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ORIGINAL ARTICLE

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Carbon cycling and sequestration in a Japanese red pine (*Pinus densiflora*) forest on lava flow of Mt. Fuji

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Abstract Biometric-based carbon flux measurements were conducted in a pine forest on lava flow of Mt. Fuji, Japan, in order to estimate carbon cycling and sequestration. The forest consists mainly of Japanese red pine (*Pinus densiflora*) in a canopy layer and Japanese holly (*Ilex pedunculosa*) in a subtree layer. The lava remains exposed on the ground surface, and the soil on the lava flow is still immature with no mineral soil layer. The results showed that the net primary production (NPP) of the forest was 7.3 ± 0.7 t C ha^{-1} $year^{-1}$, of which 1.4 ± 0.4 t C ha^{-1} $year^{-1}$ was partitioned to biomass increment, 3.2 ± 0.5 t C ha^{-1} $year^{-1}$ to above-ground fine litter production, 1.9 t C ha^{-1} $year^{-1}$ to fine root production, and 0.8 ± 0.2 t C ha^{-1} $year^{-1}$ to coarse woody debris. The total amount of annual soil surface CO_2 efflux was estimated as 6.1 ± 2.9 t C ha^{-1} $year^{-1}$, using a closed chamber method. The estimated decomposition rate of soil organic matter, which subtracted annual root respiration from soil respiration, was 4.2 ± 3.1 t C ha^{-1} $year^{-1}$. Biometric-based net ecosystem production (NEP) in the pine forest was estimated at 2.9 ± 3.2 t C ha^{-1} $year^{-1}$, with high uncertainty due mainly to the model estimation error of annual soil respiration and root respiration. The sequestered carbon being allocated in roughly equal amounts to living biomass (1.4 t C ha^{-1} $year^{-1}$) and the non-living C pool (1.5 t C ha^{-1} $year^{-1}$). Our estimate of biometric-based NEP was 25 % lower than the eddy covariance-based NEP in this pine forest, due partly to the underestimation of NPP and difficulty of estimation of soil and root respiration in the pine forest on lava flows that have large heterogeneity of soil depth. However, our results indicate that the mature pine forest acted as a significant carbon sink even when established on lava flow with low nutrient content in immature soils, and that sequestration strength, both in biomass and in soil organic matter, is large.

Keywords Carbon cycling · Net ecosystem production · Net primary production · *Pinus densiflora* · Soil respiration

Introduction

The net exchange of carbon (C) by an ecosystem over a given period of time is termed net ecosystem production (NEP), which is the difference between two large fluxes: gross primary production (GPP) and ecosystem respiration (ER). Long-term monitoring of eddy covariance-based NEP, such as AsiaFlux, has been established to quantify the role of terrestrial ecosystems in the global C cycle (Saigusa et al. 2008). However, eddy covariance-based NEP measurements need to be validated independently against ecological approaches before the data can be scaled up to the level of land-use confidence (Black et al. 2007; Gough et al. 2008; Luyssaert et al. 2009; Peichl et al. 2010). The calculation of NEP from ecological inventories of various C compartments, which is described as the balance between net primary production (NPP) and heterotrophic respiration (Rh), is called biometric-based NEP (Randerson et al. 2002; Curtis et al. 2002).

Stand-level studies of both eddy covariance and biometric-based NEP provide important process-level information of forest C dynamics as well as local validation of regional estimates. The few pioneer studies that have conducted concurrent biometric and eddy covariance-based assessments of NEP in forest ecosystems have often reported poor agreement between the

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two methods (Ehman et al. 2002; Hirata et al. 2008; Kolari et al. 2004; Kominami et al. 2008). On the other hand, multi-year measurements may be required to make robust estimates of C storage (Gough et al. 2008; Ohtsuka et al. 2007). For example, eddy covariance-based NEP in a temperate deciduous forest (Takayama Forest) was found to vary interannually by a factor of 2 or more, and averaged at 2.37 ± 0.9 t C ha^{-1} $year^{-1}$ from 1994 to 2003 (Saigusa et al. 2005). A high annual NEP at the Takayama Forest was due mainly to the high CO_2 uptake observed during the first half of the growth period of plants. Saigusa et al. (2005) suggested that earlier leaf expansion due to an unusually warm spring under the influence of El Niño resulted in a higher NEP. Ohtsuka et al. (2007) measured biometric-based NEP over 5 years at the Takayama Forest, which was estimated at 2.1 ± 1.2 t C ha^{-1} $year^{-1}$, agreeing well with the eddy covariance-based NEP. Moreover, linking multiyear biometric measurements of tree growth with eddy covariance-based NEP at the Takayama Forest revealed that interannual variability in the ecosystem carbon exchange was directly responsible for much of the interannual variation in autotrophic production (Ohtsuka et al. 2009).

Spatial variability in NEP among temperate forests has been related to stand age or prior disturbance. Chronosequence studies of net CO_2 exchange have become widespread in recent years in boreal and temperate regions (Clark et al. 2004; Kowalski et al. 2003; Litvak et al. 2003; Noormets et al. 2007; Zha et al. 2009). In general, a forest stand is expected to be a carbon source for several years at the beginning of secondary succession, which is often initiated by disturbance such as fires, hurricanes or clear cuttings (Chapin III et al. 2002). Middle-aged forests are usually carbon sinks, and the sink strength declines as forests mature. For example, Clark et al. (2004) reported that the annual NEP along a chronosequence of slash pine (*Pinus elliottii* var. *elliottii*) plantations changed from −1,269 to −882 g C m^{-2} $year^{-1}$ during the years immediately after clear-cut but recovered to 576 and 603 g C m^{-2} $year^{-1}$ at the mid-rotation (10-year-old) forest.

Large areas of the lower slopes of Mt. Fuji (temperate region) are covered with coniferous forests rather than with temperate deciduous broad-leaved forests. These coniferous forests, e.g., Japanese cypress (*Chamaecyparis obtusa*) and hemlock (*Tsuga sieboldii*) forests (Ohtsuka et al. 2008) or Japanese red pine (*Pinus densiflora*) forests (Ohtsuka et al. 2003), became established on lava flow. Compared with secondary succession, there have been few studies on ecological inventories on C cycling in the sere of primary succession on immature soils. Here, we conducted annual C storage estimates using biometric methods over 9 years (1999–2006) at a cool-temperate pine forest located in the lower slopes of Mt. Fuji, central Japan. Our study site is part of the AsiaFlux network of long-term C cycle research facilities (Mizoguchi et al. 2012). Our primary objectives were to estimate multiyear measurements of biometric-based NEP beneath a flux tower, and to validate the convergence of NEP. We also examined the contribution of different biological processes to the C budget, and show where and how C was sequestered in the temperate pine forest on lava flow.

Materials and methods

Study site

Japanese red pine (*P. densiflora*) dominates the Ken-Marubi lava flow in the lower north slopes of Mt. Fuji from 850 to 1,200 m a.s.l., and is distributed over an area of around 520 ha (Fig. 1a, b). The annual mean air temperature is 9.7 °C, with a minimum monthly mean temperature at the Yamanashi Institute of Environmental Sciences (YIES) of −0.7 °C in February and maximum monthly mean temperature of 21.4 °C in August. Annual precipitation is 2,025 mm and snow-depth is usually less than 50 cm in winter. The study area has a seasonal cool-temperate climate.

Pine tree age on the lava flow was mature, i.e., around 90–100 years (Ohtsuka et al. 2003). The lava flow was still exposed on the surface ground area in the mature pine forest, and the soil remains immature with an A0 layer without a mineral soil layer (Fig. 1c). There was little herbaceous vegetation on the forest floor, except for moss or lichen on the lava flow (Fig. 1b). To examine C cycling, a permanent plot of 80 m × 80 m was created in the pine forest near the YIES (35°27′N, 138°46′E, 1,030 m a.s.l.) in 1999. Detailed ground-based biometric measurements were performed in this plot. A flux tower for the eddy-covariance method is adjacent to the permanent plot, and CO_2 and energy exchange have been measured since May 1999 (Ohtani et al. 2005).

Net primary production

Biometric-based estimation of NEP determines the balance between NPP and Rh in an ecosystem, as follows:

$$\begin{aligned}\mathrm{NEP} &= \mathrm{GPP} - \mathrm{ER} = (\mathrm{NPP} + \mathrm{AR}) - (\mathrm{AR} + \mathrm{Rh}) \\ &= \mathrm{NPP} - \mathrm{Rh}\end{aligned}$$

where AR is autotrophic respiration. NPP of tree species was calculated using the following equation:

$$\mathrm{NPP} = \Delta B + L + M + P_{\mathrm{fr}}$$

where ΔB is the change in biomass of trees, L is litter production, M is necromass from tree mortality and P_{fr} is production of tree fine roots. We measured the annual diameter growth of all tree stems in the permanent plot in late autumn each year at the same painting position on all living stems > 5 cm from 1999 to 2008. The biomass of stems < 5 cm DBH was omitted from the NPP estimation. We defined net stand increments (SI) of above-ground (boles and branches) and below-ground (coarse roots) biomass as follows:

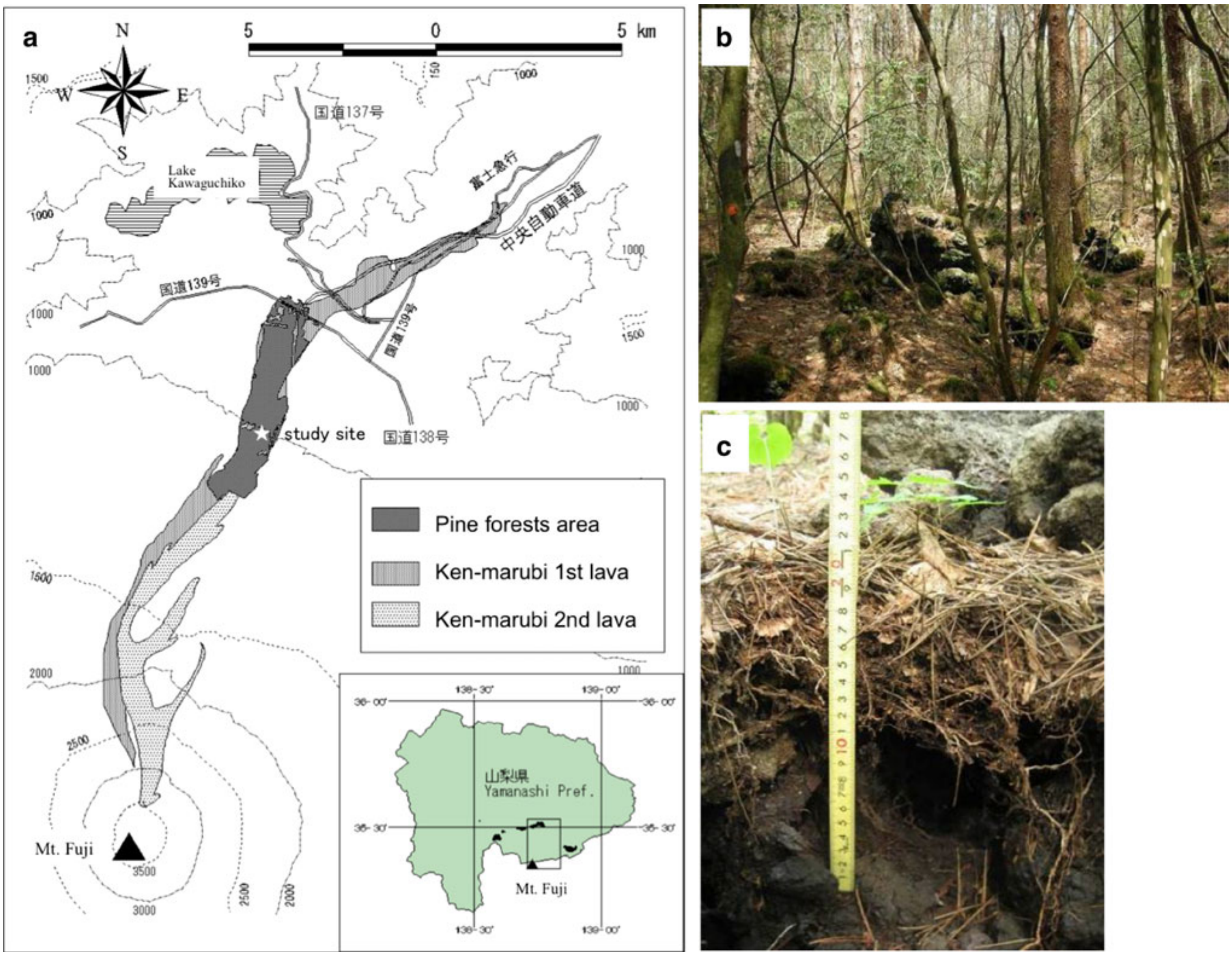


Fig. 1 **a** Map of the northern slope of Mt. Fuji and the Ken-Marubi lava flow; 1st lava was formed by the eruption of 937, and 2nd lava by the eruption of 1033 (Koyama 1998). *Pinus densiflora* is dominant on the Ken-Marubi 1st lava flow and is distributed across an area of around 520 ha from 850 to 1,200 m (a.s.l.). *White star* Permanent plot created for this study. **b**, **c** Images showing the physiognomy of the pine forest established on the Ken-Marubi 1st lava flow (**b**) and the soil profile (**c**). *Pinus densiflora* dominates the forest along with a dense evergreen subtree layer including, e.g., *Ilex pedunculosa*. Soil of the A0 layer is still immature and there is no mineral soil layer with the lava flow still being exposed on the surface

$$\begin{aligned}\text{Net stand increment (SI)} \\ &= \Sigma\ (\text{increments of surviving trees}) \\ &\quad + \Sigma\ (\text{increments(s) of ingrowth}).\end{aligned}$$

The increment for each tree was calculated as the difference between its estimated biomass at the beginning and end of the interval. The allometric relationship of tree organs (above-ground boles and branches, leaves and coarse roots) with DBH has been developed previously for the pine forest at a site near the permanent plot (Tanabe et al. 2003). The summed increments of ingrowth (recruit over 5 cm DBH during an interval) were added to SI. We did not measure DBH of ingrowth trees in the previous year and, thus, we assumed biomass at the beginning as the tree biomass of minimum diameter (5 cm). Woody mortality (M) was derived from a tree census, conducted every summer, in the plot. Necromass (including dead coarse roots) was derived from the allometric equations for live trees. ΔB is conceptually the same as net stand increment minus tree mortality. The foliage biomass is in a steady state in mature pine stands (Hatiya et al. 1989) and, therefore, it was assumed that the foliage biomass in 1999 was not altered over the study period in the plot. Dry biomass was assumed to be 50 % of the carbon content in live wood and foliage.

Litter production (L) was estimated from 10 litter traps (area 1 m^2) set in the permanent plot. Litterfall was collected monthly during the snow-free period, and also in early spring during the snow season from 1999 to 2007. Litterfall was divided into foliage, woody materials (bark and twigs) and others (flowers and seeds etc.), and was oven-dried to a constant mass and weighed. Five sub-plots (each 10 m × 10 m) were created in the permanent plot to trap branches larger than 2 cm in diameter, because such large, dead branches were not included in the litter traps. All dead branches in the five sub-plots were removed in early spring 2000 and cleared from the sub-plots monthly, during the snow-free period from 2000 to 2004. The large branches collected were oven-dried to a constant mass and then weighed. The dried litter samples, including the large branches, were measured using a CN analyzer to estimate their carbon content (g C g^{-1}).

Production of fine roots (P_{fr}) in the pine forest has been estimated to be 1.92 t C ha^{-1} $year^{-1}$, using sequential monthly core sampling from May 2000 to 2001 (Tanabe et al. 2003). P_{fr} was calculated using the following equation: $P_{\mathrm{fr}} = \Sigma P_{\mathrm{i}}$, where i is the month and P_{i} is the monthly change in both live (ΔL) and dead (ΔD) fine root biomass. P_{i} is calculated by the following rules: when both ΔL and ΔD are positive, $P_{\mathrm{i}} = \Delta L + \Delta D$; when ΔL is positive and ΔD is negative, $P_{\mathrm{i}} = \Delta L$; when ΔL is negative, $P_{\mathrm{i}} = 0$.

Soil respiration and heterotrophic respiration

Heterotrophic respiration in forest ecosystems includes decomposition of soil organic matter (SOM) ($\mathrm{Rh_{SOM}}$) and coarse woody debris ($\mathrm{Rh_{CWD}}$). Herbivore respiration was not included in our Rh calculation because of the small upward flux. Soil respiration (Rs), which can be observed as CO_2 efflux from the soil surface, consists of CO_2 emission due to autotrophic respiration by plant roots (Rr) and heterotrophic respiration by microbes ($\mathrm{Rh_{SOM}}$).

Rs was measured with a LiCor 6200 gas exchange analyzer with a soil chamber attachment (LiCor, Lincoln, NE). The LiCor 6200 is a closed-system infrared gas analyzer that measures the amount of CO_2 flux from the soil (detection limit 0.2 mmol CO_2 m^{-2} s^{-1}). PVC soil collars (10.5 cm in diameter, 4.5 cm in height) were installed into the soil at 20 locations in 0.05 ha subplots to a depth of about 1 cm to avoid severing the roots. These measurements were taken at monthly intervals, around noon, during the snow-free period from April to December in 2006 and 2007. Each time, three replicate Rs measurements were taken at the collar and the soil temperature at 5 cm depth was measured in close proximity to the collar, using a handheld temperature probe (TR-71S; T&D, Tokyo, Japan). Annual Rs ($\mathrm{Rs_{an}}$) was calculated based on the hourly monitoring of soil temperature at 5 cm depth in the permanent plot, and the relationship between Rs and soil temperature. Lava flows occupied 17.6 % of the surface ground area (Negishi 2008) and the estimated annual Rs in the permanent plot was thus corrected as $\mathrm{Rs_{an}} \times (1 - 0.176)$.

Root respiration of trees was estimated using fresh roots in the permanent plot. The fine and middle-sized root biomass was estimated by taking soil samples (10 cm × 10 cm, $n = 5$) to the depth of the parent rocks (lava flows) at the study site during the snow-free period six times (July, August, September, October, November and December) in 2005 for fine roots, and five times (June, August, September, October and December) in 2006 for fine and middle-sized roots. Roots found in each soil sample were washed in running water and separated into two classes based on their size, i.e., maximum diameter: fine (0–2 mm) and middle-sized roots (>2 mm). These were oven-dried for 2 days and then weighed.

Rr per unit biomass was measured using fresh roots five times (December 2006, May, September, October and December 2007) for fine roots, and twice (December 2006 and August 2007) for middle-sized roots. The severed fine roots (<2 mm) and middle-sized roots (>2 mm) were washed carefully by running water over the roots gently to remove the soil. The Rr measurements were performed in the laboratory within 24 h using an open-flow gas exchange system. The cut surfaces of the samples were sealed with silicone grease and the samples were then wrapped in wet paper sheets and placed in cylindrical chambers (3.5 cm internal diameter, 22 cm in length) connected to the system. Ambient air flowed into the system at a rate of 0.7 L min^{-1}. Measurements were taken to investigate Rr temperature dependence in a water bath under various temperatures, determined by considering the in situ temporal variation in soil temperature during each season. Differences in CO_2 concentrations of the inlet and outlet gas lines were determined with two infrared gas analyzer probes (GMP343; Vaisala, Helsinki, Finland). Once respiration was measured, the samples were oven-dried to calculate their dry weight.

Annual Rr ($\mathrm{Rr_{an}}$) was calculated based on hourly monitoring of soil temperature at 5 cm depth in the permanent plot, and the temperature dependence of Rr and mean fine and middle-sized root biomass per unit area in the permanent plot was also assessed. Total root biomass in the permanent plot was corrected because lava flows occupied 17.6 % of the surface ground area.

The size of the chamber was so small that decomposition of coarse woody debris (CWD) such as snags or large, dead branches could not be included in the Rs measurements. It was assumed that the C pool of CWD on the forest floor was in a steady state. Therefore, $\mathrm{Rh_{CWD}}$ was adapted from the mean annual dead branch litter, larger than 2 cm in diameter, which was estimated from branch traps (0.2 t C ha^{-1} $year^{-1}$).

Compartment model and carbon sequestration

A compartment model (Kira 1978; Ohtsuka et al. 2007) was applied to construct the C budget for the pine forest. The pine forest has three main C pools: tree biomass (B), CWD and SOM. The SOM pool was considered to include humus and fine litter (mainly leaf litter from the A0 layer), but to exclude CWD because $\mathrm{Rh_{CWD}}$ was not included in our Rs measurements. Accumulation of carbon in each compartment (pool) depends on the balance between carbon inputs and carbon losses. Annual ΔC in each carbon pool was estimated from changes in pool sizes by which carbon enters or leaves the pool, based on biometric-based flux measurements, as follows (see also below):

$$\Delta B = \mathrm{SI} - M$$
$$\Delta\mathrm{CWD} = \mathrm{CWD\ recruitment} - \mathrm{Rh}_{\mathrm{CWD}}$$
$$\Delta\mathrm{SOM} = \mathrm{SOM\ recruitment} - \mathrm{Rh}_{\mathrm{SOM}}.$$

Fine root production was adopted as a below-ground detritus production recruitment into the SOM pool in our study, since it was assumed that the fine root biomass is in an approximate steady state in a mature pine forest. Inputs of dead trees and large dead branches to the soil, as detritus, were excluded from SOM recruitment, as was the CWD component. In this case, CWD and SOM recruitment is the same as $M + L + P_{\mathrm{fr}}$ and, thus, biometric-based NEP is conceptually equivalent to the sum of the change in each carbon pool as follows:

$$\begin{aligned}\Delta B + \Delta\mathrm{CWD} + \Delta\mathrm{SOM} &= (\Delta B + M + L + P_{\mathrm{fr}}) \\ &\quad - (\mathrm{Rh}_{\mathrm{CWD}} + \mathrm{Rh}_{\mathrm{SOM}}) \\ &= \mathrm{NPP} - \mathrm{Rh}.\end{aligned}$$

Uncertainty analysis for biometric estimates

We examined potential uncertainties (σ) associated with the model and sampling errors of the biometric estimates. The uncertainty in biometric tree biomass increments (ΔB), tree mortality and litter production was computed from the SD around the year-to-year variability. Uncertainty associated with allometric equations was not estimated because coefficient standard error was not published in Tanabe et al. (2003). The uncertainty of the annual Rs and Rr ($\mathrm{Rr}_{\mathrm{an}}$) was determined from the % root mean square error (RMSE) given by the model output for the respective respiration model. The total uncertainty of NPP, Rh and NEP were estimated as:

$$\sigma^2\mathrm{NPP} = \sigma^2\Delta B + \sigma^2 L + \sigma^2 M$$
$$\sigma^2\mathrm{Rh} = \sigma^2\mathrm{Rs} + \sigma^2\mathrm{Rr}$$
$$\sigma^2\mathrm{NEP} = \sigma^2\mathrm{NPP} + \sigma^2\mathrm{Rh}.$$

Results

Forest structures and net primary production

Table 1 shows the species composition and the community structures of the pine forest over 5 cm DBH in the 0.64 ha permanent plot in 1999. The basal area (BA) of *P. densiflora* was 42.5 m^2 ha^{-1}, occupying 84.5 % of the total BA, with a density of 920 stems ha^{-1}. The largest DBH was 47.9 cm and the mean DBH was 23.3 cm; there were no small pine trees with a DBH of less than 10 cm. *P. densiflora* was mono-dominant in the forest but many deciduous tree species occurred in the permanent plot, such as *Quercus serrata* (2.2 % of BA), *Quercus mongolica* (1.0 % of BA), *Prunus maximowiczii* (0.8 % of BA) and *Carpinus japonica* (0.8 % of BA). A dense evergreen sub-tree layer (around 6 m high), developed under the canopy of pine trees (around 19 m high) and included plants such as *Ilex pedunculosa* (5.4 % of BA with 686 stems ha^{-1}), *Clethra barbinervis* (0.7 % of BA with 120 stems ha^{-1}) and *Lyonia ovalifolia* (0.7 % of BA with 120 stems ha^{-1}).

Over the period of 9 years (1999–2008), the number of pine trees (>5 cm) decreased from 920 to 872 stems ha^{-1} due to tree mortality and lack of recruitment of pine trees into the permanent plot (Table 2). Other tree species also decreased slightly from 391 to 381 stems ha^{-1} irrespective of some recruit stems. In contrast, the stem number of sub-tree species increased, especially for *Ilex pedunculosa* because of high recruitment, although the overall number of stems >5 cm decreased slightly from 2,556 to 2,544 stems ha^{-1}. The above-ground (except for foliage) biomass increased from 98.1 to 107.9 t C ha^{-1}, and below-ground (coarse root) biomass increased from 30.0 to 33.3 t C ha^{-1} over the period of 9 years in the permanent plot. Leaf biomass in the pine forest was 2.1 t C ha^{-1}. The mean above-ground (except for foliage) net stand increment was 1.5 ± 0.3 t C ha^{-1} year^{-1} and that of coarse roots was 0.5 ± 0.1 t C ha^{-1} year^{-1} based on allometric equations (Table 3). The mean annual ΔB including aboveground and coarse root biomass amounted to 1.4 ± 0.4 t C ha^{-1} year^{-1}, which was less than the net stand increment because the annual mortality including aboveground and coarse roots was 0.6 ± 0.2 t C ha^{-1} year^{-1} over the 9 years.

Annual above-ground litter production was averaged across the 8 years (Table 4): 1.4 ± 0.3 t C ha^{-1} year^{-1} for pine leaves, 0.6 ± 0.1 t C ha^{-1} year^{-1} for other leaves, 0.8 ± 0.3 t C ha^{-1} year^{-1} for woody materials and 0.3 ± 0.1 t C ha^{-1} year^{-1} for other materials (e.g., flowers and cones). Annual woody litter production varied from year to year by a factor of more than four, whereas foliage litter production was less variable. Annual litter of branches larger than 2 cm in diameter (estimated using branch traps) amounted to 0.2 ± 0.1 t C ha^{-1} year^{-1} during the 5 years from 2000 to 2004 and showed less year-to-year variability. The mean NPP was calculated as follows:

$$\begin{aligned}\mathrm{NPP} &= \Delta B + L + M + P_{\mathrm{fr}} \\ &= 1.4 + (3.2 + 0.2) + 0.6 + 1.9 \\ &= 7.3 \pm 0.7\,\mathrm{t\,C\,ha^{-1}year^{-1}}.\end{aligned}$$

Soil respiration and root respiration

Soil respiration rates displayed clear seasonal variation, and peaked in summer depend on soil temperature variation during the experimental period in 2006 and 2007. Measured Rs was correlated significantly with exponential soil temperature at 5 cm depth in the field

Table 1 Species composition and community structures in the permanent plot [diameter at breast height (DBH) > 5 cm], 1999

	Basal area		DBH (cm)		No of stems	
	$m^2\ ha^{-1}$	%	Mean	Max	ha^{-1}	%
Evergreen trees						
Pinus densiflora	42.51	84.49	23.3	47.9	920	36.0
Tsuga sieboldii	0.17	0.33	26.2	27.3	3	0.1
Deciduous trees						
Quercus serrata	1.12	2.23	10.0	24.3	122	4.8
Quercus mongolica	0.51	1.01	8.2	18.6	84	3.3
Prunus maximowiczii	0.42	0.83	9.5	20.6	50	2.0
Carpinus japonica	0.39	0.78	7.5	22.4	78	3.1
Tilia japonica	0.14	0.27	7.9	16.1	25	1.0
Larix kaempferi	0.13	0.27	23.0	27.3	3	0.1
Quercus acutissima	0.09	0.18	11.6	17.2	8	0.3
Betula platyphylla var. *japonica*	0.05	0.10	10.9	14.6	5	0.2
Alnus hirsuta	0.03	0.07	16.8	16.8	2	0.1
Acer sieboldianum	0.03	0.05	14.6	14.6	2	0.1
Cornus controversa	0.02	0.04	7.6	9.0	5	0.2
Acanthopanax sciadophylloides	0.02	0.03	11.1	11.1	2	0.1
Populus sieboldii	0.01	0.02	9.3	9.3	2	0.1
Acer mono var. *marmoratum*	0.01	0.02	8.3	8.3	2	0.1
Subtotal	45.64	90.72	19.1	47.9	1311	51.3
Evergreen subtree						
Ilex pedunculosa	2.71	5.38	6.9	15.0	686	26.8
Juniperus rigida	0.21	0.41	10.7	18.1	20	0.8
Deciduous subtree						
Clethra barbinervis	0.36	0.71	6.1	8.9	120	4.7
Lyonia ovalifolia	0.33	0.67	5.9	10.4	120	4.7
Acer crataegifolium	0.26	0.51	7.6	13.4	53	2.1
Euonymus macropterus	0.25	0.50	6.6	9.2	72	2.8
Fraxinus sieboldiana	0.15	0.30	5.8	7.4	56	2.2
Sorbus alnifolia	0.12	0.23	7.1	11.4	28	1.1
Ilex macropoda	0.08	0.16	7.0	9.1	20	0.8
Rhus trichocarpa	0.03	0.07	6.2	6.8	11	0.4
Lindera obtusiloba	0.02	0.05	5.6	6.4	9	0.4
Prunus incisa	0.02	0.04	6.6	8.1	6	0.2
Malus toringo	0.004	0.01	6.0	6.0	2	0.1
Subtotal	4.55	9.04	6.7	18.1	1205	47.1
Evergreen shrub						
Pieris japonica	0.04	0.09	6.7	8.1	13	0.5
Deciduous shrub						
Hydrangea paniculata	0.07	0.15	5.7	7.4	28	1.1
Subtotal	0.12	0.24	6.0	8.1	41	1.6
Total	50.31	100.00	13.1	47.9	2556	100.0

Table 2 Forest dynamics (dead and recruit stems) in the pine forest under study during 1999–2008

Years	Number of stems (ha^{-1})			
	Live (1999)	Dead (1999–2008)	Recruit (1999–2008)	Live (2008)
Tree species				
Pinus densiflora	920	48	0	872
Others	391	18	8	381
Subtree species				
Ilex pedunculosa	686	20	67	733
Others	519	62	67	524
Shrub species	41	8	1	34
Total	2556	156	143	2544

The change of tree stem number (ha^{-1}, DBH > 5 cm) were indicated

(Fig. 2). The Q_{10} value of soil respiration was 2.92. The respiration rates of fine roots in laboratory experiments varied greatly depending on the season, being higher in September 2007 and lower in May 2007 (Fig. 3a). The respiration rate of fine roots (Fig. 3a) was much higher than that of middle-sized roots (Fig. 3b). Both the respiration rates by fine and middle-sized roots were significantly correlated exponentially with temperature. The Q_{10} values of fine and middle-sized root respiration were 2.98 and 1.52, respectively.

Figure 4 shows the seasonal change in soil temperature at 5 cm depth and the monthly summed soil respiration and root respiration calculated by the Q_{10} function and driven by soil temperature (Figs. 2, 3). The monthly summed soil respiration showed a sharp increase from April to August, reached a peak in August (1.3 t C ha^{-1} month^{-1} in 2006 and 1.2 t C ha^{-1} month^{-1} in 2007) and then decreased in autumn (Fig. 4b). Total annual soil respiration after correction of the lava flow area was 6.3 t C ha^{-1} year^{-1} in 2006 and was 5.9 t C ha^{-1} year^{-1} in 2007.

The mean root biomass was 1.55 ± 0.2 t C ha^{-1} for fine roots and 4.27 ± 6.2 t C ha^{-1} for middle-sized roots in the permanent plot (Table 5). Spatial variations of middle-sized roots biomass were much larger than the fine root biomass. Root respiration by fine and middle-sized roots per unit area was interpolated by means of the Q_{10} function (Fig. 3), soil temperature at 5 cm depth (Fig. 4a) and mean root biomass per unit area for each root. The monthly summed root respiration also showed a clear seasonal change (Fig. 4b). Total annual fine root respiration was 1.1 t C ha^{-1} year^{-1} in 2006 and 1.0 t C ha^{-1} year^{-1} in 2007, and total annual middle-sized root respiration was 0.8 t C ha^{-1} year^{-1} both in 2006 and 2007 (assuming that fine and middle-sized root biomass was constant and that the Q_{10} function was driven by soil temperature at 5 cm depth throughout the year). Total annual root respiration (Rr_{an}) was estimated as 1.9 ± 1.0 t C ha^{-1} year^{-1} with high uncertainty.

Table 3 Biometric based annual carbon budget over 9 years (1999–2008) in the pine forest under study (t C ha^{-1} year^{-1})

	Carbon fluxes (SD or RMSE)
ΔBiomass	+1.4 ± 0.4
Aboveground	
Stand increment	1.5 ± 0.3
Mortality	−0.4 ± 0.2
Subtotal	1.1 ± 0.3
Belowground	
Stand increment	0.5 ± 0.1
Mortality	−0.1 ± 0.1
Subtotal	0.4 ± 0.1
ΔDead Wood	+0.6 ± 0.2
Mortality	
Trees	0.6 ± 0.2
Branches	0.2 ± 0.1
Respiration	−0.2[a]
ΔSOM	+0.9 ± 3.1
Litter input	
Above-ground	3.2 ± 0.5
Fine root production	1.9[b]
Respiration	−4.2 ± 3.1
Soil respiration	−6.1 ± 2.9
Root respiration	−1.9 ± 1.0
Δ*C* = NEP	+2.9 ± 3.2

Cumulative error was determined using squared sum of the standard deviation (SD) or root mean square error (RMSE) of component parameters. *SOM* Soil organic matter, *NEP* net ecosystem production

[a] Respiration of dead wood was adapted from the mean annual dead branch litter, which was estimated from branch traps

[b] Fine root production was estimated by Tanabe et al. (2003) during the period May 2000 to May 2001 and was adopted as a below-ground detritus production

Contribution of root respiration to soil respiration showed large seasonal variations (Fig. 4c); the contribution was large in winter (around 53 %) and small in summer (20 %). The annual soil respiration (Rs_{an}) was estimated as 6.1 ± 2.9 t C ha^{-1} year^{-1}, and the average contribution of root respiration to soil respiration was 30.4 %. Thus, the annual mean Rh_{SOM} was estimated to be 4.2 ± 3.1 t C ha^{-1} year^{-1}.

Carbon cycling and sequestration in the pine forest

Annual NPP amounted to 7.3 ± 0.7 t C ha^{-1} year^{-1} including fine root production. The NPP allocation was as follows: 1.4 ± 0.4 t C ha^{-1} year^{-1} to living biomass, 0.8 ± 0.2 t C ha^{-1} year^{-1} to CWD production including tree mortality and dead large branches, 3.2 ± 0.5 t C ha^{-1} year^{-1} to above-ground fine litter production for SOM recruitment, and P_{fr} (1.9 t C ha^{-1} year^{-1}). Fine root production was adopted as a below-ground detritus production recruitment into the SOM pool. Heterotrophic respiration (Rh_{SOM} and Rh_{CWD}) was estimated to be 4.2 ± 3.1 t C ha^{-1} year^{-1} and 0.2 t C ha^{-1} year^{-1}, respectively. Thus, biometric-based NEP including fine root production was calculated as follows:

$$\begin{aligned} \mathrm{NEP} &= \mathrm{NPP} - \mathrm{Rh} = 7.3 - (4.2 + 0.2) \\ &= 2.9 \pm 3.2\,\mathrm{t\,C\,ha^{-1}year^{-1}}. \end{aligned}$$

Table 4 Annual above-ground detritus production[a] (t C ha^{-1} year^{-1}) in the pine forest under study

	2000	2001	2002	2003	2004	2005	2006	2007	Average (±SD)
Foliage									
Pinus densiflora	1.37	1.28	1.40	1.36	1.55	1.03	1.77	1.79	1.44 ± 0.3
Other trees	0.71	0.65	0.64	0.62	0.65	0.61	0.55	0.74	0.64 ± 0.1
Subtotal	2.07	1.93	2.04	1.97	2.20	1.64	2.31	2.53	2.09 ± 0.3
Woody materials									
Barks	0.26	0.19	0.32	0.30	0.38	0.18	0.46	0.36	0.31 ± 0.1
Twigs	0.61	0.15	0.62	0.49	1.04	0.41	0.28	0.38	0.50 ± 0.3
Subtotal	0.87	0.35	0.94	0.79	1.42	0.59	0.74	0.74	0.80 ± 0.3
Others	0.28	0.21	0.47	0.37	0.41	0.28	0.32	0.34	0.33 ± 0.1
Total	3.23	2.48	3.45	3.14	4.02	2.51	3.37	3.61	3.23 ± 0.5
Branches (*D* > 2 cm)	0.23	0.12	0.23	0.27	0.36	ND	ND	ND	0.24 ± 0.1

[a] Detritus production was measured using ten litter traps in the permanent plot (dead branches were excluded). Annual dead branch litter was cleared from five sub-plots (each 10 m × 10 m) that acted as branch traps

Estimated NEP had large uncertainty and that was due mainly to the large RMSE of Rs and Rr given by the model output (Figs. 2, 3).

Mizoguchi et al. (2012) measured the eddy covariance-based NEP at the same pine forest on Mt. Fuji from 2000 to 2008. The NEP (−NEE) varied from year to year and the mean NEP over 9 years was 3.88 t C ha^{-1} year^{-1}. Year-to-year variability of NEP depended mainly on air temperature and photosynthetically active radiation in summer, and the dependence of the deviation of annual NEP on that of GPP was greater than that of ER. Our estimate of biometric-based NEP (2.9 t C ha^{-1} year^{-1} in 2000–2007) was 25 % lower than the eddy covariance-based NEP in this pine forest.

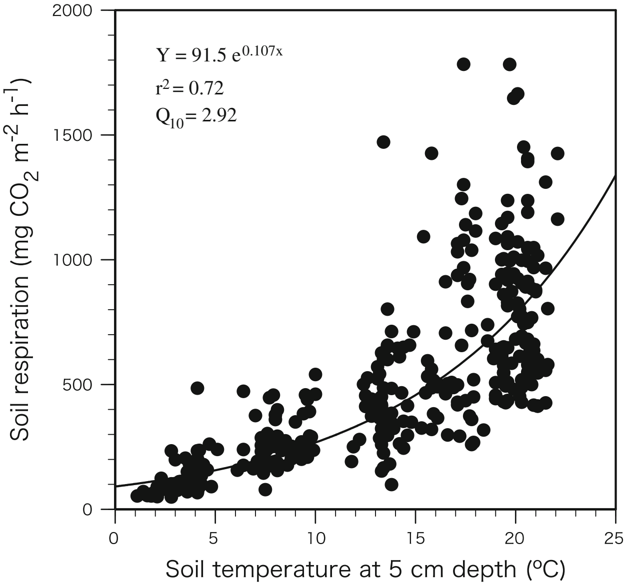


Fig. 2 Relationship between soil respiration and soil temperature at 5 cm depth at the study site during the snow-free period in 2006 and 2007

Biometric NEP is conceptually equivalent to the sum of the changes in following carbon pools:

$$\Delta C = \Delta B + \Delta \mathrm{CWD} + \Delta \mathrm{SOM}.$$

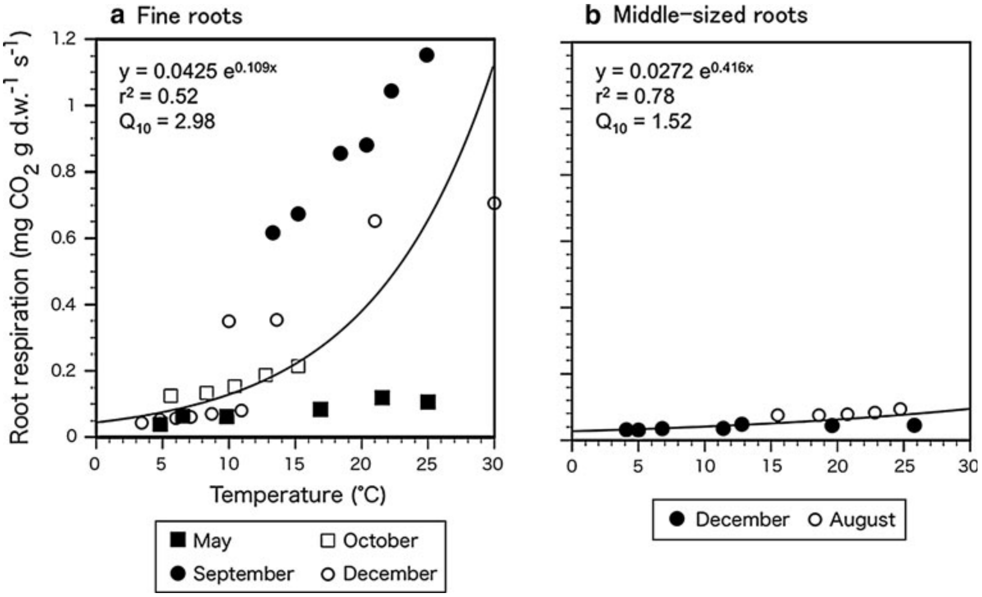
ΔB amounted to 1.1 ± 0.3 t C ha^{-1} year^{-1} for above-ground biomass excluding foliage and 0.4 ± 0.1 t C ha^{-1} year^{-1} for coarse root biomass from the balance between net stand increments and tree mortality (Table 3). ΔCWD was estimated from the balance between CWD recruitment including tree mortality and dead branches and Rh$_{\mathrm{CWD}}$, which was estimated to be 0.6 ± 0.2 t C ha^{-1} year^{-1}. ΔSOM was also estimated as the balance between SOM recruitment and Rh$_{\mathrm{SOM}}$. SOM recruitment includes above-ground fine litter production (3.2 t C ha^{-1} year^{-1}) and fine root production (1.9 t C ha^{-1} year^{-1}). The mean annual rate of Rh$_{\mathrm{SOM}}$ was 4.2 ± 3.1 t C ha^{-1} year^{-1}. Thus, the change of SOM pool in the pine forest under study (0.9 ± 3.1 t C ha^{-1} year^{-1}) had high uncertainty, due mainly to respiration measurements errors.

Discussion

Biometric and eddy covariance-based NEP estimates

One of the possible reasons for the difference between eddy covariance- and biometric-based NEP is that not all C fluxes produced in a year have been accounted for in relation to biometric NPP in field studies (Clark et al. 2001). Most frequently, measurements are restricted to aboveground litterfall and biomass increment, and their sum is considered equivalent to aboveground NPP. We

Fig. 3 Relationship between root respiration (**a** fine roots, **b** middle-sized roots) and temperature in a chamber in laboratory experiments. *Symbols* indicate the sampling month of the roots



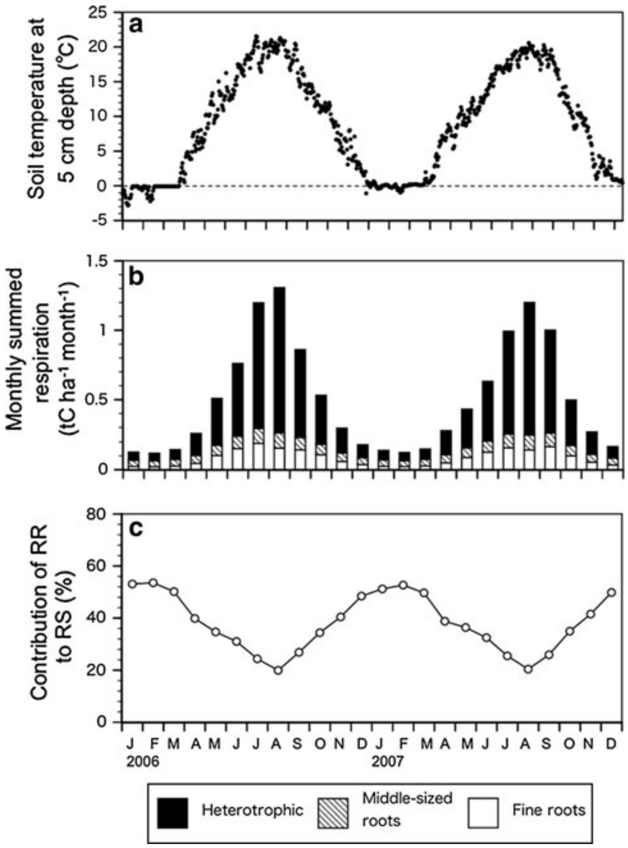


Fig. 4 **a** Seasonal changes in soil temperature at 5 cm depth, and **b** summed soil respiration (Rs) and root respiration (Rr), calculated monthly at the study site in 2006 and 2007. The monthly summed soil respiration was calculated using the regression equation in Fig. 2 and soil temperature was noted hourly. The monthly summed fine and middle-sized root respirations were calculated using the regression equation in Fig. 3, soil temperature logged at hourly intervals as well as the fine and middle-sized root biomass per hectare. Average values of the observed root biomass in 2005 and 2006 (Table 5) were used for the calculation. Heterotrophic respiration (Rh_{SOM}) was subtracted Rr from Rs, and contribution of total Rr to Rs is also shown (**c**)

Table 5 Fine (< 2 mm diameter) and middle-sized (> 2 mm) root biomass (t C ha^{-1}) in the pine forest under study

	Fine roots	Middle-sized roots
June	1.73 ± 0.19	7.09 ± 8.95
July	1.51 ± 0.15	ND
August	1.20 ± 0.11	2.03 ± 3.58
September	1.49 ± 0.14	7.11 ± 7.32
October	1.66 ± 0.19	3.57 ± 5.38
November	2.08 ± 0.21	1.55 ± 1.77
December	1.61 ± 0.18	ND
Average	1.55 ± 0.18	4.27 ± 6.22

Root biomass was estimated by taking soil samples (10 cm × 10 cm area) to a depth of the parent rocks (lava flows) in the permanent plot during the snow-free period, 2005 and 2006. Values are mean ± 1 SE of 5–10 replicates each

included below-ground (coarse roots) biomass increment and fine root production in biometric NPP, but did not include losses to consumers or volatile and leached organics, and these resulted in a slight underestimation of NPP in our study.

Estimates of both fine root production (P_{fr}) and fine root biomass are still highly uncertain because of the considerable temporal and spatial variability (Vogt et al. 1998). In the last two decades, the use of minirhizotron, based on sequential video images recorded by a camera within a buried transparent tube, has become a favourite method of many researches (e.g., Aerts et al. 1989; Steele et al. 1997). The minirhizotron approach enables direct observation of the growth and mortality of fine roots. The sequential root coring method, applied by Tanabe et al. (2003) at our study site, was the most commonly used method in the past and is still common, although this method should be conducted with a large number of replicate samples taken on a few dates per season. Hertel and Leuschner (2002) applied four different approaches to determine P_{fr} in an old-growth temperate forest. When compared to the C budget data, the sequential coring approach overestimated P_{fr}, whereas the in-growth core and minirhizotron approach grossly underestimated P_{fr}. They concluded that the most reliable estimates of P_{fr} would be obtained by applying the sequential coring/minimum–maximum approach in conjunction with direct root growth observation by minirhizotrons, although it is difficult to install the required tubes in immature soils on lava flow under study.

Other major uncertainties in the results from biometric methods were associated with Rs measurements in the field. As all natural ecosystems are heterogeneous at some scale, the question arises as to whether or not estimation of soil respiration based on a limited number of samples represents the average of the total ecosystem (Ehman et al. 2002; Ohtsuka et al. 2007). Rs should have varied greatly in the pine forest on lava flow, which has a large heterogeneity of soil depth. There are only few studies of Rs in an ecosystem on a lava flow, and methods for scaling up of Rs and correction of lava flow occupation on the soil surface need to be improved, for example, by using more chambers of a smaller size to detect correlations between Rs and soil depth.

Partitioning Rs into autotrophic root respiration and heterotrophic respiration is also controversial. Three primary methods have been used to partition: root exclusion (e.g., trenched plot), root extraction (measuring root respiration), and application of stable or radioactive isotopes (Hanson et al. 2000). We used the root extraction method, measuring Rr per unit biomass using cut fresh roots in the laboratory, and partitioned Rs into Rr (1.9 t C ha^{-1} year^{-1}) and Rh_{SOM} (4.2 t C ha^{-1} year^{-1}). However, Rr, especially for fine roots, had large RSME, due mainly to the temporal (seasonal) changes and spatial change (size or species) of fine root activities.

Many studies have attempted to partition Rs into these two components, with highly variable results. Bond-Lamverty et al. (2004) analyzed published data encompassing 54 forests and showed that Rh values using three primary methods are strongly correlated to annual Rs across a wide range of forest ecosystems: ln (Rh) = 1.22 + 0.73 ln (Rs), (unit of g C m^{-2} $year^{-1}$, $r^2 = 0.81$, $n = 53$). Using the formula of Bond-Lamberty et al. (2004), the Rh was estimated to be 3.7 t C ha^{-1} $year^{-1}$ and thus the biometric-based NEP is 7.3–3.7 = 3.6 t C ha^{-1} $year^{-1}$, which agrees well with the cumulative sum of eddy covariance-based NEP (3.88 t C ha^{-1} $year^{-1}$). Therefore, the current method in partitioning may overestimate Rh due to some uncertainty: both the root biomass and respiration might have temporal variation that we had not considered (Satomura et al. 2006), while root respiration can differ between laboratory and field measurements (Bekku et al. 2009). In addition, method-specific issues in the eddy-covariance method (e.g., choice of u* threshold, advection loss etc.) may also be responsible for the differences between the two methods.

Carbon sequestration in the pine forest

Long-term studies of carbon cycling in temperate regions, not only of eddy covariance but also of biometric measurements, conducted at Harvard (Urbanski et al. 2007) and Takayama (Ohtsuka et al. 2009) Forests, have helped demonstrate the temporal variation in NEP and where and how the forest stores carbon (Table 6). There are two contrasting C pools in forest ecosystems: biomass pool and non-living pools (CWD and SOM pools). For example, the mean annual NEP in the Takayama Forest was partitioned into 0.3 t C to the biomass pool, 1.0 t C to the CWD pool, and 0.8 t C to the SOM pool (Table 6; Ohtsuka et al. 2007). Annual woody NPP (1.3 t C ha^{-1} $year^{-1}$), which sequestered C to woody parts (annual net stand increment in Table 3) did not dominate C uptake, accounting for less than half of eddy covariance-based NEP (2.8 t C ha^{-1} $year^{-1}$). Non-living C pools play important roles in carbon sequestration, partly due to litter production by dense forest floor vegetation and high tree mortality in the Takayama Forest (Ohtsuka et al. 2009). In contrast, the mean woody NPP (1.7 t C ha^{-1} $year^{-1}$) comprised more than 80 % of the eddy covariance-based NEP (2.0 t C ha^{-1} $year^{-1}$) in the Harvard Forest (Table 6; Barford et al. 2001). This was also suited to the Michigan (Gough et al. 2008), Takayama cedar plantation (Yashiro et al. 2010; Saito et al. 2010) and Yamashiro (Kominami et al. 2008) sites, although the mean annual woody NPP has slightly larger values than eddy covariance-based NEP. In these cases, almost all the annual C uptake (NEP) sequestered in the biomass pool of woody trees in ecosystems, and non-living C pools is nearly steady state.

Table 6 Comparison of the forest carbon fluxes (t C ha^{-1} $year^{-1}$) of temperate region beneath a flux tower (except for Takayama young forest)

Latitude	Yamashiro[a]	Fujiyoshida[b]	Takayama young forest[c]	Takayama forest[d]	Takayama cedar plantation[e]	Harvard forest[f]	Michigan[g]
	34°47′N	35°27′N	36°07′N	36°08′N	36°08′N	42°54′N	45°35′N
Annual mean temperature	15.5 °C	9.7 °C		7.3 °C	11.2 °C		5.5 °C
Altitude	220 m	1,030 m	1,160 m	1,420 m	800 m	340 m	
ΔBiomass	+1.3	+1.4	+2.5	+0.3	+4.1	+1.0	+2.1
Aboveground							
Net stand increment		1.5	2.4	1.1	3.3	1.4	
Mortality		−0.4	−0.4	−0.8	−0.2	−0.6	
Subtotal	1.1	1.1	2.0	0.3	3.1	0.8	1.7
Belowground							
Net stand increment		0.5	0.7	0.2	1.1	0.3	
Mortality		−0.1	−0.2	−0.2	−0.1	−0.1	
Subtotal	0.2	0.4	0.5	0.0	1.0	0.2	0.4
ΔDead wood	+0.1	+0.6		+1.0		+0.4	
Mortality	0.6	0.8	0.5	1.5	0.3	0.7	0.2
Respiration	−0.5	−0.2	ND	−0.5	ND	−0.3	ND
ΔSOM	+0.3	+0.9	−1.6	+0.8	±0	+0.2	−0.8
Litter input							
Foliage	2.6	2.1	1.6	1.8	2.7	1.4	1.5
Others		3.0	1.6	2.9	0.9		2.7
Respiration	−3.7	−4.2	−4.9	−3.9	−3.6		−5.0
ΔC = NEP	1.7	2.9	0.9–1.4	2.1	4.0–4.3	1.6	1.4–1.5
-NEE	1.2	3.9	ND	2.8	3.4	2.0	1.5

[a] Kominami et al. (2008)

[b] This study and Mizoguchi et al. (2012)

[c] Ohtsuka et al. (2010)

[d] Ohtsuka et al. (2007) and Saigusa et al. (2005)

[e] Yashiro et al. (2010) and Saito et al. (2010)

[f] Barford et al. (2001) and Urbanski et al. (2007)

[g] Gough et al. (2008)

During the early stages of succession, forest NPP increases greatly due to the rapid increase in biomass of pioneer trees. The Japanese red pine (*P. densiflora*) is a typical pioneer tree species, both in secondary (e.g., Higo et al. 1995; Kamada and Nakagoshi 1991) and primary (e.g., Tagawa 1965; Tsujimura and Hara 1995) succession in temperate Japan. Hatiya et al. (1989) summarized primary production processes in 11 *P. densiflora* forests of different age ranged from 7 to 120 years and analyzed relationships between aboveground NPP (ANPP) and stand age in temperate Japan. ANPP of pine forests reached a maximum of 22–25 t ha^{-1} $year^{-1}$ [dry weight (dw) basis] followed by a substantial decline to 13 t dw ha^{-1} $year^{-1}$ in 50-year-old and 10 t dw ha^{-1} $year^{-1}$ in 120-year-old mature forests. The ANPP of our study site (excluding coarse and fine root production) was 5.1 t C (ca. 10 t dw) ha^{-1} $year^{-1}$. This value corresponds well with the results of Hatiya et al.'s (1989) study of mature pine stands.

Forest NPP and its allocation to woody components of temperate forest ecosystems also vary dramatically at successional stages. In temperate pioneer deciduous forests, annual aboveground woody NPP was 1.4 t C ha^{-1} $year^{-1}$ in a shrubby stage of 7 years after clear-cutting, and then increased to 2.0 t C ha^{-1} $year^{-1}$ at 11 years site after clear-cutting in a cool-temperate region (Shizu et al. 2012). Takayama young forest site of 18 years after clear-cutting (Table 6) also had a large annual aboveground net stand increment of 2.4 t C ha^{-1} $year^{-1}$ due to rapid growth of pioneer trees with low mortality (Ohtsuka et al. 2010). Compared to the young Takayama forest site, woody NPP is small in the middle-aged site of Takayama Forest of a 50–60 years pioneer forest (Ohtsuka 2012), and Harvard Forest with 50–70 years mixed forest (Urbanski et al. 2007). A temperate coniferous forest (Takayama cedar plantation site in Table 6) has large aboveground woody NPP (3.3 t C ha^{-1} $year^{-1}$) compared to other temperate deciduous

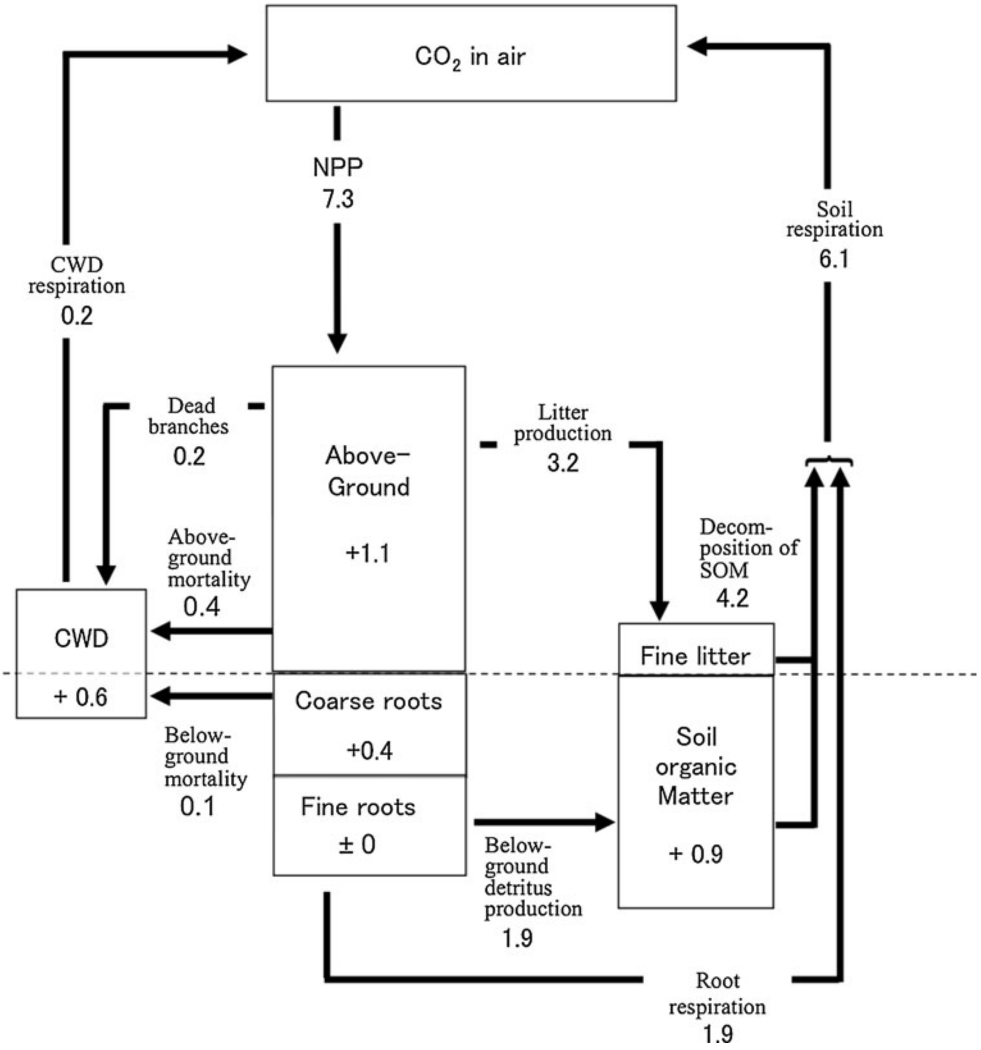


Fig. 5 Compartment model of carbon pools and fluxes in a pine forest established on a lava flow. *Squares* Carbon pools, *arrows* carbon fluxes measured or estimated in this study. *Numbers* Mean annual carbon fluxes (t C ha^{-1} $year^{-1}$) and carbon budget of each carbon pool in the permanent plot

or mixed forests due to higher tree growth of the planted evergreen trees (Yashiro et al. 2010). The above-ground woody NPP of the evergreen pine forest under study was 1.5 t C ha^{-1} year^{-1}, which was nearly the same as the other deciduous or mixed forests irrespective of the mature age (ca. 100 years) of pine trees with low nutrient content in immature soils (Tanabe et al. 2006).

Foliage litter production is the annual carbon allocation of NPP to the foliage component (foliage NPP that recruited C to SOM pools). The mean leaf biomass (annual leaf litter production) in Japanese deciduous broad-leaved forests is 3.1 ± 1.5 t ha^{-1} (dry weight basis). The maximum rate of annual leaf-fall in fully closed stable stands may be around 5 t ha^{-1} year^{-1} (dry weight basis) in Japanese temperate forests (Shidei and Kira 1977). Foliage NPP of the temperate deciduous broad-leaved forests beneath flux towers was rather uniform, ranging from 1.4 to 1.8 t C ha^{-1} year^{-1}, which falls within the range of the previous data. The Yamashiro site, with its warm-temperate deciduous-evergreen mixed forests, has the largest foliage NPP (2.6 t C ha^{-1} year^{-1}) among the sites (Table 6). These values correspond to foliage NPP in evergreen coniferous forests beneath flux towers at Takayama cedar plantation (2.7 t C ha^{-1} year^{-1}) and our study site (2.1 t C ha^{-1} year^{-1}).

In our study site, woody NPP (2.0 t C ha^{-1} year^{-1}) also did not dominate C uptake, which comprised only 51 % of eddy-covariance based NEP (3.9 t C ha^{-1} year^{-1}) despite a large proportion of woody NPP compared to the Takayama Forest. This may indicate that both the biomass pool and non-living C pools play an important role in carbon sequestration in the pine forest established on the lava flow. Our results (Fig. 5) indicate that the mature pine forest on lava flow is forecast as a significant carbon sink (NEP = 2.9 t C ha^{-1} year^{-1}) with sequestered carbon being allocated in roughly equal amounts to the biomass pool and the non-living carbon pools. However, as mentioned above, the current methods in Rs and Rr measurements in this study may have added large uncertainty. Therefore, further studies of heterotrophic respiration in SOM decomposition and below-ground detritus production are still needed.

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