Carbon cycling and net ecosystem production at an early stage of secondary succession in an abandoned coppice forest

Toshiyuki Ohtsuka · Yoko Shizu · Ai Nishiwaki · Yuichiro Yashiro · Hiroshi Koizumi

Abstract Secondary mixed forests are one of the dominant forest cover types in human-dominated temperate regions. However, our understanding of how secondary succession affects carbon cycling and carbon sequestration in these ecosystems is limited. We studied carbon cycling and net ecosystem production (NEP) over 4 years (2004–2008) in a cool-temperate deciduous forest at an early stage of secondary succession (18 years after clear-cutting). Net primary production of the 18-year-old forest in this study was 5.2 tC ha^{-1} year^{-1}, including below-ground coarse roots; this was partitioned into 2.5 tC ha^{-1} year^{-1} biomass increment, 1.6 tC ha^{-1} year^{-1} foliage litter, and 1.0 tC ha^{-1} year^{-1} other woody detritus. The total amount of annual soil surface CO_2 efflux was 6.8 tC ha^{-1} year^{-1}, which included root respiration (1.9 tC ha^{-1} year^{-1}) and heterotrophic respiration (RH) from soils (4.9 tC ha^{-1} year^{-1}). The 18-year forest at this study site exhibited a great increase in biomass pool as a result of considerable total tree growth and low mortality of tree stems. In contrast, the soil organic matter (SOM) pool decreased markedly (-1.6 tC ha^{-1} year^{-1}), although further study of below-ground detritus production and RH of SOM decomposition is needed. This young 18-year forest was a weak carbon sink (0.9 tC ha^{-1} year^{-1}) at this stage of secondary succession. The NEP of this 18-year forest is likely to increase gradually because biomass increases with tree growth and with the improvement of the SOM pool through increasing litter and dead wood production with stand development.

Keywords Carbon cycling · Net ecosystem production · Net primary production · Secondary succession · Soil respiration · Takayama

Introduction

Secondary mixed forests are one of the dominant forest cover types in temperate regions because the utilization of forested areas, e.g., as grasslands, arable land and coppice forests for charcoal production, is an integral part of these forest ecosystems. Temperate deciduous forests play a critical role in terrestrial ecosystems as carbon sinks (Wofsy et al. 1993; Yamamoto et al. 1999; Wilson and Baldocchi 2001; Carrara et al. 2003), especially in Asian terrestrial ecosystems (Hirata et al. 2008; Kato and Tang 2008). Carbon cycling in a forest varies markedly during stand development (Odum 1969; Shidei and Kira 1977), and thus carbon sequestration on the landscape scale is influenced strongly by forest age and successional stage (Hudiburg et al. 2009).

Chronosequence studies of net CO_2 exchange have become widespread in recent years (Clark et al. 2004; Kowalski et al. 2003; Law et al. 2001; Litvak et al. 2003; Noormets et al. 2007; Zha et al. 2009). The forest ecosystem becomes a large carbon source soon after clear-cutting. Large emissions decrease following vegetation development as gross primary production (GPP) increases, while the effects of a disturbance on CO_2 emission can last from a

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few years to decades. For example, Takagi et al. (2009) studied the effects of clear-cut harvesting and replanting on CO_2 exchange in a cool-temperate region of Hokkaido using the eddy covariance method. They concluded that the mixed forest became a large carbon source [net ecosystem production (NEP) = -569 gC m^{-2} year^{-1}] after clear-cutting, and emissions decreased rapidly in the following 2 years (NEP = -153 gC m^{-2} year^{-1}).

NEP is the balance between two opposing biological processes: autotrophic photosynthetic activity and heterotrophic decomposition activity. Successional processes greatly affect both autotrophic and heterotrophic processes, and thus ecosystem carbon pools vary markedly in the short term after clear-cutting. The growth (biomass increment) of a forest typically changes with forest age, reaching a peak relatively soon in stand development followed by a substantial decline (Binkley et al. 2002; Ryan et al. 1997; Smith and Long 2001). Chronosequence studies, mainly in even-aged single-species stands, have revealed that above-ground net primary production (ANPP) peaks early in stand development and then declines gradually by as much as 76%, with a mean reduction of 34%, as a result of decreasing soil nutrient availability and increasing stomatal limitation, leading to reduced photosynthetic rates (Gower et al. 1996). Moreover, secondary succession also affects the dynamics of soil carbon pools (Marin-Spiotta et al. 2009; Tang et al. 2009; Yanai et al. 2003). Generally, soil carbon stocks decline sharply after disturbance (Covington 1981). The apparent losses of organic matter were attributed to increased decomposition rates and decreased litter input soon after clear-cutting. An abrupt decrease in soil organic matter (SOM) pools then increased asymptotically as above- and below-ground detritus production recovered with development of vegetation during succession (Kawaguchi and Yoda 1986).

Compared with chronosequence studies of net CO_2 exchange using the eddy covariance method, there have been few studies on ecological inventories of carbon cycling and biometrically based flux measurements in the early stages of secondary succession in temperate regions. The dynamics of carbon pools in forest ecosystems during vegetation development are crucial in revealing the cause of the dramatic change in net CO_2 exchange after clear-cutting. We therefore conducted a study of carbon cycling and carbon budget over 4 years (2004–2008) of measurements in a cool-temperate deciduous forest at an early stage of secondary succession (18 years old) in an abandoned coppice forest. Our objectives were (1) to clarify carbon cycling in a young secondary mixed forest, and (2) to show where and how the forest stores carbon in the early stages of secondary succession.

Materials and methods

Study sites

The study site is located on the middle slope of Mt. Norikura (36°07′N, 137°23′E, 1,160 m a.s.l.) approximately 3 km from the Takayama Forest Research Station, Institute for Basin Ecosystem Studies, Gifu University, in central Japan. The study area has a seasonal cool-temperate climate. Annual mean air temperature at the Takayama Forest Research Station (36°08′N, 137°25′E, 1,420 m a.s.l.) is 7.3°C, annual precipitation is about 2,400 mm and snow depth is usually 1–2 m in winter (December–April). Air temperature was measured within the canopy during the study period at the study site; annual mean air temperature was 8.7 and 9.4°C in 2005 and 2006, respectively.

The primary climax vegetation around the area was cool-temperate deciduous broad-leaved forests dominated by Japanese beech (*Fagus crenata*) or oak (*Quercus crispula*). However, these climax forests have been largely replaced by coppice chestnut or oak forests for producing charcoal. The study site was abandoned after clear-cutting in October 1986. Thus, the area was covered by oak and chestnut coppice with deciduous pioneer trees of 8–10 m canopy height, which represent an early stage of secondary succession. A permanent plot of 20 m × 30 m was set on a southeast-facing steep slope to study carbon cycling and NEP in 2004, 18 years after clear-cutting.

Net primary production

Net primary production (NPP) of overstory tree species was calculated using the following equation:

$$NPP = \Delta B + L + M$$

where ΔB is the change in living biomass (except for foliage) of trees, L is above-ground (foliage and other woody material) litter production, and M is above- and below-ground necromass resulting from tree mortality during the study period. Herbivore loss was assumed to be negligible during the study period. All trees in the permanent plot taller than 1.3 m in height were numbered and identified in autumn 2004. Tree diameter at breast height (DBH) was measured using a steel tape measure, or in case of small tree stems (diameter usually less than 1 cm), using a vernier calliper. DBH was measured in two directions in each stem when using the vernier calliper and averaged. The DBH of all living stems was remeasured in autumn 2008 to estimate ΔB in the permanent plot. The allometric relationship of above-ground parts (boles and branches) with DBH was developed from data on a deciduous broad-leaved forest (ca. 50 years old) near the Takayama Forest Research Station (Ohtsuka et al. 2005). The above-ground

woody increment was determined as the average increment during 4 years (2004–2008). The increment in coarse roots (stumps and large lateral roots) was also derived from allometric equations relating DBH to woody root mass (Ohtsuka et al. 2005). Dry biomass was assumed to be 50% of the carbon content in live wood and foliage.

Above-ground litter production (L) was estimated from nine litter traps (area 1 m^2) in the permanent plot. Litter fall was collected monthly in snow-free seasons. Litter fall was separated into foliage (leaf litter) and other woody material (coarse litter), oven-dried to constant mass and weighed. Woody mortality (M) was derived from a tree census in summer 2008 in the plot, and the necromass, including dead coarse roots, was derived from allometric equations for live trees. The dried litter samples were measured using a CN analyser (Sumigraph NC-800; Sumika Chemical Analysis Service, Tokyo, Japan) to estimate the carbon content (gC g^{-1}).

Soil carbon pool

The carbon pool of litter in the A0 layer was sampled in 2005 for an area of 1 m^2 in both the upper and lower part of the site near the permanent plot; the sampled material was oven dried to constant mass and weighed. Bulk soils were collected to a depth of 1 m from a pit near the permanent plot in 2005 to estimate the SOM pool. A 100-mL cylindrical soil corer (approximately 5 cm in diameter and 5 cm in length) was used to collect a sample of topsoil beneath the litter (0–5 cm) and at seven successive depths (5–10, 10–15, 15–20, 20–25, 35–40, 65–70 and 95–100 cm) with three replicates. Soil samples were oven dried for the measurement of bulk density (g cm^{-3}). The dried soils were passed through a 2-mm mesh sieve, and the sieved soils were measured using a CN analyser (Sumigraph NC-800) to estimate the total soil carbon content (gC g^{-1}). The standing stocks of soil organic carbon were estimated in each 5-cm slice. Soil carbon contents in the unsampled layers were interpolated as the average of the upper and lower depths. The volumetric soil mass of total carbon (tC ha^{-1}) was evaluated from the product of gravimetric carbon content and soil bulk density in each layer.

Soil surface CO₂ efflux and heterotrophic respiration in soil

Soil surface CO_2 efflux (RS, soil respiration) includes autotrophic respiration by roots (RR) and decomposition of SOM as primarily heterotrophic respiration (RH) by microbes and the soil fauna. RS was measured by the dynamic closed chamber method with an LI-6400 portable photosynthesis system (Li-Cor, Lincoln, NE) fitted with a soil respiration chamber (6400-09; Li-Cor). Measurements

were made at 12 locations; polyvinyl chloride collars (10.5 cm diameter, 4.5 cm high) were installed 10 m apart at each corner of a 10 m × 10 m subplot. The collars were inserted approximately 1 cm into the soil layer so as to avoid severing roots. Measurements were conducted monthly from May 2005 to November 2006 in the snow-free season. Soil temperature (1 cm depth) was measured with a soil temperature probe at the same time as the CO_2 evolution measurements were made. Annual RS was extrapolated from hourly continuous soil temperature (depth 1 cm) measurement in the permanent plot.

To evaluate the contribution of root respiration to total soil respiration, we measured the respiration rates of roots by the following procedure. Adachi (2001) derived the following empirical equation for cut root respiration (RR: mgCO₂ g dw^{-1} h^{-1}) as an exponential function of temperature (t) in laboratory experiments in an early stage of secondary succession:

$$RR = R_0 e^{kt}$$

$R_0 = 0.0735$, $k = 0.0879$, $Q_{10} = 2.41$, $r^2 = 0.79$ for fine roots (<2 mm diameter)
$R_0 = 0.0694$, $k = 0.0629$, $Q_{10} = 1.88$, $r^2 = 0.99$ for middle-sized roots (2–10 mm diameter)
$R_0 = 0.0395$, $k = 0.0598$, $Q_{10} = 1.82$, $r^2 = 0.99$ for large roots (>10 mm diameter)

We calculated the total annual respiration of the tree roots in the field from the below-ground biomass and continuous measurements of soil temperature (depth 5 cm). Root standing crop was estimated by soil sampling. Six soil samples (two samples in 2005 and four in 2006) were dug out near the permanent plot (1 m × 1 m, 1 m depth). The roots in the soil samples were washed in running water and separated into three size classes depending on the diameter: fine roots (0–2 mm), middle-sized roots (2–10 mm) and large roots (more than 10 mm). They were oven dried for 2 days and then weighed.

Compartment model and net ecosystem production

A compartment model (Kira 1978; Ohtsuka et al. 2007) was used to construct the carbon budget for the forest ecosystem (Fig. 1). There were three main carbon pools in the site: biomass of trees (B), SOM including fine litter in the A0 layer, and coarse woody debris (CWD). The understory at the site was sparse, and therefore we did not estimate the biomass and production of understory vegetation in this study. Accumulation of carbon in each compartment (pool) depends on the balance between carbon inputs and carbon losses. NEP is conceptually equivalent to the sum of the change in each carbon pool ($\Delta B + \Delta SOM$) if the losses of carbon other than RH (such
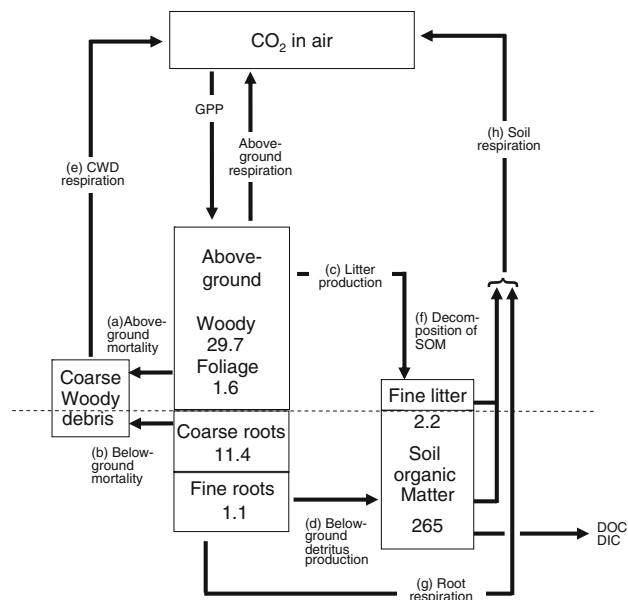
Fig. 1 Compartment model of carbon pools and fluxes in an 18-year mixed forest stand. *Squares* Carbon pools (tC ha^{-1}), *arrows* carbon fluxes (*a–h*) measured or estimated in this study, except for gross primary production (GPP), above-ground tree respiration and coarse woody debris (CWD) respiration. Fine root biomass refers to roots less than 2 mm in diameter

as elution of DOC by soil water flow or evaporation of volatile organic compounds) in the forest are low. Dead wood respiration was not measured in this study, and carbon sequestration in CWD (ΔCWD) is therefore excluded from the calculation of NEP. Annual ΔC was estimated from changes in these fluxes, by which carbon enters or leaves the pools, as follows:

$$\Delta B = \text{above- and belowground woody increment} - M(a+b)$$

$$\Delta SOM = \text{above- and belowground litter production} (c+d) - \text{RH} (h-g)$$

$$\text{NEP} (\Delta C) = \Delta B + \Delta SOM$$

Results

Community structure and carbon pools

A total of 37 species were present in the plot in 2004 (Table 1), including 13 tree species (including an evergreen conifer tree), 17 subtrees (including an evergreen broad-leaved species) and 7 deciduous shrubs. The dominant top three species in terms of summed relative basal area (RBA) were *Betula platyphylla* var. *japonica*, *Castanea crenata* and *Quercus crispula* (Table 1). The combined RBA of

these three species was 58.9%. Almost all species were deciduous broad-leaved species, and only two evergreen species, *Pinus parviflora* and *Ilex pedunculosa*, were present (less than 0.1% RBA). The total number of tree stems higher than 1.3 m was 1,199 plot^{-1} (19,983 ha^{-1}) in 2004. More than half of the total stems were of subtree species (692 plot^{-1}), which accounted for 32% of RBA. The number of stems of tree species was 288 plot^{-1}, which accounted for 64% of RBA. Maximum DBH was 16.3 cm (*Castanea crenata*), and the mean DBH of all stems was 2.9 cm. The total summed basal area of all tree stems was 22.1 m^2 ha^{-1}.

The tree biomass of the permanent plot in 2004 was 29.7 tC ha^{-1} of above-ground woody biomass and 11.4 tC ha^{-1} of below-ground coarse root biomass (Fig. 1). Total woody biomass in the stand was 41.2 tC ha^{-1}. The total mean leaf biomass was 1.6 tC ha^{-1}, as estimated from annual leaf fall during the study period. The mean fine root (diameter less than 2 mm) biomass was 1.1 tC ha^{-1}. The fine litter pool of the A0 layer was 2.2 tC ha^{-1} and the total amount of SOM in the mineral soil layer at a depth of 1 m was 265 tC ha^{-1}.

Net primary production in the stand

Table 2 shows the number of stems and tree biomass in the permanent plot during the study period. Stem mortality was high during the study period (52 stems plot^{-1} year^{-1}). However, dead wood production (M) of above-ground and coarse root necromass was low (0.5 tC ha^{-1} year^{-1}) because almost all dead stems were less than 5 cm DBH. Ninety-four stems (23 stems plot^{-1} year^{-1}) were over 1.3 m high during the study period (2004–2008); thus, the number of stems in the permanent plot decreased from 1,199 to 1,085.

The biomass of trees (except for foliage and fine roots) increased from 41.2 to 51.4 tC ha^{-1} during the study period, and ΔB was therefore 2.5 tC ha^{-1} year^{-1}. Annual above-ground litter production (L), averaged across the 4 years, was 1.60 ± 0.18 tC ha^{-1} year^{-1} for foliage and 0.49 ± 0.18 ha^{-1} year^{-1} for other litter (Table 3). The mean NPP was calculated as follows:

$$\Delta B + L + M = 2.5 + 2.1 + 0.5 = 5.2 \text{ tC ha}^{-1} \text{ year}^{-1}$$

Heterotrophic respiration

Measured soil respiration rate in 2005 and 2006 correlated significantly with soil temperature as an exponential function (Fig. 2). The Q_{10} value of soil respiration rate was 2.64. Figure 3 shows the seasonal change in temperature and the daily value of RS estimated by the Q_{10} function driven by soil temperature at 1 cm depth in the snow-free season. The daily RS was moderate in spring (0.81–1.76 gC m^{-2} day^{-1}

Table 1 Species composition in the permanent plot (20 m × 30 m) of an 18-year mixed forest after clear-cutting

Species	Basal area		DBH (cm)		Number of stems	
	($m^2\ ha^{-1}$)	(%)	Mean	Maximum	($Plot^{-1}$)	(%)
Trees						
Betula platyphylla var. *japonica*	6.2	28.2	5.7	13.3	127	10.6
Castanea crenata	4.1	18.7	7.1	16.3	48	4.0
Quercus crispula	2.7	12.0	5.3	15.9	51	4.3
Quercus serrata	0.5	2.1	4.4	9.9	14	1.2
Magnolia obovata	0.2	0.8	4.4	7.3	6	0.5
Carpinus japonica	0.2	0.7	2.3	3.7	20	1.7
Acanthopanax sciadophylloides	0.1	0.6	4.9	8.4	3	0.3
Acer rufinerve	0.1	0.5	2.7	7.1	7	0.6
Others (five species)	0.1	0.4	2.0	5.2	12	1.1
Sub total	14.2	64.0	5.3	16.3	288	24.3
Subtrees						
Clethra barvinervis	1.7	7.7	2.2	12.1	185	15.4
Hamamelis japonica	1.2	5.6	2.9	7.7	99	8.3
Prunus grayana	0.9	4.2	3.1	7.1	61	5.1
Fraxinus sieboldiana	0.8	3.6	2.2	15.9	71	5.9
Ilex macropoda	0.4	1.9	2.3	5.4	50	4.2
Lindera obtusiloba	0.4	1.7	1.8	4.8	71	5.9
Acer sieboldianum	0.3	1.5	2.2	4.6	45	3.8
Acer crataegifolium	0.3	1.4	2.0	12.1	25	2.1
Magnolia salicifolia	0.2	1.0	1.9	4.9	35	2.9
Lyonia ovalifolia	0.2	1.0	3.2	8.4	12	1.0
Maackia amurensis	0.2	0.9	3.8	6.3	8	0.7
Populus sieboldii	0.1	0.5	3.4	5.2	6	0.5
Others (five species)	0.2	0.9	2.3	5.7	24	2.1
Sub total	6.9	31.9	2.4	15.9	692	57.9
Shrubs						
Symplocos coreana	0.5	2.2	1.5	10.1	105	8.8
Hydrangea paniculata	0.2	0.8	1.6	4.0	41	3.4
Others (five species)	0.3	1.3	1.4	5.3	73	6.2
Sub total	1.0	4.3	1.5	10.1	219	18.4
Total	22.1	100	2.9	16.3	1,199	100

DBH Diameter at breast height

Table 2 Number of stems and tree biomass in the permanent plot of an 18-year mixed forest after clear-cutting

	November 2004	November 2008
Number of stems (600 m^{-2})	1,199	1,085
Biomass (tC ha^{-1})		
Aboveground	29.7	37.7
Coarse roots	11.4	13.6
Total (except for foliage)	41.2	51.4

Table 3 Annual aboveground litter production (tC $ha^{-1}\ year^{-1}$) in the permanent plot of an 18-year mixed forest after clear-cutting

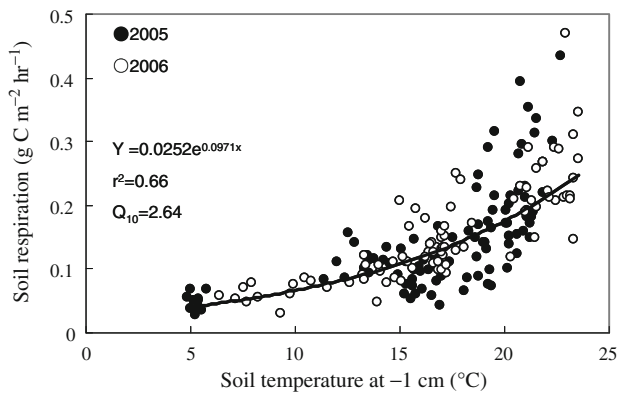|	2005	2006	2007	2008	Average ± SD
Leaf litter	1.50	1.40	1.71	1.78	1.60 ± 0.18
Other litter	0.73	0.50	0.42	0.31	0.49 ± 0.18
Total	2.23	1.90	2.13	2.10	2.09 ± 0.14

Fig. 2 Relationship between soil CO_2 efflux (2005 and 2006) and soil temperature (depth 1 cm) in the snow-free season in the permanent plot of an 18-year mixed forest after clear-cutting
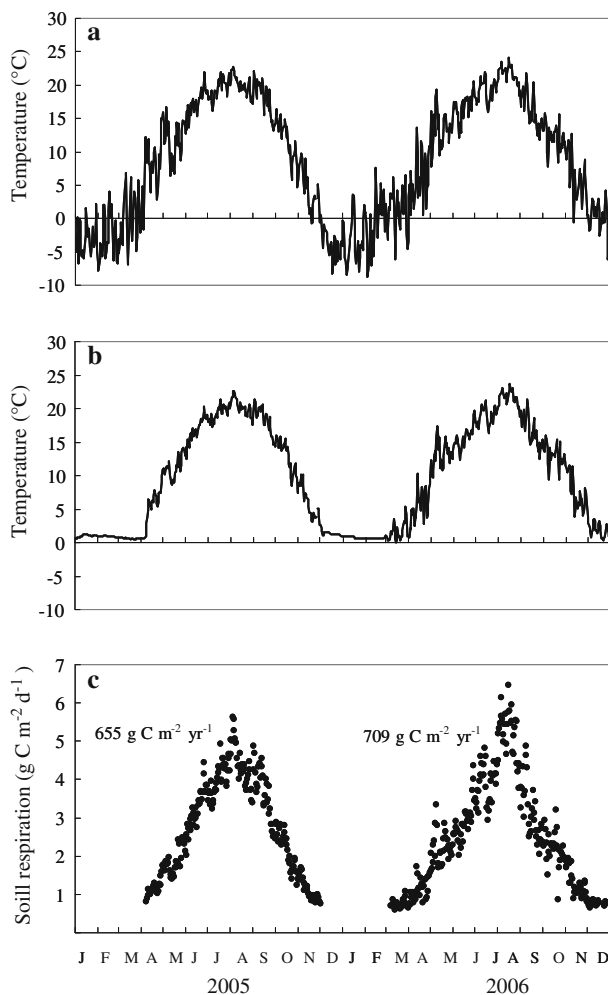

Fig. 3 Seasonal changes in temperature (air and soil) and estimated daily CO_2 efflux in the permanent plot in an 18-year mixed forest after clear-cutting. Air temperature in the canopy (**a** height approximately 1.5 m) and soil temperature (**b** depth 1 cm) were obtained from data recorded continuously every hour in the permanent plot. Estimated effluxes (**c**) were calculated from the regression equation in Fig. 2

Table 4 Annual carbon budget in the permanent plot of an 18-year mixed forest over 4 years (2004–2008)

	Carbon fluxes (tC ha^{-1} year^{-1})
ΔB	
Aboveground (boles and branches)	
Growth	2.4
Mortality (a)[a]	0.4
Subtotal	2.0
Belowground (coarse roots)	
Growth	0.7
Mortality (b)	0.2
Subtotal	0.5
ΔDead wood	
Mortality $(a + b)$	0.5
ΔSOM	
Aboveground litter (c)	2.1
Fine roots (d)	1.1
Respiration (f)	4.9
Subtotal $(c + d - f)$	−1.6
ΔC $(\Delta B + \Delta$SOM$)$ = NEP	0.9

NEP Net ecosystem production, *SOM* soil organic matter

[a] Italicised letters $(a$–$f)$ refer to the carbon fluxes shown in Fig. 1

in April 2005), increased sharply to a peak in summer (3.45–5.63 gC m^{-2} day^{-1} in August 2005), and then decreased in autumn (0.60–1.65 gC m^{-2} day^{-1} in November 2005). Total annual soil surface CO_2 efflux in 2005 and 2006 was 6.55 and 7.09 tC ha^{-1} year^{-1}, respectively.

The mean root biomass was 1.1 tC ha^{-1} for fine roots, 1.3 tC ha^{-1} for middle-sized roots and 0.6 tC ha^{-1} for large roots in the permanent plot. RR was extrapolated by means of a Q_{10} function of RR, soil temperature and root biomass for each size of root. Total annual RR was 1.0 tC ha^{-1} year^{-1} for fine roots, 0.7 tC ha^{-1} year^{-1} for middle-sized roots and 0.2 tC ha^{-1} year^{-1} for large roots if we assume that the biomass of roots was constant during the study period. Fine roots (less than 2 mm) made the largest contribution (53%) to total RR (1.9 tC ha^{-1} year^{-1}) at the site, though the biomass of the fine roots was smaller than that of the middle-sized roots. The annual soil respiration averaged across the 2 years of recording was 6.8 tC ha^{-1} year^{-1}. The contribution of RR to the total soil surface CO_2 efflux was 28%, and thus, the annual mean RH at the study site was estimated to be 4.9 tC ha^{-1} year^{-1}.

Carbon cycling and net ecosystem production

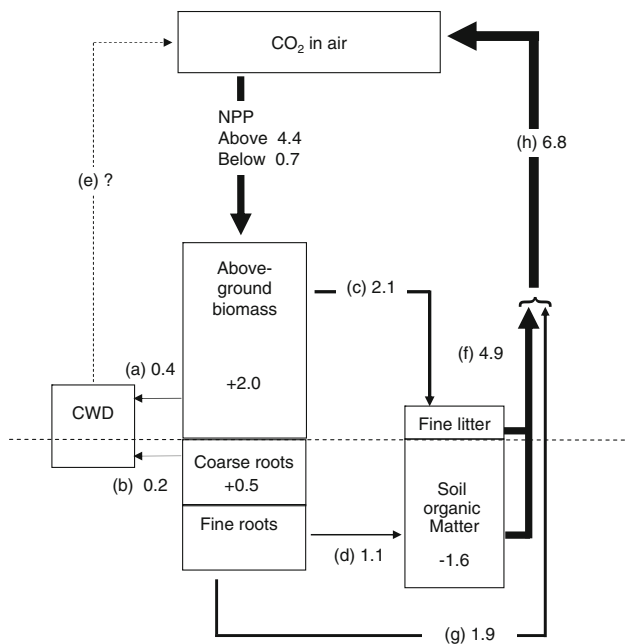Table 4 shows the annual carbon budget of each carbon pool. Above- and belowground woody increments for

Fig. 4 Mean annual carbon fluxes (tC ha^{-1} year^{-1}) and carbon budget of each carbon pool in the permanent plot of an 18-year mixed forest over 4 years (2004–2008). *Arrow thickness* is proportionally to the amount of each carbon flux

trees were large (2.4 and 0.7 tC ha^{-1} year^{-1}, respectively) compared with the biomass losses (0.4 and 0.2 tC ha^{-1} year^{-1}, respectively) as a result of tree mortality during the study period. The biomass pool of trees at the site increased greatly during the 4 years of the study (Table 2). ΔB was 2.5 tC ha^{-1} year^{-1}: 2.0 for aboveground and 0.5 for belowground. ΔSOM was estimated as the balance between SOM recruitment and RH. SOM recruitment includes both above- and below-ground litter production. The fine root biomass (1.1 tC ha^{-1} year^{-1}) was adopted as belowground litter production at the study site, since we assumed that the turnover time of the fine roots was 1 year. The mean annual rate of RH was 4.9 tC ha^{-1} year^{-1}, and thus the SOM pool decreased by 1.6 tC ha^{-1} year^{-1} in this forest ecosystem.

Figure 4 shows the results of carbon cycling at the site over the 4 years of the study. Annual NPP (except for fine roots) allocated 2.5 tC ha^{-1} year^{-1} to living biomass and 2.6 tC ha^{-1} year^{-1} to detritus production, including tree mortality. The mean total carbon sequestration (NEP = $\Delta B + \Delta$SOM) of the site amounted to 0.9 tC ha^{-1} year^{-1} during the period from 2004 to 2008. NEP was lower than the biomass increments because RH from soil was high compared with detritus production, although it included below-ground dead fine roots.

Discussion

Recovery of living biomass pool and NPP with stand development

Net primary production of the 18-year young mixed forest in this study site was 5.2 tC ha^{-1} year^{-1}, including below-ground coarse roots. If the decomposition of standing dead trees is negligible over the short term, the woody increment ($\Delta B + M$) is the annual carbon allocation to the woody component in the ecosystem (woody NPP), and NPP was thus partitioned as 3.6 tC ha^{-1} year^{-1} to woody production (2.5 for ΔB and 1.0 for woody detritus) and 1.6 tC ha^{-1} year^{-1} to foliage production. Ohtsuka et al. (2007) also studied carbon cycling and the carbon budget in a secondary deciduous broad-leaved forest aged approximately 50 years at the Takayama flux site (TKY site), which was located at an altitude 260 m higher than the 18-year forest stand of this study. The tree NPP of the TKY site, except for fine root production, was 3.6 tC ha^{-1} year^{-1}, partitioned half and half to woody NPP and foliage NPP (1.8 tC ha^{-1} year^{-1} each). Thus, foliage biomass (production) in the 18-year young mixed forest recovered rapidly after clear-cutting as a result of the development of a pioneer community, which contributed to greater recovery of production.

In contrast, woody biomass in the 18-year forest stand in this study was only 41.1 tC ha^{-1}, which is only just half of that of the 50-year TKY site (76.8 tC ha^{-1}). The biomass increment (ΔB) of the 18-year site (2.5 tC ha^{-1} year^{-1}) was more than seven times larger than that at the 50-year TKY site (0.3 tC ha^{-1} year^{-1}). The large biomass increment of the 18-year site was caused by both higher woody NPP and lower tree mortality, and thus the 18-year forest sequestrated carbon to a great extent in the living woody biomass pool. Kawaguchi and Yoda (1986, 1989) studied the change in carbon dynamics during regeneration of a deciduous broad-leaved forest after clear-cutting. Leaf biomass in a 12-year young forest (2.6 t dw ha^{-1}) was nearly the same as that in a 100-year forest (2.4 t dw ha^{-1}) and mature beech forest (3.0 t dw ha^{-1}) in central Japan. In contrast, biomass increased gradually from the 12-year forest to the 100-year forest, even in a mature beech forest. Leaf biomass in secondary deciduous forests increased rapidly within a decade after clear-cutting with the full closure of forest canopy, while woody biomass increased monotonously and gradually. These trends in the living biomass pool along the secondary succession are examples of the hypothetical trends suggested by Kira and Shidei (1967).

In general, the NPP of a forest ecosystem typically changes with age; it reaches a peak relatively sooner in stand development, and this is followed by a substantial decline (Binkley et al. 2002; Ryan et al. 1997; Smith and

Long [2001]). For example, Marks ([1974]) reported that the first peak of NPP due to dense pioneer communities of pin cherry (*Prunus pensylvanica*) was observed several years after disturbance in northern hardwoods in the United States. Tree NPP in the 18-year forest we studied was higher than that of the 50-year TKY site, and thus NPP recovered rapidly soon after clear-cutting with development of the vegetation of pioneer communities, which might decrease during the maturing pioneer stage. However, a change in species composition is a common phenomenon in the natural secondary succession in temperate forest regions. Kawaguchi and Yoda ([1989]) suggested that the secondary succession in mixed deciduous forests has several peaks in NPP corresponding to changes in species composition, contrary to the hypothetical trends suggested by Kira and Shidei ([1967]) for even-aged pure stands. Further studies of trends in NPP during secondary succession are needed because a few climax trees (e.g., Japanese beech) invaded both the 18-year forest of this study and even the 50-year TKY site.

Carbon dynamics in the non-living necromass pools

The SOM pool in the 18-year forest of this study site decreased greatly (-1.6 tC ha^{-1} year^{-1}), while much carbon (2.5 tC ha^{-1} year^{-1}) accumulated in the woody biomass pool. Covington ([1981]) reported that forest floor mass declined sharply after harvesting, with 50% of the forest floor organic matter lost in the first 20 years in the White Mountains of New Hampshire in the context of the Hubbard Brook Ecosystem. Kawaguchi and Yoda ([1986]) also studied successional changes in SOM pools: the SOM pool decreased from a 12-year forest to a 45-year forest. Chronosequence studies of the net CO_2 exchange using the eddy covariance method (e.g., Takagi et al. [2009]; Zha et al. [2009]) revealed that forest ecosystems became a large carbon source after clear-cutting. These large CO_2 emissions corresponded to a decrease in SOM pools, which in general resulted from both accelerated decomposition rates and decreased litter inputs. Our 18-year young forest was a weak carbon sink (0.9 tC ha^{-1} year^{-1}); however, the SOM pool decreased during the study period as a result of the high level of RH and small above- and below-ground litter production compared with the 50-year TKY site.

On the other hand, the low contribution of root respiration to total RS in the 18-year young site (28%) compared with the 50-year TKY site (44%) resulted in a higher RH at the young site. The method used to quantify the contribution of roots to total RS differed between the two sites. We measured direct root respiration in the laboratory at our study site, but the trenching method (Lee et al. [2003]) was used at the TKY site. We assumed that biomass and respiration rate were constant during the study period;

however, root biomass and root respiration change during the seasons of the year according to tree growth (Satomura et al. [2006]). Moreover, the respiration of cut roots in a laboratory is different from root respiration in situ (Bekku et al. [2009]). Therefore, estimating ΔSOM solely from the balance between the two fluxes by which carbon enters and leaves the SOM pool is unreliable because of both scaling-up error in estimation and the method of root respiration measurement. The SOM pool in the 18-year forest stand decreased during the study period, although there is a need for more studies on root respiration and belowground detritus production, especially for fine root turnover.

In general, after an abrupt decrease in the early stage of secondary succession, the SOM pool increases gradually with vegetation development, as indicated by an increase in the amount of leaf litter and dead fine roots (Covington [1981]; Kawaguchi and Yoda [1986]; Yanai et al. [2003]). In contrast to the 18-year young forest, carbon in non-living pools (CWD and SOM) played significant roles in carbon sequestration in the 50-year TKY site because of high tree mortality and above- and below-ground litter production by the dense dwarf bamboo at the site (Ohtsuka et al. [2009]). Luyssaert et al. ([2008]) recently showed that old-growth forests are usually carbon sinks, contrary to the long-standing view that old-growth forests are carbon neutral (Odum [1969]). Luyssaert et al. ([2008]) suggested that in old-growth forests, carbon accumulates in non-living detritus pools, such as in soils, CWD and charcoal. The total necromass of dead tree production will increase over time in natural secondary forests of mixed species, and thus tree mortality and CWD dynamics constitute an important part of the carbon cycle.

Young forests show a great increase in the biomass pool because of the large amount of total tree growth (woody NPP) and low mortality of tree stems. In contrast, the SOM pool decreased markedly in the 18-year forest, although further study on belowground detritus production and the RH of SOM decomposition is needed. As a result, the 18-year forest was a weak carbon sink (0.9 tC ha^{-1} year^{-1}), which is less than half that of the 50-year TKY site (2.1 tC ha^{-1} year^{-1}). The NEP of the young forest is likely to increase gradually because of the increase in biomass increment resulting from tree growth and also through the improvement of the SOM pool by increasing above- and below-ground litter production and woody detritus production as a result of increasing mortality as the stand develops.

References

Adachi T (2001) Carbon dynamics in a cool-temperate deciduous forest soon after clear-cutting (in Japanese). Master Thesis, Gifu University

Bekku YS, Sakata T, Nakano T, Koizumi H (2009) Midday depression in root respiration of *Quercus crispula* and *Chamaecyparis obtusa*: its implication for estimating carbon cycling in forest ecosystems. Ecol Res 24:865–871

Binkley D, Stape JL, Ryan MG, Barnard HR, Fownes J (2002) Age-related decline in forest ecosystem growth: an individual-tree, stand-structure hypothesis. Ecosystems 5:58–67

Carrara A, Kowalski AS, Neirynck J, Janssens IA, Yuste J, Ceulemans R (2003) Net ecosystem CO_2 exchange of mixed forest in Belgium over 5 years. Agric For Meteorol 119:209–227

Clark KL, Gholz HL, Castro MS (2004) Carbon dynamics along a chronosequence of slash pine plantations in north Florida. Ecol Appl 14:1154–1171

Covington WW (1981) Changes in the forest floor organic matter and nutrient content following clear cutting in northern hardwoods. Ecology 62:41–48

Gower ST, McMurtie RE, Murty D (1996) Aboveground net primary production decline with stand age: potential causes. Trends Ecol Evol 11:378–382

Hirata R, Saigusa N, Yamamoto S, Ohtani Y, Ide R, Asanuma J, Gamo M, Hirano T, Kondo H, Kosugi Y, Li S-G, Nakai Y, Takagi K, Tani M, Wang H (2008) Spatial distribution of carbon balance in forest ecosystems across East Asia. Agric For Meteorol 148:761–775

Hudiburg T, Law B, Turner DP, Cambell J, Donato D, Duane M (2009) Carbon dynamics of Oregon and Northern California forests and potential land-based carbon storage. Ecol Appl 19:163–180

Kato T, Tang Y (2008) Spatial variability and major controlling factors of CO_2 sink strength in Asian terrestrial ecosystems: evidence from eddy covariance data. Glob Chang Biol 14:2333–2348

Kawaguchi H, Yoda K (1986) Carbon-cycling changes during regeneration of a deciduous broadleaf forest after clear-cutting I. Changes in organic matter and carbon storage. Jpn J Ecol 35:551–563

Kawaguchi H, Yoda K (1989) Carbon-cycling changes during regeneration of a deciduous broadleaf forest after clear-cutting II. Aboveground net production. Ecol Res 4:271–286

Kira T (1978) Carbon cycling. In: Kira T, Ono Y, Hosokawa T (eds) Biological production in a warm-temperate evergreen oak forest of Japan, JIBP Synthesis 18. University of Tokyo Press, Tokyo, pp 272–276

Kira T, Shidei T (1967) Primary production and turnover of organic matter in different forest ecosystems of the western Pacific. Jpn J Ecol 17:70–87

Kowalski AS, Sartore M, Burlett R, Berbigier P, Loustau D (2003) The annual carbon budget of a French pine forest (*Pinus pinaster*) following harvest. Glob Chang Biol 9:1051–1065

Law BE, Thornton PE, Irvine J, Anthoni PM, Van Tuyl S (2001) Carbon storage and fluxes in ponderosa pine forests at different developmental stages. Glob Chang Biol 7:755–777

Lee M-S, Nakane K, Nakatsubo T, Koizumi H (2003) Seasonal changes in the contribution of root respiration to total soil respiration in a cool-temperate deciduous forest. Plant Soil 255:311–318

Litvak M, Scott M, Wofsy SC, Goulden M (2003) Effect of stand age on whole ecosystem CO_2 exchange in the Canadian boreal forest. J Geophys Res 108(D3):8225, doi:10.1029/2001JD000854

Luyssaert S, Schulze E-D, Börner A, Knohl A, Hessenmöller D, Law BE, Ciais P, Grace J (2008) Old-growth forests as global carbon sinks. Nature 455:213–215

Marin-Spiotta E, Silver WL, Swanston CW, Ostertag R (2009) Soil organic matter dynamics during 80 years of reforestation of tropical pastures. Glob Chang Biol 15:1584–1597

Marks PL (1974) The role of pin cherry (*Prunus pensylvanica* L.) in the maintenance of stability in northern hardwood ecosystems. Ecol Monogr 44:73–88

Noormets A, Chen J, Crow TR (2007) Age-dependent changes in ecosystem carbon fluxes in managed forests in Northern Wisconsin, USA. Ecosystems 10:187–203

Odum EP (1969) The strategy of ecosystem development. Science 164:262–270

Ohtsuka T, Akiyama T, Hashimoto Y, Inatomi M, Sakai T, Jia S, Mo W, Tsuda S, Koizumi H (2005) Biometric based estimates of net primary production (NPP) in a cool-temperate deciduous forest stand beneath a flux tower. Agric For Meteorol 134:27–38

Ohtsuka T, Mo W, Satomura T, Inatomi M, Koizumi H (2007) Biometric based carbon flux measurements and net ecosystem production (NEP) in a temperate deciduous broad-leaved forest beneath a flux tower. Ecosystems 10:324–334

Ohtsuka T, Saigusa N, Koizumi H (2009) On linking multiyear biometric measurements of tree growth with eddy covariance-based net ecosystem production. Glob Chang Biol 15:1015–1024

Ryan MG, Binkley D, Fownes JH (1997) Age-related decline in forest productivity: pattern and process. Adv Ecol Res 27:213–262

Satomura T, Hashimoto Y, Koizumi H, Nakane K, Horikoshi T (2006) Seasonal patterns of fine root demography in a cool-temperate deciduous forest in central Japan. Ecol Res 21:741–753

Shidei T, Kira T (1977) Primary productivity of Japanese forests—productivity of terrestrial communities. JIBP synthesis, vol 16. University of Tokyo Press, Tokyo

Smith FW, Long JN (2001) Age-related decline in forest growth: an emergent property. For Ecol Manag 144:175–181

Takagi K, Fukuzawa K, Linag N, Kayama M, Nomura M, Hojyo H, Sugata S, Shibata H, Fukazawa T, Takahasi Y, Nakaji T, Oguma H, Mano M, Akibayashi Y, Murayama T, Koike T, Sasa K, Fujinuma Y (2009) Change in CO_2 balance under a series of forestry activities in a cool-temperate mixed forest with dense undergrowth. Glob Chang Biol 15:1275–1288

Tang J, Bolstad PV, Martin JG (2009) Soil carbon fluxes and stocks in a Great Lakes forest chronosequence. Glob Chang Biol 15:145–155

Wilson KB, Baldocchi DD (2001) Comparing independent estimates of carbon dioxide exchange over 5 years at a deciduous forest in the southeastern United States. J Geophys Res 106:34167–34178

Wofsy SC, Goulden ML, Munger JW, Fan S-M, Bakwin PS, Daube BC, Bassow SL, Bazzaz FA (1993) Net exchange of CO_2 in a mid-latitude forest. Science 260:1314–1317

Yamamoto S, Murayama S, Saigusa N, Kondo H (1999) Seasonal and inter-annual variation of CO_2 flux between a temperate forest and the atmosphere in Japan. Tellus 51B:402–413

Yanai RD, Currie WS, Goodale CL (2003) Soil carbon dynamics after forest harvest: and ecosystem paradigm reconsidered. Ecosystems 6:197–212

Zha T, Barr AG, Black TA, McCaughy JH, Bhatti J, Hawthorne I, Krishnan P, Kidston J, Saigusa N, Shashkov A, Nesic Z (2009) Carbon sequestration in boreal jack pine stands following harvesting. Glob Chang Biol 15:1475–1487