leaf

litterfall was further divided into leaves of canopy tree species (hinoki cypress trees in CO1 and CO2, konara oak trees in QS2 and QS3) and other leaves of from other tree species. The sorted litterfall was oven-dried at 65 °C for 72 h and weighed.

Fine roots (< 2 mm) measurement

We used the ingrowth core method ('ic' denotes the ingrowth core method) to estimate fine root production (FRPic), mortality (FRMic) and decomposition (FRDic) in all study plots (CO1, CO2, QS2, and QS3). The ingrowth core method uses measurements of fine root growth into a root-free medium placed in the soil profile to estimate production (Vogt and Persson 1991; Nadelhoffer and Raich 1992). Three parallel sampling lines, which were separated from each other by at least 10 meters, were established in all plots except CO1. Each sampling line had four points placed at five-meter intervals for the ingrowth core. In the case of CO1, six subplots with a size of 5 m × 5 m were randomly selected for ingrowth core installation, and two points from each subplot were randomly selected for ingrowth cores. In total, 48 ingrowth cores (12 ingrowth cores in each plot) were installed in early June 2013 in all plots. At the beginning of ingrowth core installation, the hole that was needed to place a cylindrical tube 32 mm in diameter and 21 cm in length was excavated by pounding a stainless steel tube (38 mm in diameter and 45 cm in length) into the ground. The cylindrical tube, which is used for the ingrowth core frame, is made of plastic mesh, with approximately 3 mm mesh openings and a mesh bottom made of the same material as the cylinder wall (Osawa and Aizawa 2012). The cylinder was placed in the hole and filled separately with a root-free soil to a soil depth between the upper (0–5 cm in depth) and lower layer (5–21 cm in depth). To make a root-free soil, soil divided into the upper and lower layers was collected from the study site; the soil profile of the Ryukoku Forest was distinguished by its color between the upper and lower layer at a depth of approximately 5 cm, although the properties of the soil were not analyzed. The soil was sieved through a sieve with a mesh size in 5 mm and then remaining root particles were visually handpicked from the sieved soil to remove all living and dead roots. The gap between the cylinder and the inner wall of the cored hole was also filled with the same soil that was used to fill the ingrowth cores. In December 2013, six ingrowth cores were chosen randomly, removed from the ground by cutting around the periphery of the ingrowth cores approximately 2 cm away from the ingrowth core wall with a knife, and pulling the cores out by hand. In June 2014, the remaining six ingrowth cores were collected using the same method in each plot. The collected ingrowth cores were placed in plastic bags and stored in a freezer until the time of processing. The cylinders

were divided into the upper (0–5 cm) and lower (5–21 cm) soil layers, woody fine roots were extracted from the upper and lower layers of the soil samples, and the sorted roots were washed carefully with tap water. Living and dead roots were separated and further sorted into two diameter classes (very fine root, 0–0.5 mm; fine root 0.5–2 mm). Dead fine roots are distinguished by their dark color, low strength, and low resilience (Vogt and Persson 1991; Hishi and Takeda 2005a, b). The microscope was used when it was difficult to distinguish dead roots. The washed roots were oven-dried at 65 °C for 72 h and weighed.

To investigate fine root dynamics, a total 140 soil cores were collected sequentially ('sc' denotes the sequential core method) at 2-month intervals in CO2 and QS3 using the same stainless steel tube that was used for the ingrowth core study from June 2013 to June 2014. Twelve parallel sampling lines, which were separated from each other by at least 1 m, were established in each plot. Each sampling line included ten points placed at two-meter intervals for sequential soil cores. Every 2 months (totally for a total of seven times for over a year), ten soil cores, which were placed to a depth of 21 cm, were collected from randomly selected points in each plot. Collected soil cores were processed in the same way described for the ingrowth cores; however, the soil cores were not divided by soil depth.

In this study, we collected soil cores in upper soil layer (0–21 cm) because of practical difficulties in collecting soil core samples below 20 cm due to the presence of gravel. According to previous studies conducted in the same research site, fine roots in the upper soil layer accounted for approximately 70% of those in 0–50 cm soil depth (Hattori 2011). Thus, we assumed that belowground fine roots in 0–21 cm soil depth covered a high proportion of total belowground productivity in this research site.

Root litterbag experiment

To estimate the decomposition ratio of dead fine roots, we conducted root litter bag experiments in all plots for 1 year from June 2013. Regardless of species, living fine roots were collected from each plot at the study site, washed, dried at room temperature, divided into three diameter classes, and used as dead fine roots in the litter bags in this experiment. We used flat, square litter bags made of a 'root-impermeable water-permeable (RIWP) sheet®' (Toyobo Co., Osaka, Japan). The bags had a pore size of approximately 6 µm to prevent fine roots from growing into the bag; however, fine particles of soil, rain water, and other microorganisms could penetrate through the sheet (Osawa and Aizawa 2012). A known amount of dead fine roots of three diameter classes was added to each of the root litter bags separately, and a root-free soil divided by soil depth was also included in the litter bags to improve the physical contact of the soil

particles with the dead roots in the bag. In June 2013, 36 root litter bags (3 diameter classes \times 2 soil depths \times 6 replicates = 36 bags) were buried separately at different soil depths at randomly selected points in each plot. In December 2013, litter bags that were buried for 6 months were collected, moved to the laboratory and processed. Decomposing dead fine roots were removed from the litter bag, carefully washed with tap water, oven-dried at 65 °C for 72 h and weighed. In January 2014, the same procedure that was used for the root litter bag experiment was repeated to estimate the decomposition ratio of dead fine roots from January to June 2014.

Calculation of root production, mortality, decomposition

For ingrowth cores, fine root production (g_{ij}), mortality (m_{ij}) and decomposition (d_{ij}) were calculated using the continuous inflow estimate method (Osawa and Aizawa 2012), as follows:

$$\text{Fine root production : } g_{ij} = \Delta B + \Delta N + d_{ij}$$

$$\text{Fine root mortality : } m_{ij} = \Delta N + d_{ij}$$

$$\text{Fine root decomposition : } d_{ij} = -\Delta N - (\Delta N/\gamma_{ij} + N_i) \cdot \ln(1 - \gamma_{ij})$$

where ΔB and ΔN are the change in fine root biomass and necromass between times i and j ($i < j$), respectively; N_i is the amount of fine root necromass in the core at time i ; and γ_{ij} is the decomposition ratio of fine root necromass estimated from the root litterbag experiment, as follows:

$$\text{Decomposition ratio of fineroot necromass : } \gamma_{ij} = 1 - N_j^C/N_i^C$$

where N_i^C and N_j^C are the mass of dead fine roots in the litter bag at times i and j , respectively. Details of the calculation are described in a previous study (Osawa and Aizawa 2012). The 68% confidence limits of the estimated means were calculated using the bootstrap method with the bias-corrected percentile approach by randomly sampling a set of mass data n times with replacement (when the sample size is n) to obtain the means. The process was then repeated 1000 times to generate the 68% confidence interval (CI) (Efron 1979; Efron and Gong 1983; Osawa and Aizawa 2012).

For sequential soil cores in CO₂ and QS3, fine root production (FRPsc), mortality (FRMsc), and decomposition (FRDsc) were calculated using the simplified decision matrix (Table 2) of Yuan and Chen (2013), because many negative values occurred when we applied the continuous inflow estimate method and the bootstrap method. The simplified decision matrix proposed by Yuan and Chen (2013) is modified version from Fairley and Alexander (1985). The decision matrix is a widely used method to estimate fine root

Table 2 Simplified decision matrix (Yuan and Chen 2013) for calculating production, mortality and decomposition of fine roots in CO₂ and QS3 in the Ryukoku Forest

If	Production	Mortality	Decomposition
$\Delta B + \Delta N \geq 0$			
$\Delta N \geq 0$	$\Delta B + \Delta N$	ΔN	0
$\Delta N < 0$	ΔB	0	$ \Delta N $
$\Delta B + \Delta N < 0$			
$\Delta N \geq 0$	ΔB	0	$ \Delta N $
$\Delta N < 0$	0	$ \Delta B $	$ \Delta B + \Delta N $

Δ = changes in root biomass or necromass, B = living root biomass, N = dead root necromass

If $\Delta B + \Delta N \geq 0$ and $\Delta N \geq 0$, the fine root production is calculated as $\Delta B + \Delta N$

production, mortality, and decomposition during a certain period, based on the changes of living and dead fine root mass.

NPP estimation

The total NPP was calculated based on the sum of changes in the biomass of aboveground organs (stems and branches) and coarse roots, as well as amounts of annual litterfall mass and annual fine root production. We defined aboveground net primary production (ANPP) as the sum of aboveground (stems and branches) biomass increment and litterfall mass for 1 year. Litterfall mass was combined into leaf (sum of dominant species and other species leaf) and other litterfall (sum of twigs and others). Belowground production was calculated as the sum of coarse root biomass increment, and fine root production estimated by the ingrowth core method.

Statistical analyses

We tested the significance of differences in each litterfall fraction across the stands using one-way analysis of variance (ANOVA). Three-way ANOVA was conducted to examine the effects of stand, sampling time (month), and root diameter on fine root biomass, necromass, production, mortality, and decomposition. Tukey's HSD (honestly significant difference) test was applied to determine significant differences between means ($p < 0.05$). We used a linear regression model analysis to test the relationships between above- and belowground mass or production, such as the relationship between basal area and fine root biomass and the relationship between leaf litterfall mass and fine root production. When necessary, data was transformed properly before the statistical analyses. All statistical analyses were performed using the SAS 9.2 software (SAS Institute, Inc., USA).

Results

Above- and belowground production in hinoki cypress and konara oak forests

The total NPP ranged from 8.2 to 13.9 t ha⁻¹ yr⁻¹, with means of 11.8 and 8.4 t ha⁻¹ yr⁻¹ in hinoki cypress forest and konara oak forest, respectively (Fig. 2a). The above-ground NPP (ANPP) ranged from 6.7 to 11.0 t ha⁻¹ yr⁻¹, which accounted for an average of 81% of the total NPP. Belowground production ranged from 1.6 (in QS3) to 2.8 (in CO1) t ha⁻¹ yr⁻¹, which represented an average of 19% of the total NPP. The proportion of FRP_{ic} to belowground production in all stands was higher than that of coarse

root production to belowground production, which ranged from 51 to 53% (Fig. 2b). FRP_{ic} accounted for 9 to 11% of total NPP. Annual FRP_{sc} values were 5.4 ha⁻¹ yr⁻¹ in CO₂ and 4.0 t ha⁻¹ yr⁻¹ in QS3 (Table S2). The proportions of fine root production estimated using sequential soil cores were 53 and 36% of belowground production, resulting in 30 and 22% of the total NPP, in stands CO₂ and QS3, respectively.

Annual litterfall mass

The annual litterfall mass ranged from 436 to 560 g m⁻² yr⁻¹ and did not differ significantly among stands ($p=0.42$; Table 3). Leaf litterfall of canopy tree species (hinoki cypress trees in CO1 and CO2; konara oak trees in QS2 and

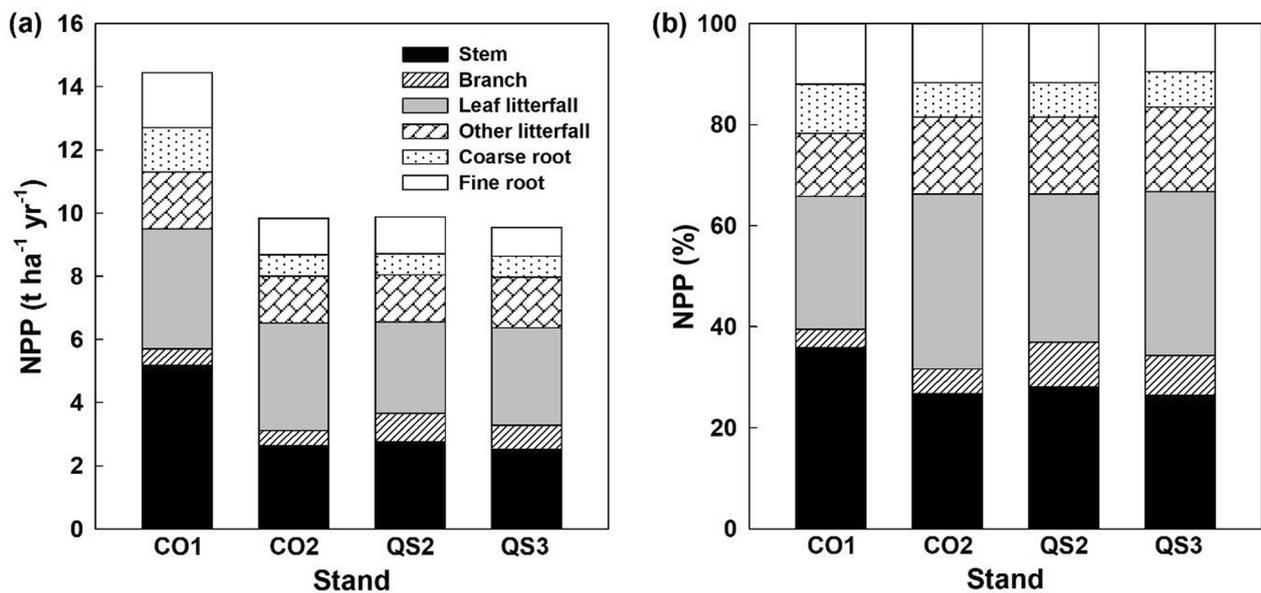


Fig. 2 Above- and belowground net primary production (NPP) in all stands in the Ryukoku Forest. NPP was calculated based on the sum of changes in the biomass of aboveground stem, branches and coarse roots, as well as annual litterfall mass and fine root production. Biomass increment of stem, branches and coarse roots was calculated

by the allometric equations. Annual litterfall mass was estimated by the litter traps. Annual fine root production was estimated by the ingrowth core method and the continuous inflow estimated method (Osawa and Aizawa 2012). **a** NPP (t ha⁻¹ yr⁻¹) and **b** NPP (%)

Table 3 Annual litterfall mass (g m⁻²) sorted into four parts (leaves (hinoki cypress in CO1 and CO2, konara oak in QS2 and QS3), other leaves, twigs, and the remaining fraction) for all study plots in the Ryukoku Forest

	Leaves	Other leaves	Twigs	Others	Total
Hinoki cypress					
CO1	356.5 (36.7)a	26.6 (7.1)b	67.3 (12.3)a	109.7 (19.1)a	560.1 (72.3)a
CO2	266.3 (60.1)a	69.0 (22.4)b	62.1 (11.2)a	85.8 (11.0)a	483.1 (64.5)a
Konara oak					
QS2	133.1 (17.8)b	154.8 (21.8)a	85.0 (21.9)a	62.9 (14.1)a	435.8 (14.1)a
QS3	135.5 (16.6)b	179.3 (36.5)a	101.7 (21.6)a	63.1 (9.5)a	479.5 (24.2)a

Standard errors are shown in parentheses ($n=6$). Mean values presented with the same letters are not significantly different among stands within each column ($p < 0.05$; Tukey’s HSD test)

QS3) and other leaf litterfall differed significantly among stands ($p < 0.05$). Regardless of tree species, the leaf litterfall mass was a major fraction of the total litterfall, with values of 69 and 66% of total litterfall mass in hinoki cypress stands and konara oak stands, respectively. Other leaf litterfall mass was higher than leaf litterfall mass for konara oak trees in QS2 and QS3, accounting for an average of 55% of the total leaf litterfall. In contrast, other leaf litterfall mass comprised an average of 14% of the total leaf litterfall in hinoki cypress stands. The proportion of twigs and other fractions, such as bark and seeds, to total litterfall mass for both types of stand was 16%, on average.

Annual fine root (< 2 mm) production, mortality, and decomposition

The annual FRP_{ic} ranged from 90 to 159 g m⁻² yr⁻¹, 50 to 88 g m⁻² yr⁻¹ for FRM_{ic}, and 1 to 8 g m⁻² yr⁻¹ for FRD_{ic}, respectively (Table S1). No roots larger than 2 mm in diameter were found in the 1-year ingrowth cores. The values of FRP_{ic} and FRM_{ic} were high in hinoki cypress stand, CO1 which had high density of canopy tree. Annual FRP_{ic}, FRM_{ic}, and FRD_{ic} of less than 2 mm in diameter accounted for averages of 83, 94, and 89% of the total FRP, FRM, and FRD for all diameter classes, respectively (Table S1).

The annual FRP_{sc}, FRM_{sc}, and FRD_{sc} values were 540, 585, and 671 g m⁻² yr⁻¹ in CO2 and 400, 410, and 499 g m⁻² yr⁻¹ in QS3, respectively. All values were higher in CO2 than in QS3 ($p < 0.05$; Table S2). Compared with the annual FRP_{ic} values, the annual FRP_{sc} values were 5.8 and 4.4 times greater in CO2 and QS3, respectively.

Seasonal dynamics of fine root bio- and necromass in hinoki cypress and konara oak stands

Fine root biomass estimated by the sequential soil core method differed significantly between stands ($p = 0.008$), sampling times ($p < 0.0001$) and root diameter ($p < 0.0001$; Table 4). In both stands, fine root biomass was about two times higher in February 2014 than in October 2013 (Fig. 3a and b) and it was attributed to high biomass of larger fine root (0.5–2 mm) in February 2014 (Fig. 3a). Fine root necromass was also significantly different between stands ($p < 0.0001$), sampling times ($p < 0.0001$) and root diameter ($p = 0.002$; Table 4). Also, the three-way interaction between stand and time related to root diameter significantly affected fine root necromass ($p = 0.03$). In this study area, seasonal patterns of fine root necromass between stands were significantly influenced by root diameter. Very fine root (< 0.5 mm) necromass was higher in summer season (June–August in 2013) than other seasons and this tendency was remarkable in hinoki cypress stand CO2 (Fig. 3c and d). On the other hand, larger fine root necromass was only significantly

different among sampling times in hinoki cypress stand, representing the higher necromass in early winter (November) than summer and spring (August and April) (Fig. 3c).

Seasonal patterns of fine root production, mortality, and decomposition in hinoki cypress and konara oak stands

Seasonal FRP_{sc} was not significantly different between stands ($p = 0.12$), months ($p = 0.18$), and root diameter ($p = 0.09$) according to the result of a three-way ANOVA (Table 5). However, FRM_{sc} was significantly different between stands ($p = 0.008$) and months ($p = 0.006$) with the interaction effect between month and diameter, and FRD_{sc} differed significantly across months ($p = 0.03$; Table 5). In hinoki cypress stand CO2, the mortality of very fine root (< 0.5 mm) was high in early summer (Fig. 4c) resulted from high necromass of very fine root in August 2013.

Relationships between above- and belowground production

FRP_{ic} showed no significant correlations with the leaf litterfall mass ($p = 0.18$, $r^2 = 0.67$) and the basal area increment ($p = 0.29$, $r^2 = 0.50$) (Fig. 5a, b). However, there was a positive tendency for the relationship between above- and belowground production ($p = 0.06$, $r^2 = 0.87$) (Fig. 5c). Also, the relationship between NPP and FRP_{ic} was not statistically significant but approached trend levels of significance ($p = 0.058$, $r^2 = 0.89$).

Discussion

Litterfall and fine roots, which represent major carbon fluxes in forest ecosystems, contributed about 60% of the total NPP in hinoki cypress and konara oak stands in the Ryukoku Forest, confirming the significance of above- and belowground litter for forest NPP as inputs of detritus to the decomposer system. In addition, belowground production accounted for 19% on average of NPP in this study area. Tateno et al. (2004) conducted a study of biomass and net primary production in a cool-temperate deciduous forest in Japan in relation to topographical changes. They also estimated fine root production using the ingrowth core method. According to their results, the total NPP ranged from 8.8 to 14.1 t ha⁻¹ yr⁻¹, and the proportion of fine root production to total belowground production was 60 to 90%; those levels are higher than the percentages reported in this study. Moreover, their results showed that the belowground production tended to increase with decreasing soil N availability and that fine root production was the main contributor to this tendency. The general allocation pattern of NPP indicates

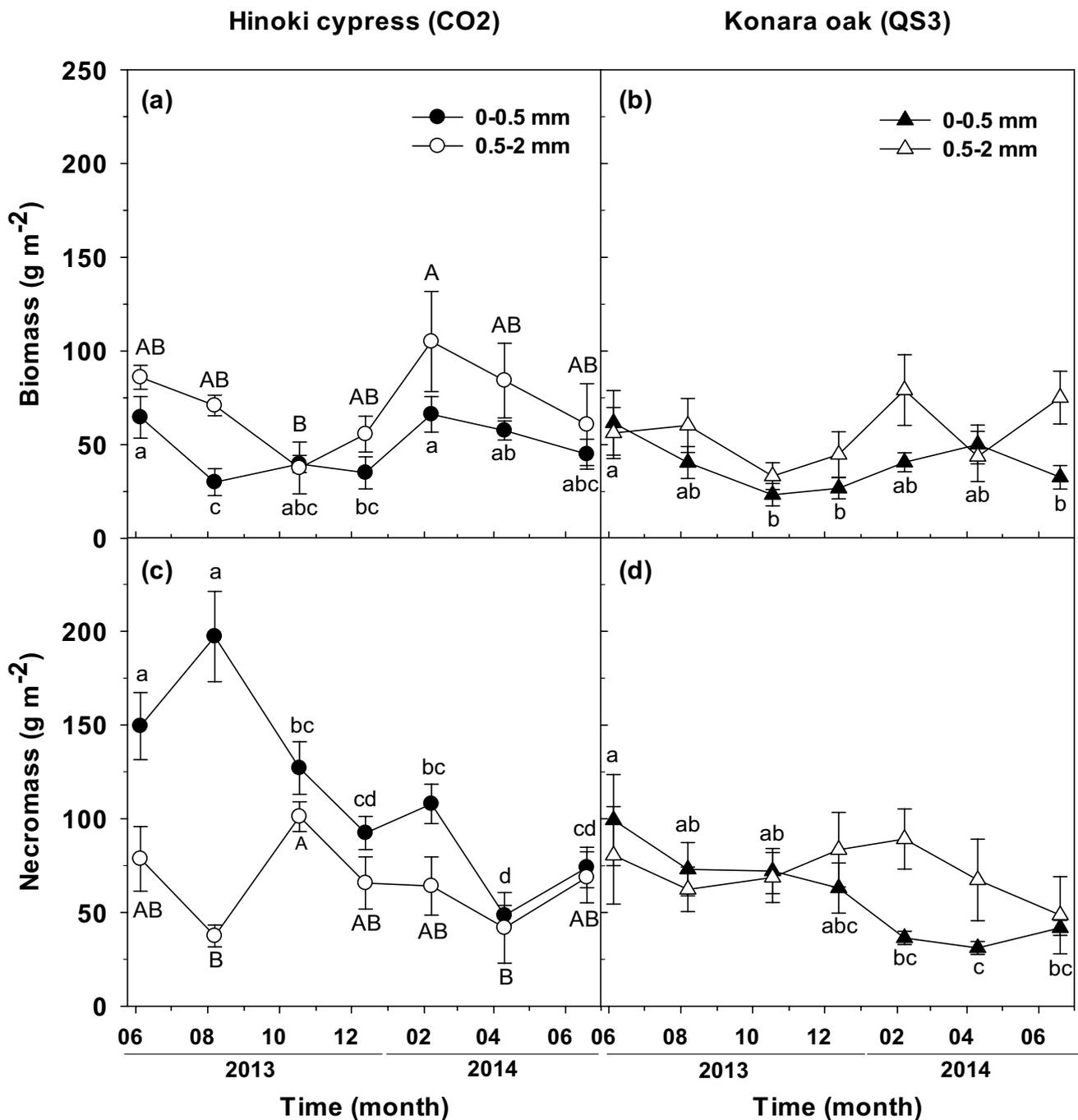


Fig. 3 Seasonal dynamics of fine root biomass (a, b) and necromass (c, d) measured by sequential soil cores from Jun 2013 to June 2014 in the CO2 (a, c) and QS3 (b, d) stands. Vertical bars indicate standard errors ($n=10$). Mean values with the same letters do not differ

significantly across months within each stand ($p < 0.05$; Tukey's HSD test). No significant differences were detected in fine root (0.5–2 mm) biomass and necromass in QS3 across sampling times

that more NPP is allocated to the roots under unfavorable site conditions (Keyes and Grier 1981; Vogt et al. 1987). In contrast, Yuan and Chen (2012a, b) reported that fine root production increased along natural N and P soil gradients in terrestrial ecosystems through a global analysis study. They also implied that the proportion of root production to NPP

decreased with soil nutrients, resulting in changes of carbon allocation pattern, although the absolute value of fine root production may increase with increasing soil nutrients. Understanding patterns of belowground carbon allocation can improve our insights into plant nutrient demand in forest ecosystems (Iversen and Norby 2008). Because fine roots

Table 4 F and p values of the effects of stand (S), sampling time (T), and fine root diameter (D) on fine root biomass and necromass measured by the sequential soil core in CO₂ and QS3 using a three-way ANOVA

	df	F value	p value
Biomass			
Stand (S)	1	7.17	0.0079
Time (T)	6	5.39	<0.0001
Diameter (D)	1	19.33	<0.0001
S*T	6	0.78	0.5875
S*D	1	0.51	0.4764
T*D	6	1.21	0.3026
S*T*D	6	0.82	0.5553
Necromass			
Stand (S)	1	16.88	<0.0001
Time (T)	6	6.51	<0.0001
Diameter (D)	1	9.73	0.002
S*T	6	1.51	0.175
S*D	1	26.52	<0.0001
T*D	6	5.14	<0.0001
S*T*D	6	2.34	0.0322

take a role of nutrient acquisition from soil resources, nutrient requirements of forest trees may be implied by allocation of more carbon to belowground structures than aboveground parts, based on the balanced-growth hypothesis (Shiple and Meziane 2002). Although we cannot suggest that low belowground production/NPP implies high nutrient availability or high site productivity without soil or stand productivity data in this study, belowground production or its proportion to NPP may become one of indicators for site productivity if further data about site factors is supported.

In this study, fine root production was estimated in the upper soil layer up to 21 cm depth, because soil core samples could not be collected below 20 cm in gravel soil of the study site. Previous study reported that over 70% of fine roots were concentrated in the upper soil layer in this study site. Although soil core technique is an effective method for fine root study and many previous studies investigated fine roots in the top of the soil profile using this technique, it can underestimate fine root production and mortality (Clark et al. 2001a, b). However, most of the roots are more likely to be present in the top soil layer, decreasing exponentially with increasing soil depth in most ecosystems (Zhou et al. 2016a, b). Also, deep roots probably play a relatively small role in belowground carbon budget (Hendrick and Pregitzer 1996) as shown by other studies of temperate tree species which reported an increase in fine root turnover time with depth, with the most rapid fine root turnover occurring in the

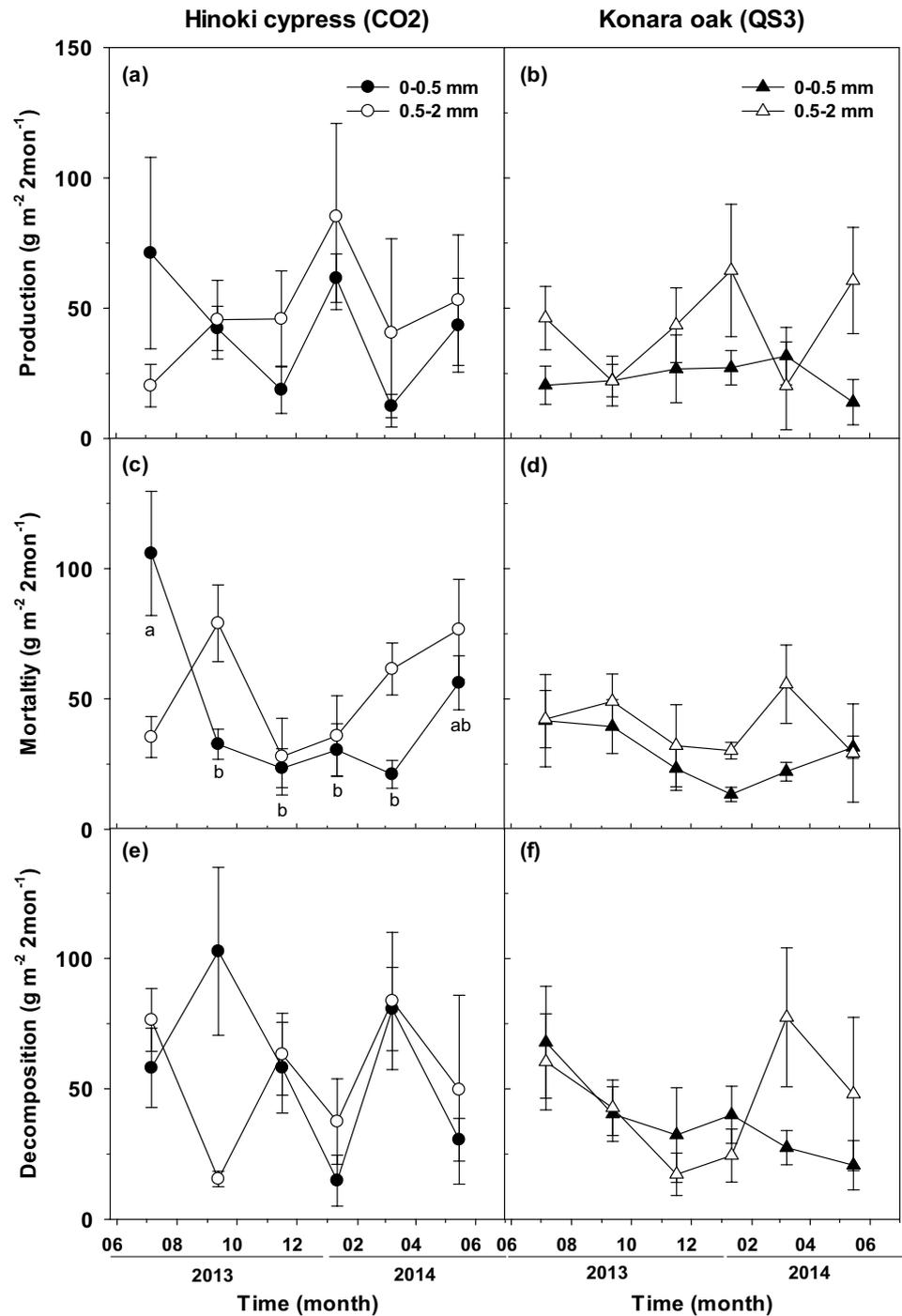
upper 20 cm (Gaudinski et al. 2001; Baddeley and Watson 2005a, b).

The annual FRP_{ic} was significantly lower than that estimated using the sequential soil core method in this study. Several researchers have reported obtaining lower estimated values of fine root production when using the ingrowth core method than when using the sequential soil core method (Makkonen and Helmisaari 1999; Ostonen et al. 2005). Makkonen and Helmisaari (1999) reported that the fine root production in the ingrowth cores after 3 years of installation was similar to the value estimated using soil cores in Scots pine stands. The production of fine roots, as estimated using the ingrowth core method, tended to have lower estimates in the first year of the ingrowth core than in the following year (Persson 1980; Yin et al. 1989; Messier and Puttonen 1993; Ostonen et al. 2005). The reason for the low fine root production estimated using the ingrowth core method may involve unfavorable soil conditions for starting root growth, the absence of older roots, and delayed root re-colonization (Joslin and Henderson 1987; Vogt and Persson 1991; Idol et al. 2000).

Noguchi et al. (2007) reviewed studies of fine root biomass and production in Japanese forests. The estimated values of fine root production for hinoki cypress plantations ranged from 122 to 306 g m⁻² yr⁻¹ (Kasuya et al. 1993; Tokuchi et al. 2002; Hishi and Takeda 2005a, b), and the values of FRP in deciduous broadleaved forests ranged from 90 to 680 g m⁻² yr⁻¹ (Satomura 2003; Tateno et al. 2004; Tripathi et al. 2005). The estimates of FRP obtained in this study were in the range of reported values and the values obtained in this study do not appear to deviate significantly from the reported range. The study of fine root dynamics was also conducted in konara oak stand of Ryukoku Forest from March to September 2012 (Van Do et al. 2015a; Do et al. 2015b). They reported that the FRP_{sc} values ranged from 232 to 311 g m⁻² for 174 days according to root size classes and calculation intervals. Compared with our results, the all values were higher than the FRP_{sc} value (181 g m⁻² for 188 days from June to December 2013) in this study.

The temporal patterns of fine root dynamics may be affected by changes in stand conditions, such as soil temperature, moisture, and nutrients, as well as carbon allocation patterns (Makkonen and Helmisaari 1998; Pregitzer et al. 2000; Lopez et al. 2001). In this study, significant differences in fine root bio- and necromass were observed between the two forests and sampling times. Also, the seasonal patterns of fine root bio- and necromass varied between root diameter classes. The low fine root biomass observed during early summer and high necromass of very fine root in August 2013 in CO₂ might be attributable to very low precipitation during early summer. On the other hand, the fine root necromass in hinoki cypress stands showed significantly different

Fig. 4 Seasonal dynamics of fine root production (a, b), mortality (c, d), and decomposition (e, f) estimated by sequential soil cores and calculated by the simplified decision matrix (Yuan and Chen 2013). Vertical bars indicate standard errors ($n=10$). Mean values with the same letters do not differ significantly across months within each stand ($p<0.05$; Tukey's HSD test)



peak from June to August 2013 and from October 2013 to June 2014. According to a study performed by Hattori (2011), which was conducted in a nearby konara oak forest at the same study site, the maximum fine root biomass and necromass values were observed in October and in November, respectively. The peaks and troughs of fine root mass

reported by Hattori (2011) do not exactly correspond to the patterns of fine root mass observed in this study, whereas the relatively high fine root biomass observed in February 2014 is consistent with that previous study. Meanwhile, although several researchers hypothesized that deciduous trees have a higher fine root biomass than coniferous trees

Table 5 *F* and *p* values of the effects of stand (S), month (M), and fine root diameter (D) on fine root production, mortality, and decomposition estimated by the sequential soil core method and the simplified decision matrix in CO2 and QS3 using a three-way ANOVA

	<i>df</i>	<i>F</i> value	<i>p</i> value
Production			
Stand (S)	1	2.37	0.1248
Month (M)	5	1.53	0.1817
Diameter (D)	1	2.91	0.0894
S*M	5	0.39	0.852
S*D	1	0.65	0.4198
M*D	5	0.82	0.5392
S*M*D	5	1.18	0.3202
Mortality			
Stand (S)	1	7.1	0.0083
Month (M)	5	3.34	0.0062
Diameter (D)	1	2.97	0.0862
S*M	5	1.22	0.3028
S*D	1	0.1	0.7571
M*D	5	3.4	0.0056
S*M*D	5	1.94	0.0884
Decomposition			
Stand (S)	1	3.2	0.0752
Month (M)	5	2.47	0.0332
Diameter (D)	1	0.06	0.814
S*M	5	0.69	0.6284
S*D	1	0.4	0.5295
M*D	5	1.62	0.1569
S*M*D	5	1.6	0.162

in the temperate zone (Vogt et al. 1986, 1996; Leuschner and Hertel 2003; Finér et al. 2007; Noguchi et al. 2007), the higher fine root biomass in the hinoki cypress stand than in the konara oak stand is not consistent with previously reported results.

Several researchers reported that the seasonal dynamics of fine root production are affected by nutrient availability, environmental conditions (Vogt et al. 1996; Alvarez-Uria and Körner 2007; Finér et al. 2011), species composition (Lei et al. 2012), and stand age (Helmisaari et al. 2002; Yang et al. 2010; Yuan and Chen 2012a, b). Fine root production

(< 2 mm) did not show clear pattern in both stands of this study. Nakahata (2016) investigated long-term observation of fine root production using a root scanner method in hinoki cypress and konara oak stands in the Ryukoku Forest. He found a summer unimodal pattern with a high production rate from July to August in hinoki cypress stand in 2013 and a bimodal pattern with two peaks between mid-spring and early summer, and between mid-summer and early autumn, respectively, in hinoki cypress stand in 2014 and konara oak stand in 2013 and 2014. The fine root mortality was relatively high from April to June, and it might be induced by low soil temperature rather than air temperature in March 2014 as a result of suppressing fine root growth.

We found no significant relationships between fine root production and basal area increment or leaf litter-fall production. Previously, Santantonio (1989) found a linear relationship between fine root and foliage biomass for several conifer species, and a positive linear relationship between annual leaf litterfall and fine root mass in semi-arid tree species was observed by Jha and Mohapatra (2010). Also, a positive linear relationship between fine root production and litterfall was reported in a warm-temperate evergreen broadleaved forest (Van Do et al. 2015a; Do et al. 2015b). Contrary to previous studies, Nadelhoffer and Raich (1992) observed no overall relationship between aboveground production and fine root production with a large data set. However, a marginally positive correlation between above- and belowground net primary production was detected in this study, even though the data are only from four stands. Belowground production increased with aboveground production, given that independent analyses of forest C and N budgets suggest a linkage between these two components of net primary production (Nadelhoffer and Raich 1992). This finding is consistent with the significant relationship observed between above- and belowground NPP in this study. Furthermore, we found that fine root production might increase with increasing NPP suggesting high allocation to belowground in high productive stands. Similar to our results, Litton et al. (2007) reviewed literature and reported that a positive correlation between ANPP and total belowground carbon flux was observed across a broad productivity gradient, and carbon fluxed to belowground production increased with increasing GPP.

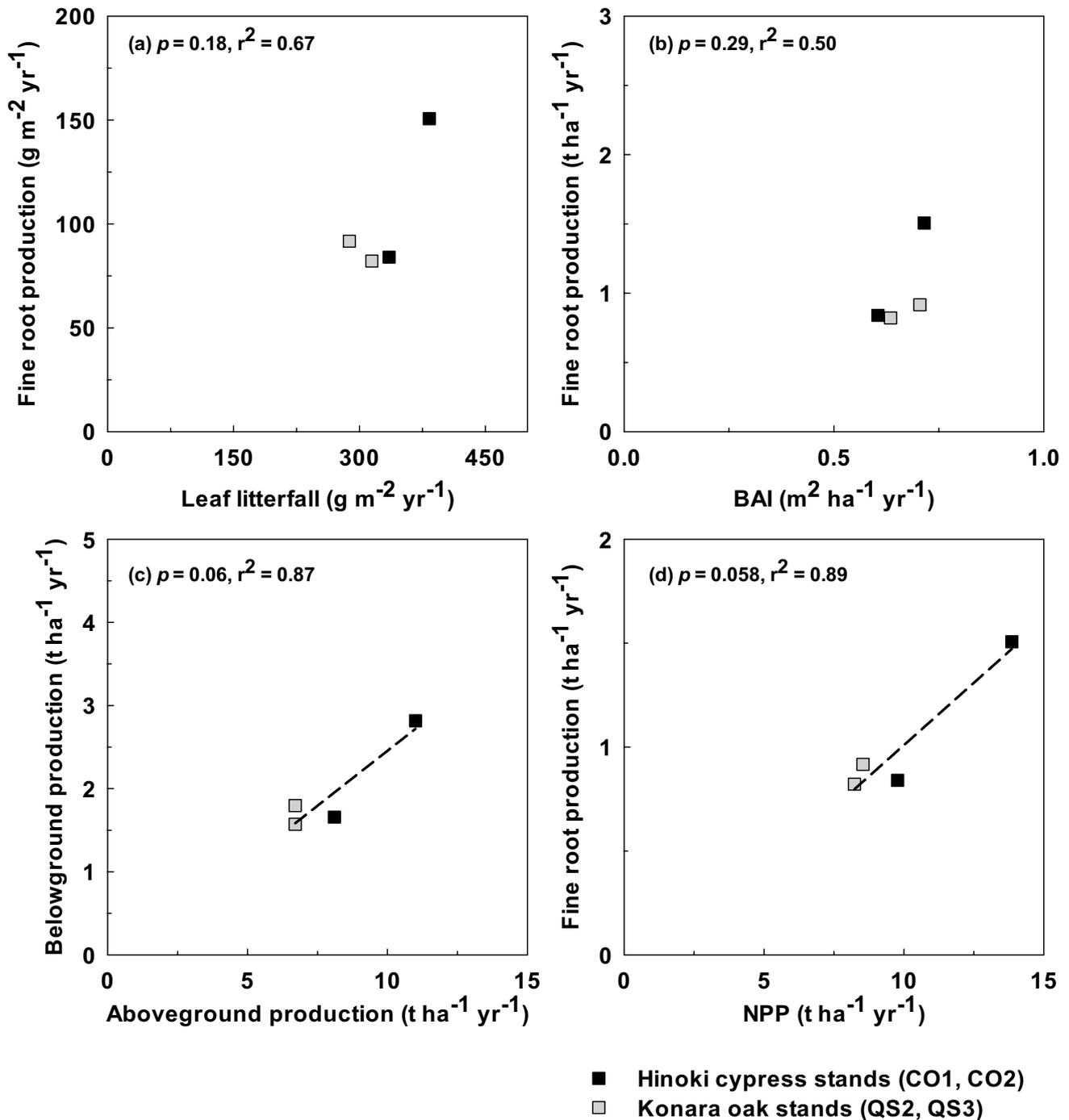


Fig. 5 Relationships between **a** leaf litterfall and fine root production, **b** basal area increment (BAI) and fine root production, **c** above- and belowground production, **d** net primary production (NPP) and fine

root production in hinoki cypress (CO1 and CO2) and konara oak (QS2 and QS3) stands in the Ryukoku Forest. Dashed lines show a marginally significant relationship (**c**, **d**)

Conclusions

We clarified the role and significance of fine roots in forest ecosystems through a stand-level study. The probable ranges of fine root production, mortality, and

decomposition were estimated using two soil core techniques for hinoki cypress and konara oak forests in Japan. The estimated values of fine root characteristics varied depending on the measurement method, representing lower production values by ingrowth coring than sequential soil

coring. Seasonal patterns of fine root bio- and necromass differed between two forest types and thinner root showed more distinct seasonal changes than thicker root. No overall seasonal patterns of fine root production were found regardless of forest types. However, we found that carbon allocation to belowground fine roots seemed to be positively related with forest productivity. This study can contribute to improve our understanding of carbon allocation patterns in temperate forest ecosystems.

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Author contributions statement JYA and AO contributed to the study conception and design. Material preparation, data collection and analysis were performed by JYA. The first draft of the manuscript was written by JYA and AO commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

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