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ORIGINAL ARTICLE

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Role of coarse woody debris in the carbon cycle of Takayama forest, central Japan

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Abstract Coarse woody debris (CWD) is an important component of the forest carbon cycle, acting as a carbon pool and a source of CO_2 in temperate forest ecosystems. We used a soda-lime closed-chamber method to measure CO_2 efflux from downed CWD (diameter ≥5 cm) and to examine CWD respiration (R_{CWD}) under field conditions over 1 year in a temperate secondary pioneer forest in Takayama forest. We also investigated tree mortality (input to the CWD pool) from the data obtained from the annual tree census, which commenced in 2000. We developed an exponential function of temperature to predict R_{CWD} in each decay class (R^2 = 0.81–0.97). The sensitivity of R_{CWD} to changing temperature, expressed as Q_{10}, ranged from 2.12 to 2.92 and was relatively high in decay class III. Annual C flux from CWD (F_{CWD}) was extrapolated using continuous air temperature measurements and CWD necromass pools in the three decay classes. F_{CWD} was 3.0 (class I), 17.8 (class II), and 13.7 g C m^{-2} $year^{-1}$ (class III) and totaled 34 g C m^{-2} $year^{-1}$ in 2009. Annual input to CWD averaged 77 g C m^{-2} $year^{-1}$ from 2000 to 2009. The budget of the CWD pool in the Takayama forest, including tree mortality inputs and respiratory outputs, was 0.43 Mg C ha^{-1} $year^{-1}$ (net C sink) owing to high tree mortality in the mature pioneer forest. The potential CWD sink is important for the carbon cycle in temperate successional forests.

Keywords AsiaFlux network · CO_2 efflux · CWD · Net ecosystem production · Soda-lime

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Introduction

Forest inventory and eddy covariance-based flux measurements have shown that mid-latitude temperate forests may account for an important fraction of the terrestrial carbon (C) sequestration (Kato and Tang 2008; Pan et al. 2011; Wofsy et al. 1993). Coarse woody debris (CWD) is often overlooked in forest C inventories, although it is an important component of C pools (Harmon et al. 1986) and may comprise 4–18 % of the total C in the ecosystem (Vogt 1991) in mid-latitude forests. Recently, comprehensive estimates of ecosystem C storage that account for all C pools, particularly at tower flux sites, have revealed the importance of CWD pools in temperate forests (Barford et al. 2001; Kominami et al. 2008; Ohtsuka et al. 2007). For example, Barford et al. (2001) estimated the carbon budget of Harvard forest biometrically, and concluded that the forest sequestered C into biomass (1.0 Mg C ha^{-1} $year^{-1}$), dead wood (0.4 Mg C ha^{-1} $year^{-1}$), and soil (0.2 Mg C ha^{-1} $year^{-1}$).

Many studies estimating CWD mass and density loss have emphasized the ecological roles of CWD such as nutrient supply and wildlife habitat (Harmon and Hua 1991; Harmon and Prescott 2008; Mattson et al. 1987). However, few studies have examined respiratory C flux from CWD (CWD respiration) in temperate forests (Gough et al. 2007). Carbon storage, or net ecosystem production (NEP), is the small difference between the two opposing large carbon fluxes of net primary production (NPP) and heterotrophic respiration (RH). Accordingly, annual CWD respiration (R_{CWD}) exerts a strong influence on the carbon budget, although R_{CWD}

generates only a small upward flux because of the longevity of the forest C pool. Accurate estimations of the fluxes into and out of CWD are expected to be important measures for the study of the C cycle and for precise estimation of biometrically based NEP in forest ecosystems.

R_{CWD} rates are sensitive to temperature and wood moisture (Bond-Lamberty et al. 2002; Wang et al. 2002), and direct field measurement of R_{CWD} using a closed dynamic chamber with an infrared gas analyzer (IRGA) has only recently been developed (Liu et al. 2006; Gough et al. 2007; Jomura et al. 2007). Liu et al. (2006) developed two linear-regression models to predict R_{CWD} from measurements of temperature and moisture. They concluded that annual R_{CWD} contributed approximately 2 % of the total ecosystem respiration (RE), whereas net C flux from CWD accounted for up to 30 % of NEP. The soda-lime method has also been used for in situ measurements of R_{CWD} (Marra and Edmonds 1994; Progar et al. 2000). The method is useful for obtaining an integrated estimate of the mean flux over a given time period at heterogeneous sites where a large number of simultaneous measurements are required to integrate the spatial variation. The method thus offers an advantage for measuring R_{CWD}, given that CWD is distributed heterogeneously across the forest floor and varies in physical conditions and species. Keith and Wong (2006) tested soil CO_2 efflux using soda-lime absorption in comparison with the IRGA method; they also provided a detailed protocol for field use of the soda-lime method that we applied in our study. They found that a regression line for the two methods did not differ significantly from the 1:1 line, and indicated that measurement of CO_2 efflux via soda-lime absorption was quantitatively similar and unbiased compared with the IRGA method.

The study site used in this paper for description of CWD dynamics, Takayama forest, is the oldest flux-measurement site in the AsiaFlux network and, it was initiated in 1993 (Yamamoto et al. 1999; Saigusa et al. 2002). Biometric measurement of forest growth and soil respiration using a 1.0-ha permanent plot beneath a flux tower was introduced in 1999 (Ohtsuka et al. 2005; Mo et al. 2005). These biometric measurements clarified the contribution of biological processes to the ecosystem carbon budget. The mean NPP at the Takayama forest was 6.5 ± 1.07 Mg C ha^{-1} year^{-1}, including the NPP of trees (5.4 Mg C ha^{-1} year^{-1}) and the forest-floor community (1.1 Mg C ha^{-1} year^{-1}), whereas the annual biomass increment (0.3 Mg C ha^{-1} year^{-1}) was relatively small because of high tree mortality (Ohtsuka et al. 2007).

Our analysis of CWD dynamics in the Takayama forest provides one of the few comprehensive inventories of C dynamics in temperate deciduous forests. In this study, our objective was to quantify CWD mass and respiration in a typical secondary deciduous forest in central Japan. Moreover, we investigated tree mortality (input to the CWD pool) using an annual tree census, and discuss the role of the CWD pool in terrestrial C storage. This study is part of the carbon cycle research conducted in the Takayama forest and operates within the AsiaFlux network of long-term carbon cycle research sites.

Materials and methods

Study site

The study site was located on the middle slopes of Mt. Norikura in the Takayama Forest Research Station (36°08′N, 137°25′E, 1,420 m a.s.l.), Institute for Basin Ecosystem Studies, Gifu University, in central Japan. The flux of CO_2 has been measured in Takayama forest, a temperate deciduous forest in the AsiaFlux network (Yamamoto et al. 1999; Saigusa et al., 2002), using the aerodynamic method since 1993 and the eddy covariance method since 1998. The annual NEP was estimated to be 237 ± 92 g C m^{-2} year^{-1} (mean ± SD) from 1994 to 2002 with large year-to-year variation (Saigusa et al. 2005).

The vegetation around the study site was secondary deciduous broad-leaved forest dominated by *Quercus crispula*, *Betula ermanii*, and *B. platyphylla* var. *japonica* (Ohtsuka et al. 2005). The primary climax forests of Japanese beech (*Fagus crenata*) around the study site have been largely replaced by coppice oak (*Q. crispula*) forests used for producing charcoal. However, these oak forests were abandoned because of the rapid decrease in charcoal demand after the 1960s. *B. ermanii* and *B. platyphylla* var. *japonica* are typical pioneer trees following abandonment, and the Takayama forest is a mature pioneer forest (approximately 50–60 years old) mixed with abandoned oak. The forest floor is mostly covered with a very dense *Sasa senanensis* (perennial evergreen dwarf bamboo) community approximately 1.5 m in height.

The study area has a seasonal cool temperate climate. Annual mean temperature and precipitation from 2000 to 2009, as measured at the Takayama Station, were 6.5 °C and 2,026 mm, respectively. Snow depth was usually 1–1.5 m during the winter seasons. The rainy season is strongly influenced by the Asian monsoon and usually occurs in early summer, such that there was no clear, dry summer season (Fig. 1).

Dead tree census

We set up a permanent 1-ha plot beneath the flux tower to estimate biomass and tree production (Ohtsuka et al. 2005). All live stems of 5 cm or more in the permanent plot were tagged and stem diameter was measured every year starting from 1999. Detailed descriptions of our biometric-based measurements at the Takayama forest have been given in our previous papers (Ohtsuka et al. 2007, 2009). Annual woody mortality (dead trees) was calculated from an annual tree census conducted in each

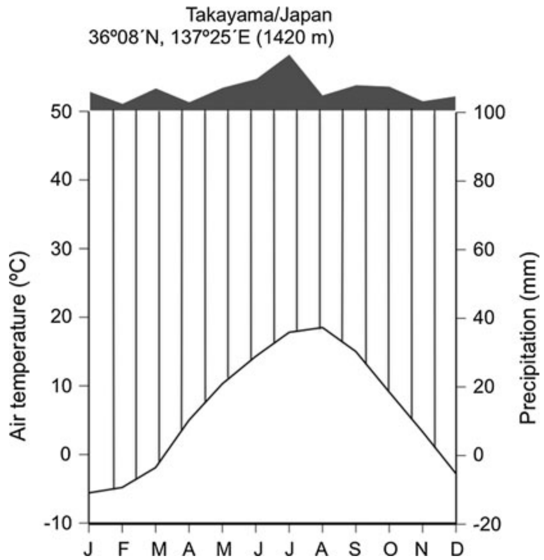

Fig. 1 Walter's climate diagram for the Takayama Forest Research Station. The *gray* portion indicates precipitation over 100 mm and the scale is 1:10 for precipitation

summer from 2000 to 2009. Aboveground litter production was estimated from 14 litter traps (1 m^2 area) in the permanent plot.

The recently dead trees are usually present as standing dead trees (snags). In time, the boles gradually fracture and eventually break off from the bases, to become downed woody debris as logs. We checked the 2009 census records for the status of not only dead or live stems, but also snags, broken boles, and complete logs for all trees that died after 2000. The necromass of the aboveground parts of trees that died in the interval was derived from allometric equations for live trees established in the site (Ohtsuka et al. 2005).

Coarse woody debris (CWD) respiration: field design

We defined CWD as aboveground dead wood consisting of stems and branches (logs) with diameter of 5 cm and more. We randomly selected logs (CWD samples) in the permanent plot in October 2008 to measure respiration in the field. We then added more samples in May 2009 after snow melt, using in total 76 samples (Table 1). Diameter of CWD samples ranged from 5 to 19.4 cm. If the samples were too long, they were cut with a hand saw in the field to 20–30 cm length in order to fit into the plastic containers used for CWD respiration (R_{CWD}) chambers (Fig. 2a). A subsample in the form of a disk 2–3 cm thick was also cut from each sample with a handsaw. After tagging each sample, we calculated the volume of all logs (V_{CWD}) from measurements of length and the diameter of the base and top using the equation for the frustum of a cone. The subsamples were transported to a laboratory, oven-dried at 70 °C to constant mass, and weighed. The wood volume of each subsample

Table 1 CWD samples randomly selected from the Takayama forest

	Decay class			Total
	I	II	III	
Betula spp.	10	16	4	30
Quercus crispula	0	5	2	7
Prunus spp.	2	2	0	4
Tilia japonica	0	2	0	2
Conifer trees	0	2	0	2
Not identify	0	24	7	31
Total	12	51	13	76

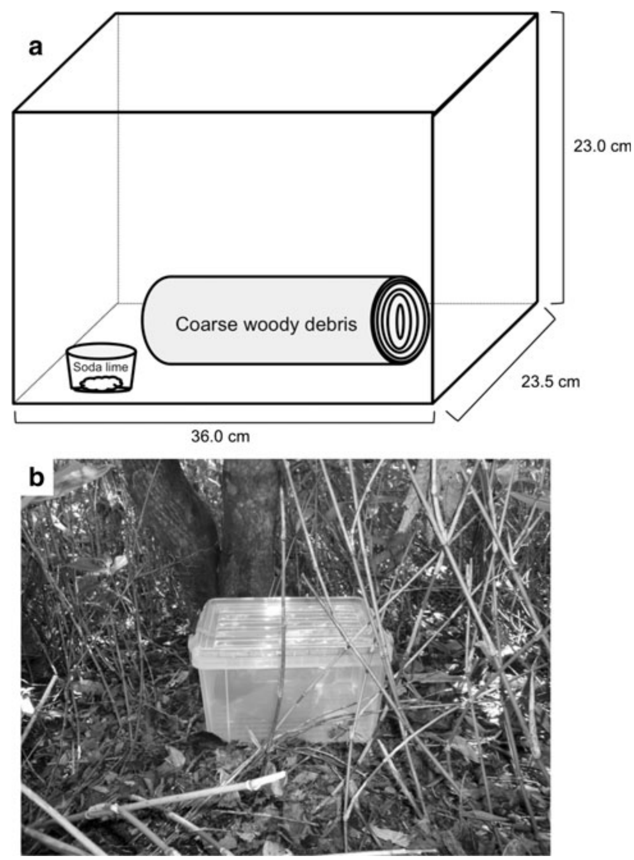

Fig. 2 Diagram illustrating the chamber design, with a dish of soda-lime (**a**). A lid is fitted on the chamber and set on the forest floor during an incubation period of about 24 h (**b**)

was measured by displacement using fine glass beads to calculate bulk density (g cm^{-3}).

The CWD samples were stratified by taxonomic groups (birch, oak, conifer, and other deciduous trees). *Betula* spp. (especially *B. platyphylla* var. *japonica)* dominated the samples (Table 1) owing to the high mortality of the pioneer species in the Takayama forest (Ohtsuka et al. 2007). However, most of the samples were difficult to identify, especially for those lacking barks. Decay state was categorized using a three-class system based on visual and physical characteristics following Lambert et al. (1980). The decay classes were: class I—a knife could not penetrate the sample with bark; class II—a knife could penetrate slightly in the sample with appreciable resistance; and class III—a knife could fully penetrate the sample with easy manual breaking of large pieces. The diameter size distributions were not significantly different among three decay classes (class I, 8.52 ± 3.0 cm; class II, 8.37 ± 3.4 cm; class III, 8.11 ± 2.9 cm).

We used the static chamber technique based on the soda-lime absorption of evolved CO_2 given in Keith and Wong (2006) for measuring soil respiration. About 25 g soda-lime granules was weighed into a dish (16 cm^2 and 3.7 cm in height), then oven-dried at 105 °C for 24 h. The dry weight of the soda-lime and the dish was recorded and the dish was sealed with PVC electrical insulation tape in the laboratory. When measuring R_{CWD}, we measured the wet weight of each CWD sample at the field and put it in the chamber (36 × 23.5 × 23 cm in height, 19.5 l). The soda-lime was rewetted with approximately 4 ml of water applied as a spray before being placed in a sealed chamber with a CWD sample for about 24 h. A lid is fitted on the chamber and set on the forest floor during an incubation period of about 24 h (Fig. 2b). Blank measurements were made to account for CO_2 absorbed by soda-lime during the experimental procedure. Dishes with soda-lime that had undergone the same process of drying and weighing were placed in blank chambers with no CWD samples and left for about 24 h in the field to simulate conditions of the incubating chambers. One blank chamber was used per ten sample chambers and located randomly.

The next day, dishes in each chamber were collected and again sealed with tape, transported to a laboratory, oven-dried at 105 °C for 24 h and reweighed. The measured CWD samples remained in the field and were reused for the next measurement at an interval of approximately 1 month. Respiration measurements were conducted nine times over 1 year: October 2, 2008; April 1, 2009; May 21, 2009; July 3, 2009; August 3, 2009; September 2, 2009; September 30, 2009; October 29, 2009; December 2, 2009. In snow season (April 1, 2009), some CWD samples were dug out from the snow and the chambers were buried in the snow depending on the snow depth in the field. We assumed that the dry weight and bulk density of these samples did not change during our measurements.

CWD respiration: modeling

Coarse woody debris respiration (R_{CWD}) in each sample at each sampling time was calculated on a weight basis as mg C g^{-1} day^{-1} as follows;

$$R_{CWD} = \frac{(W_s - W_b(1 - V_{CWD}/V_{CH}))1.69}{W_{CWD}} \times \frac{24}{T} \times \frac{12}{44} \quad (1)$$

where W_s is the sample weight gain (mg) of soda-lime, W_b is the mean blank weight gain (mg) of soda-lime, V_{CWD} is the volume of the CWD sample (cm^3), V_{CH} is the chamber volume (19,458 cm^3), W_{CWD} is the dry weight of the CWD sample (g), and T is the duration of CWD respiration measurement (i.e., duration of soda-lime exposure) (h). W_{CWD} of each sample was calculated using the bulk density (g cm^{-3}) of each subsample and V_{CWD}. The correction factor used to account for water formed during chemical absorption of CO_2 by soda-lime and released during drying was 1.69 as given by Grogan (1998). The water content of CWD samples ($Ø_{CWD}$ %) was calculated gravimetrically (g H_2O g^{-1} oven-dry wood) from W_{CWD} and wet weight of CWD samples at the time of each field measurement.

Instantaneous R_{CWD} measurements in the field were scaled to a land surface area basis to estimate annual CWD flux (F_{CWD}: g C m^{-2} year^{-1}) following procedure. An empirical equation of R_{CWD} was found as an exponential function of temperatures in each decay class as follows:

$$R_{CWD} = a\, e^{bT_c} \quad (2)$$

where a and b are fitted coefficients for each decay class, T_c is the average air temperature in the chamber during each daily measurement, and the temperature coefficient, $Q_{10} = e^{b10}$. Annual R_{CWD} (g C g^{-1} year^{-1}) was extrapolated within each decay class using Eq. (2) from continuous air temperature measurement in the Takayama forest.

We estimated ground-based F_{CWD} (g C m^{-2} year^{-1}) in the Takayama forest, using CWD necromass pools investigated by Jia and Akiyama (2005) in autumn 2001, by multiplying annual R_{CWD} (g C g^{-1} year^{-1}) by necromass (g C m^{-2}) in each decay class. The carbon content of CWD was assumed to be 50 % of dry weight, within the reported range of 46–52 % of dry weight (Yoneda et al. 1977; Yoneda and Kirita 1978).

Statistical analysis

The effect of decay class on bulk density and water content were tested using ANOVA followed by post hoc Tukey's test to make comparisons between decay classes (α = 0.10). All analysis was performed using SPSS statistical software.

Results

Environmental controls on R_{CWD}

The average CWD mass in the Takayama forest was 609 g C m^{-2}, whereas slightly decomposed downed wood of class I was a small value (76 g C m^{-2}) compared with the other decay classes (Table 2). The decrease in bulk density of CWD samples with increasing rank of the decay class ranged from 0.33 to 0.39 g cm^{-3}. However, bulk density did not significantly differ among

Table 2 Necromass pool, bulk density, and water content ($Ø_{CWD}$) of CWD for the three decay classes in the Takayama forest

Decay class	Necromass (g C m^{-2})	Bulk density (g cm^{-3})	$Ø_{CWD}$ (%)
I	76	0.39 (0.072)[a]	128.1 (20.5)[a]
II	298	0.34 (0.101)[a]	184.1 (24.1)[b]
III	235	0.33 (0.107)[a]	208.8 (17.1)[b]
Total	609		

Standard errors are shown in *parentheses* and *letters* indicate that values are significantly different ($p < 0.05$)

decay classes, owing partly to the inclusion of several species in each decay class (Table 1). $Ø_{CWD}$ of decay class I was significantly lower than those of decay class II and III. $Ø_{CWD}$ tended to increase with decay-class increase, because water absorption is greater in less-dense wood.

Field R_{CWD} increased in response to rising T_c in all decay classes (Fig. 3), although a large dispersion was observed at each measurement time especially in the summer season at high temperatures. R_{CWD} exhibited an exponential response to temperature, but the magnitude of the temperature responses, expressed as Q_{10}, was different among decay classes, ranging from 2.12 to 2.92 (Table 3). The temperature-normalized respiration rate (R_{CWD15}) of decay class I was lower (0.08 mg C g^{-1} day^{-1}) than those of the other decay classes (Table 3). Elevated R_{CWD} in more decayed wood was due not only to greater sensitivity to T_c as indicated by Q_{10} but also to the increase in $Ø_{CWD}$ with decay class (Table 2).

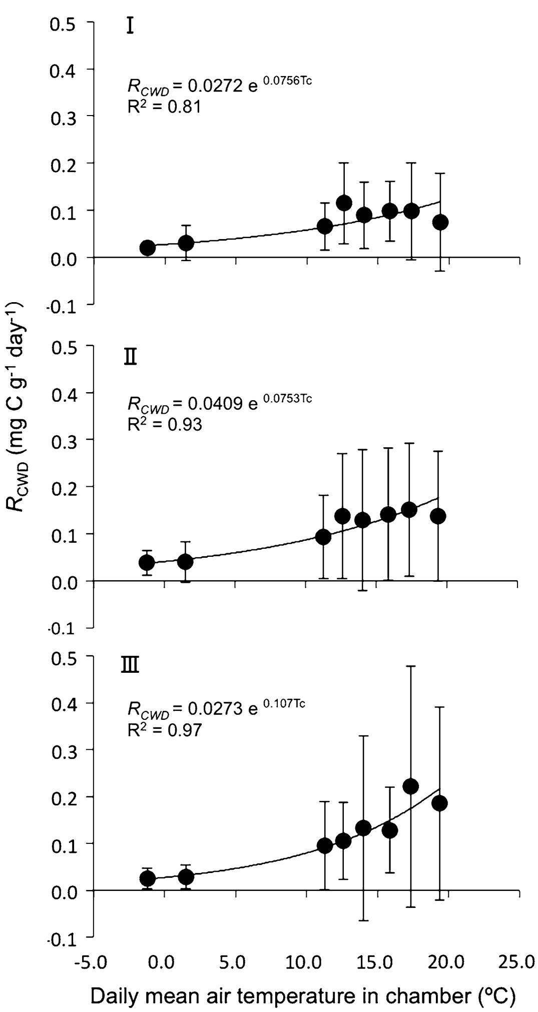

Fig. 3 The response of CWD respiration (R_{CWD}) to chamber temperature (T_c) for three decay classes (I, II, and III). *Vertical bars* denote SD of the mean

There were minor seasonal variations in $Ø_{CWD}$ under field conditions in each decay class except in early spring (April 1), whereas $Ø_{CWD}$ increased with decay-class increase (Fig. 4a). Some CWD samples were frozen on April 1 under snow cover, and had low $Ø_{CWD}$ for decay class III compared with the other seasons. Soil water content in the Takayama forest fluctuated from 40 to 50 % depending on precipitation in spring and summer after snow melt, and decreased to approximately 30 % by autumn (Fig. 4b) in 2009. However, soil water content was generally high with no clear dry season beneath canopy trees with dense *Sasa* understory at the Takayama forest, owing to the monsoon climate with higher precipitation in summer (Fig. 1).

Annual carbon flux from CWD and input to CWD

The Takayama forest has a temperate climate with clear seasonal variations of air temperature, ranging from less than −5 °C in winter to 20 °C in August 2009 (Fig. 5a), with no clear trend of precipitation. Air temperature inside the CWD respiration chamber did not differ significantly from forest air temperature during daily measurements, and was 1–1.5 °C higher even during summer at noon (Fig. 5a). This observation is due to the positioning of the chamber beneath a tree and the dense *Sasa* canopy under field conditions (see Fig. 2b). Modeled daily R_{CWD} (mg C g^{-1} day^{-1}) in every decay class varied seasonally in response to air temperature, increasing rapidly following snow melt in late April and peaking in summer at 0.12, 0.18, and 0.23 mg C g^{-1} day^{-1} for decay classes I, II, and III, respectively (Fig. 5b). The annual flux from CWD (F_{CWD}), except for standing dead trees, was 34.5 g C m^{-2} $year^{-1}$ in 2009 (Table 3), with the contribution from each decay class varying with the necromass pool. Decay classes I, II, and III contributed 8.7, 51.5, and 39.8 %, respectively, to total F_{CWD}.

Table 3 Respiration normalized to 15 °C (R_{CWD15}), temperature response coefficients (Q_{10}), and annual C respiratory flux (F_{CWD}) for the three decay classes in the Takayama forest

Decay class	R_{CWD15} (mg C g^{-1} day^{-1})	Q_{10}	F_{CWD} (g C m^{-2} $year^{-1}$)
I	0.08	2.13	3.02
II	0.13	2.12	17.75
III	0.14	2.92	13.71
Total			34.47

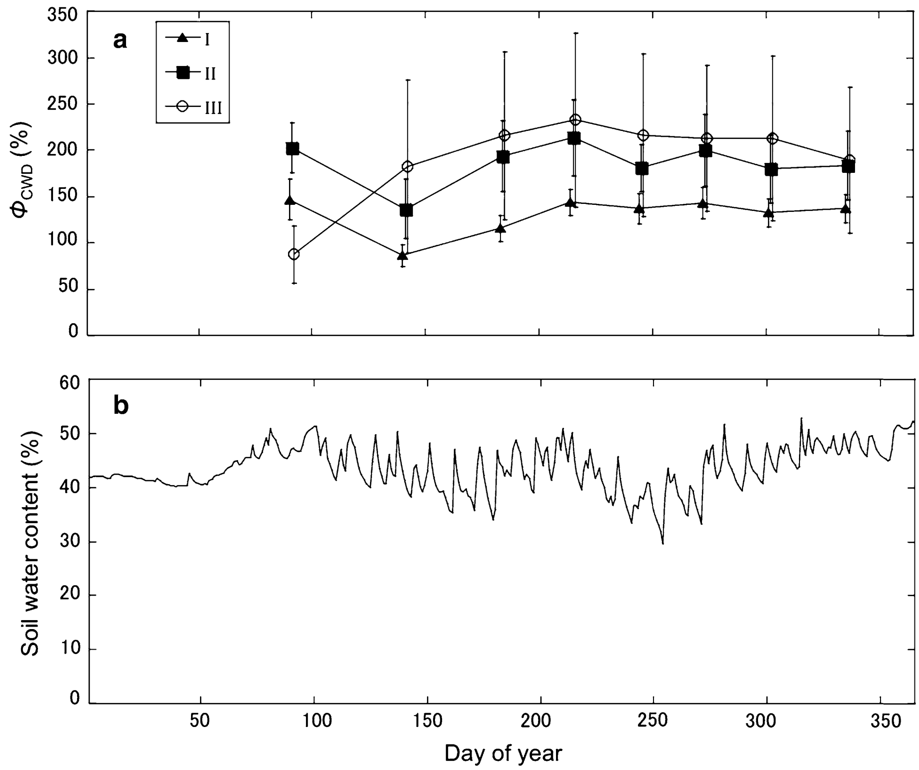

Fig. 4 Seasonal changes of water content of CWD samples ($Ø_{CWD}$) for the three decay classes under field conditions (**a**) and volumetric water content of soils (to 5 cm depth) beneath the tree canopy (**b**) during the study period in the Takayama forest

Table 4 shows the annual aboveground dead carbon fluxes by tree mortality and leaf litter over a period of 8 years for which the census in the Takayama forest was conducted. Annual tree mortality (CWD input flux) was high, ranging from 43 to 145 g C m^{-2} $year^{-1}$ and averaging at 77 ± 32 g C m^{-2} $year^{-1}$ during the study period. The CWD input flux from tree mortality was 42 % that of the leaf litter (annual leaf production) at the Takayama forest. In addition, CWD input flux was 2.3 times CWD output flux (F_{CWD}) at 34.5 g C m^{-2} $year^{-1}$, although F_{CWD} was estimated from the temperature change in 2009 (Table 3). In the Takayama forest, many canopy pioneer trees (especially *Betula platyphylla* var. *japonica*) died during the study period, and tree growth compensated for necromass production by tree mortality. Most of the dead trees (boles) were still snags for 1–3 years after death (Fig. 6). Breakage of boles increased after 4 years following death, and more than 60 % of dead trees became complete snags after 9 years.

Discussion

Environmental controls on R_{CWD}

Temperature controls on respiration of woody debris are well established in mid-latitude forests (Liu et al. 2006; Wang et al. 2002; Jomura et al. 2007; Gough et al. 2007). In general, R_{CWD} increases exponentially as temperature increases. For example, Gough et al. (2007) used chamber-based methods to measure R_{CWD} and reported that the sensitivity of R_{CWD} to temperature, expressed as Q_{10}, varied among decay classes from 2.20 to 2.57 in a temperate deciduous forest. Our Q_{10} values were nearly the same in decay classes I (2.13) and II (2.12), and increased to 2.92 in decay class III (Table 3). These values fall within the range reported for other temperate and boreal forests (Chen et al. 2000; Bond-Lamberty et al. 2002).

Wood moisture is another important variable driving R_{CWD}. Jomura et al. (2007) reported the optimal water content for maximal R_{CWD} in a temperate secondary forest in Japan; R_{CWD} increases with wood moisture, but respiration decreases at high wood moisture contents, measured using volumetric water content. Liu et al. (2006) also reported that log-transformed gravimetric wood moisture was linearly correlated with R_{CWD} in a temperate forest. Decreased water content, particularly values <100 % of gravimetric CWD moisture ($Ø_{CWD}$), greatly limited R_{CWD}. Limited R_{CWD} may be caused by the rapid response of microbial activity to wetting (Broken et al. 1999; Jomura et al. 2005b).

We used temperature alone as a predictor of R_{CWD} because seasonal change in wood moisture in snow-free seasons varied little (Fig. 4) compared with air temperature (Fig. 5). $Ø_{CWD}$ in the field was 100–250 %, representing optimal conditions for decay (Liu et al. 2006).

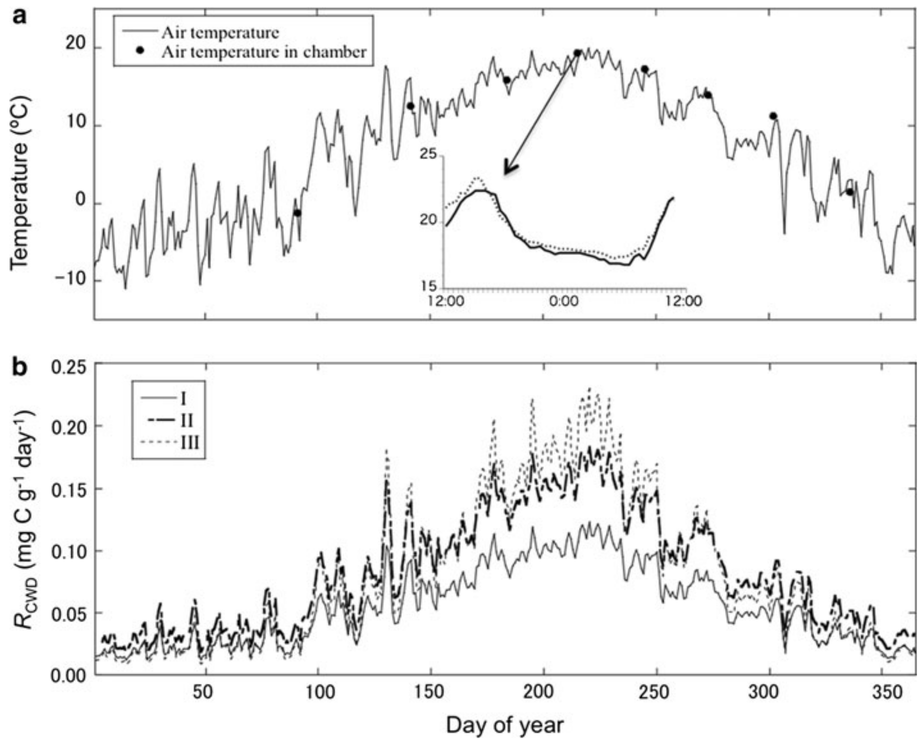

Fig. 5 Seasonal changes of mean daily air temperature of the forest and inside the chamber (*filled circles*) during the study period (**a**). An example of the daily change of forest air temperature (*solid line*) and chamber air temperature (*dotted line*) in summer is superimposed. Variation in modeled daily R_{CWD} for the three decay classes (**b**)

In addition, $Ø_{CWD}$ did not change seasonally in any decay class, although moisture increases as wood density decreases. This low variation in wood moisture is due to the monsoon climate, which has no clear dry season, and also due to the dense canopy over the forest-floor *Sasa* community that protected CWD from drying. If we estimate the temperature dependence of R_{CWD} in every decay class, expressed in Fig. 3, the influence of temperature may outweigh that of wood moisture, owing to the wide variation in temperature variables. Decay classes have also been shown to be a good proxy for both bulk density and wood moisture (Gough et al. 2007). Thus, temperature alone accounted for a large part of the variation in R_{CWD} in every decay class in the Takayama forest.

We continuously monitored soil water content (Fig. 4b), but not $Ø_{CWD}$ under field conditions. Continuous measurements of $Ø_{CWD}$ fluctuate greatly depending on daily precipitation (Gough et al. 2007). Jomura et al. (2005a) monitored R_{CWD} and $Ø_{CWD}$ of logs continuously over 12 days, using an automated open-closed chamber system, and reported that R_{CWD} decreased sharply with increased water content during rain events and then increased slowly after rain events. Jomura et al. (2007) also reported that the $Ø_{CWD}$ of logs and snags changes continuously in field conditions. In this case, CWD samples underwent wetting and drying in response to variation in precipitation, and the range of $Ø_{CWD}$ of logs fell primarily within the optimal water content for R_{CWD}. In contrast, the water content of snags was approximately 20 % of that of logs, and C emission from snags was limited by their lower water content; thus, the spatial variation in water content caused by CWD orientation (snags or logs) markedly affected the entire flux (Jomura et al. 2007).

For this reason, we did account for respiration from logs protected by the dense *Sasa* canopy from drying but not from snags, although dead trees remained standing as snags for approximately 3 years (Fig. 6). Therefore, we need to monitor $Ø_{CWD}$ in field conditions to accurately estimate F_{CWD}, including R_{CWD} for snags. Furthermore, moisture heterogeneity depends on snag height, and snag heights >15 m should be taken into consideration for estimation of respiration. Thus, annual total carbon flux from CWD was underestimated at this stage, whereas the decomposition of dead trees increased greatly after bole breakage, leaving them on the ground.

The accuracy of the soda-lime technique for in situ measurement of respiration may vary depending on the site or sample conditions (e.g., soil properties and sample decay class). We applied the method of Keith and Wong (2006) for measurement of R_{CWD}. Additional testing would be advisable if used under different conditions, particularly where soils are highly porous (Keith and Wong 2006). Hirota et al. (2011) recently compared this soda-lime technique with an automated open-closed chamber system coupled with IRGA for measurement of soil CO_2 efflux. They found that, in a temperate region

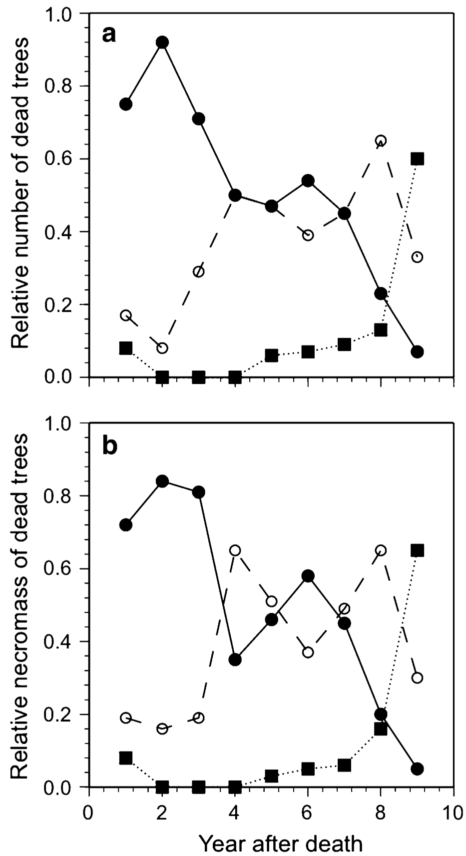

Fig. 6 The rate of stem number (**a**) and the rate of necromass (**b**) for three CWD types: standing dead trees as snags (*filled circles*), broken boles (*open circles*) and logs on the ground (*filled squares*) in 2009. CWD status was evaluated in the tree census of 2009 for all trees that died after 2000

of Japan, the daily estimated value for both methods could be represented by a simple linear regression (soda-lime value = 0.87 × IRGA value, R^2 = 0.92), although the regression line was significantly different from the 1:1 line. However, no studies have compared the two methods for measurement of R_{CWD}.

Keith and Wong (2006) originally published the method used in the present study, and addressed the issues concerning the accuracy of the soda-lime method in terms of chamber design and experimental procedure. They listed issues relating to quantification and reliable measurement of soil CO_2 efflux, and noted that variation in the CO_2 concentration inside the chamber headspace should affect the rate of CO_2 absorption by the soda-lime in an unstirred chamber. Thus, further testing of soda-lime absorption using a static chamber for measurement of R_{CWD} is necessary, particularly for measuring the effect of chamber size on a large CWD sample.

CWD flux contribution to RE

Annual C flux from CWD (F_{CWD}) at our site (0.34 Mg C ha^{-1} year^{-1}) falls within the estimated range for a temperate deciduous forest (Table 5). Annual C storage, or NEP, has been well demonstrated at our site by both eddy-covariance and biometrically based estimation. In the Takayama forest, current eddy covariance-based NEP is 2.37 ± 0.92 Mg C ha^{-1} year^{-1} and RE is 7.42 ± 0.36 Mg C ha^{-1} year^{-1} (1994–2002, Saigusa et al. 2005). The contribution of F_{CWD} to RE in our site (4.6 %) was larger than in other temperate forests, even though respiration of snags was not included. This difference is partly because of the greater CWD mass in our site than in the other temperate deciduous forests for which F_{CWD} was reported (Table 5).

Biometrically based NEP is the difference between NPP and RH. NPP at our site was 6.5 Mg C ha^{-1} year^{-1}, including trees and the forest-floor *Sasa* community (Ohtsuka et al. 2007). RH occurs primarily on the forest floor in forest ecosystems and soil CO_2 efflux (RS) is often measured using a chamber system, as was used for the long-term monitoring estimate of 7.1 Mg C ha^{-1} year^{-1} in the Takayama forest (Mo et al. 2005). The contribution of RH to the RS was estimated at 54.7 % by a trenching method (Lee et al. 2005), and thus RH was 3.9 Mg C ha^{-1} year^{-1}. However, RH measurements that focus on the decomposition of fine surface litter (e.g., leaves and twigs) and soil organic matter (SOM) are underestimates for forest ecosystems because CWD is usually larger than the soil respiration chamber. If we include the F_{CWD} (0.34 Mg C ha^{-1} year^{-1}) in the calculation of biometrically based NEP in the Takayama forest, NEP decreases by approximately 13 % to give 2.3 Mg C ha^{-1} year^{-1}. This value correlates well with the eddy covariance-based NEP. Thus, F_{CWD} is an important component of the ecosystem carbon balance, although respiratory C loss from CWD is a minor component compared with RE and soil respiration.

Role of CWD in the Takayama forest carbon cycle

Jia and Akiyama (2005) estimated the total aboveground CWD necromass in the Takayama forest in 2001

Table 4 Annual dead carbon fluxes (g C m^{-2} year^{-1}) of tree mortality and leaf litter in the Takayama forest

Year	2000	2001	2002	2003	2004–2005	2006	2007	2008	Average SD
Tree mortality	68	145	43	107	58	50	77	67	77 ± 32
Leaf litter	166	194	191	192	203	175	180	172	184 ± 12

Two-year averages for 2004 and 2005

Table 5 Annual carbon fluxes (Mg C ha^{-1} year^{-1}) of ecosystem respiration (RE), soil respiration (RS), heterotrophic respiration (RH), respiratory CWD flux (F_{CWD}), and net ecosystem production (NEP) reported from our site (Takayama forest), and compared with others in temperate forests

NEP (Mg C ha^{-1} year^{-1})	RE (Mg C ha^{-1} year^{-1})	RS (Mg C ha^{-1} year^{-1})	RH (Mg C ha^{-1} year^{-1})	F_{CWD} (Mg C ha^{-1} year^{-1})	F_{CWD}/RE (%)	CWD pool (Mg C ha^{-1})	References
				0.53		4.9	Forrester et al. (2012)
1.5	14.5		5.0	0.21	1.4	2.2	Gough et al. (2007)
2.4	11.5	6.5–7.5		0.28	2.4	5.1	Liu et al. (2006), Urbanski et al. (2007)
2.4	7.4	7.1	3.9	0.34	4.6	6.1	This study, Saigusa et al. (2005), Mo et al. (2005)
1.2		5.8	3.7	0.50		9.3	Jomura et al. (2007), Kominami et al. (2008)

CWD pool (Mg C ha^{-1}) in each forest is also presented

at 11.4 Mg C ha^{-1}, including snags (5.3 Mg C ha^{-1}) and logs (6.1 Mg C ha^{-1}). If we included snags and logs, CWD necromass of our site was higher than that reported for other temperate forests, ranging from 2.2 to 9.3 Mg C ha^{-1} (Table 5). CWD mass is affected partly by climatic variables that regulate the decay rate (Woodall et al. 2008). In addition, natural disturbances and forest succession influence CWD mass (Goulden et al. 2011). Jomura et al. (2007) reported a large CWD mass of 9.3 Mg C ha^{-1}, including snags (amounting to 60 % of the total CWD mass) in a temperate secondary forest. Most of the pine trees in the forest died of pine wilt disease and were replaced by broad-leaved species. Yan et al. (2010) also suggested that CWD necromass increases in an old-growth forest owing to natural disturbances such as typhoons in south China.

The Takayama forest is a typical pioneer-tree stage cool-temperate deciduous forest dominated by *Betula* spp. and oak (*Quercus crispula)* with dense dwarf bamboo. Tree mortality was high (0.77 Mg C ha^{-1} year^{-1}) in the Takayama forest during the study period, although mortality rates were episodic and varied annually (0.43–1.45 Mg C ha^{-1} year^{-1}). Tree mortality was greater than that in a nearby early stage cool-temperate secondary forest after 18 years of clear cutting (0.4 Mg C ha^{-1} year^{-1}) near the Takayama forest (Ohtsuka et al. 2010). The Takayama forest is a mature pioneer forest ($>$50 years) and pioneer trees, particularly *Betula*, constantly die off because of thinning and age. Moreover, the dense cover of dwarf bamboo prevents the establishment of climax beech seedlings on the forest floor (Nakashizuka 1988; Abe et al. 2002). These mature pioneer tree stages of a secondary succession characterize typical secondary forests of the temperate region of Japan, following the abandonment in the 1960s of the coppiced oak and chestnut forests that were widely exploited for charcoal production. For this reason, CWD dynamics will become increasingly important to the carbon cycle in temperate Japanese forests.

The difference between tree mortality (input to CWD) and F_{CWD} (output from CWD) is the annual net rate of C storage input into the CWD pool. We estimated that the CWD pool is currently increasing (0.77–0.34 = 0.43 Mg C ha^{-1} year^{-1}), representing net C storage and 18 % of the eddy covariance-based NEP. Accordingly, the CWD is important to the carbon cycle as a potential sink, although C storage is slightly overestimated because we did not consider the respiration from snags. CWD dynamics may also be important for SOM sequestration. The increasing trend in CWD accumulation can explain the accumulation of carbon in soils in old-growth forests in China (Zhou et al. 2006). Long-term monitoring at the Takayama forest has revealed a constant net accumulation of C in nonliving detritus pools, such as litter and SOM (Ohtsuka et al. 2009). Annual CWD input during the study period was comparable with that from leaf litter (42 % of leaf litter; Table 4), and the decomposition rate of CWD is lower than that of leaf litter. Therefore, the contribution of

CWD input to SOM should not be overlooked, particularly in temperate successional forests. Further studies are required for long-term monitoring of upward CO_2 flux from dead wood as well as of downward flux from dead wood to soil via leaching.

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