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The carbon budget of coarse woody debris in a temperate broad-leaved secondary forest in Japan

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ABSTRACT

We evaluated the carbon budget of coarse woody debris (CWD) in a temperate broad-leaved secondary forest. On the basis of a field survey conducted in 2003, the mass of CWD was estimated at 9.30 tC ha^{-1}, with snags amounting to 60% of the total mass. Mean annual CWD input mass was estimated to be 0.61 tC ha^{-1} yr^{-1} by monitoring tree mortality in the forest from 1999 to 2004. We evaluated the CWD decomposition rate as the CO_2 evolution rate from CWD by measuring CO_2 emissions from 91 CWD samples (R_{CWD}) with a closed dynamic chamber and infrared gas analysis system. The relationships between R_{CWD} and temperature in the chamber, water content of the CWD, and other CWD characteristics were determined. By scaling the measured R_{CWD} to the ecosystem, we estimated that the annual R_{CWD} in the forest in 2003 was 0.50 tC ha^{-1} yr^{-1} or 10%–16% of the total heterotrophic respiration. Therefore, 0.11 tC ha^{-1} yr^{-1} or 7% of the forest net ecosystem production was sequestered by CWD. In a young forest, in which CWD input and decomposition are not balanced, the CWD carbon budget needs to be quantified for accurate evaluation of the forest carbon cycle and NEP.

1. Introduction

CO_2 sequestration in forest ecosystems plays a key role in the global carbon cycle. Forests absorb CO_2 via photosynthesis and release CO_2 via autotrophic and heterotrophic respiration. Net ecosystem production (NEP) is the small difference between these two large fluxes (Law et al., 1999; Valentini et al., 2000). It is necessary to understand the biological and physical controls on all of the processes in a forest to estimate how the carbon cycle in that forest will respond to environmental change. Autotrophic respiration is integrated into the estimation of net primary production (NPP), but heterotrophic respiration (R_h) must be treated independently, because the amount of dead plant tissue, which may have been generated from a past stand has an impact, must be taken into account.

The primary source of R_h is dead organic matter, which varies greatly in size and other characteristics. R_h from relatively small sources such as fine litter and soil organic matter (SOM) has been much studied (e.g. Holland et al., 2000; Kelliher et al., 2004) and is treated as a significant component in soil respiration studies (e.g. Davidson et al., 2002; Irvine and Law, 2002; Pendall et al., 2004; Bond-Lamberty et al., 2005). R_h from relatively large sources such as coarse woody debris (CWD) is also a significant component of total R_h, especially when a forest is regenerating from a disturbance, such as a forest fire (Bond-Lamberty et al., 2003; Gower, 2003). However, compared with small sources, CWD has been largely ignored as a carbon source in forest carbon cycles (Gower, 2003; Chambers et al., 2004), mainly because of its slow rate of decomposition and the spatiotemporal variation in CWD accumulation, as well as because a long-term forest history is required to complete a carbon budget of CWD.

Because the decomposition rate of CWD is very slow, its weight loss through decomposition must be monitored for several years to decades, and daily or seasonal changes in the decomposition rate are difficult to determine. By measuring the CO_2 flux from CWD along with other respiration processes such as soil respiration, we can attempt to model in detail the effect of environmental factors and CWD characteristics on the decomposition rate of CWD (Yoneda, 1975, 1980; Wang et al., 2002) and to estimate the contribution of CWD decomposition to carbon emission to the atmosphere (Chambers et al., 2001; Bond-Lamberty et al., 2003).

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Accumulation and input mass of CWD change with spatiotemporal scales. The distribution of CWD in a forest is heterogeneous (Clark et al., 2002; Rubino and McCarthy, 2003), and many sampling designs for estimating forest-wide CWD accumulation have been developed and evaluated (Ståhl et al., 2001; Gove et al., 2002). Woldendorp et al. (2004) indicated that large-scale fixed-area plots are preferred for estimating CWD accumulation. The spatial orientation of the CWD, that is, whether standing or downed (snags or logs, respectively), must also be taken into account, because limited contact with the ground slows the decomposition rate of CWD in the form of snags (Næsset, 1999; Yatskov et al., 2003; Jomura et al., 2005b). Tree mortality is caused by small- and large-scale disturbances, such as competition, succession, forest fires and disease, resulting in spatial and temporal variations in CWD input. Thus, large-scale and long-term inventory observations are needed to evaluate the carbon budget of CWD at the landscape level.

Previous forest generation is a major contributor to CWD accumulation, except in old-growth forests (Fahey, 1983); thus, CWD mass cannot be estimated as a function of the living tree biomass. In some regions, CWD volume follows a general "U-shaped" temporal trend after a disturbance (Harmon et al., 1986; Spies et al., 1988; Spetich et al., 1999), but the temporal trends of CWD accumulation are complex, depending on forest age, stem growth, stand structure and disturbance regime (Sturtevant et al., 1997). Therefore, field measurements are needed to estimate the current CWD accumulation in a forest.

The object of this study was to evaluate the contribution of the CWD carbon budget to the forest carbon cycle in a temperate broad-leaved secondary forest in Japan. To evaluate spatiotemporal variation in CWD accumulation and input mass, we focused not only on logs but also on snags larger than 3 cm in diameter in a 1.7-ha forest, and we monitored tree mortality in the forest for 5 yr. To estimate the forest-wide CWD decomposition rate as the CWD respiration rate, we determined the relationship between environmental factors, CWD characteristics, and the respiration rate by measuring the CO_2 evolution rate from 91 CWD samples using an infrared gas analysis (IRGA) and a closed-chamber system.

2. Site & methods

2.1. Site

Our field study was conducted in a temperate secondary broad-leaved forest (Yamashiro Experimental Forest, YMS) in southern Kyoto, Japan (34°47′N, 135°50′E). More than 100 yr ago, this area was wasteland because of severe cutting for firewood. The land was rehabilitated by afforestation or reforestation beginning ca. 100 yr ago. Eventually, the area became dominated by *Pinus densiflora* Sieb. et Zucc. However, about 30 yr before our study, pine wilt disease spread in the area; most of the *P. densiflora* died, and broad-leaved species took their place. In 1999, the living tree biomass [diameter at breast height (DBH) $\geq$3 cm] was estimated to be 48.3 tC ha^{-1} (Goto et al., 2003). Deciduous broad-leaved tree species such as *Quercus serrata* Thunb. ex Murray, evergreen broad-leaved tree species such as *Ilex pedunculosa* Miq. and coniferous tree species such as *P. densiflora* account for 66%, 28% and 6%, respectively, of the living tree biomass (Goto et al., 2003) and *P. densiflora* dead wood, both standing and downed, are abundant in the forest. In 2002, the annual mean air temperature was 15.5 °C, and the hourly maximum air temperature in summer was 34.8 °C, whereas the wintertime hourly minimum was –3.9 °C. Annual precipitation was 1449 mm; the rainy season was in late June to early July, and some typhoons struck in summer and fall. The study site is a 1.7-ha watershed (220 m above sea level); the canopy height is approximately 12.0 m, the mean DBH and tree height of the living trees (DBH $\geq$ 3 cm) average 7.4 cm and 5.6 m, respectively. The stand density is 3209 trees ha^{-1}, and the total basal area averages 20.7 m^2 ha^{-1} (Goto et al., 2003). The forest soil is poorly developed in sandy weathered granite with thin O and A layers. A meteorological tower was constructed previously in this forest to permit measurements of the CO_2 flux between the forest ecosystem and the atmosphere (Kominami et al., 2003). Measurements of photosynthesis (Miyama et al., 2003), soil respiration (Nobuhiro et al., 2003; Tamai et al., 2005), and root respiration (Dannoura et al., 2006) have been conducted at this site using the chamber method, and databases of forest inventory, biomass, and production have been compiled (Goto et al., 2003) to evaluate the NEP from the tower measurements.

2.2. Methods

2.2.1. CWD accumulation. We defined CWD as above-ground dead wood consisting of stems and branches with diameter $\geq$3 cm. Three plots with different sizes were established for estimating the CWD biomass of three diameter (D) size classes: $7 > D \geq 3$ cm, 0.045 ha; $10 > D \geq 7$ cm, 0.188 ha; and $D \geq 10$ cm, 1.7 ha. In October 2003, we measured the DBH and height of snags and the diameter (measured at the centre) and length of logs. In addition, we recorded the species and decay class (see below), and whether the CWD item was a snag or log. Decay classes were based on the condition of the CWD bark and sapwood (Sollins, 1982). Log volume was calculated by assuming that each log was a cylinder. Snags were assumed to consist of stem only, and snag volume was estimated by using the allometric relationship between DBH and stem volume, on the basis of destructive sampling conducted in 1999 and 2000 (Goto et al., 2003). The loss of the tops of snags was estimated from the difference between past and current tree heights. The past tree height was estimated by using the relationship between DBH and tree height of current living wood (Goto et al., 2003). The current tree height was measured in October 2003. The dry weight of individual CWD items was estimated by multiplying the volume by wood density. The density of dead wood was assumed to be the mean wood density for its decay class, estimated from 159 CWD samples from both snags and logs of various species and decay classes. The wood density of each sample was calculated from its dry weight (oven-dried for 72 h at 105 °C) and volume. The carbon content of CWD has been reported to range from 46% to 49% (Yoneda and Kirita, 1978) or from 46% to 52% (Yoneda et al., 1977) of dry weight; therefore, we assumed a CWD carbon content of 50% of dry weight and calculated carbon weights for each CWD. CWD accumulation in YMS was estimated from the total estimated carbon weight of CWD items in the forest divided by the forest area (1.7 ha). The projected area of a log was estimated by assuming the log to be rectangular and multiplying the log diameter by its length. The projected area of a snag was estimated from the basal area of each snag at breast height. The total log and snag projected areas were the sums of the projected areas of the respective individual CWD items.

2.2.2. Input rate of CWD. Living stems ≥3 cm in diameter in YMS had been inventoried in 1999, and these data were used together with descriptions of the occurrence of dead wood. We identified the dead trees and classified the dead wood as either snags or logs in 2000, 2001, 2003 and 2004. The dry weight of dead wood was estimated from the allometric relationship between DBH and the dry weight of living stems and branches (Goto et al., 2003), and the carbon content of dead wood was assumed to be 50% of that value, as mentioned above. The input rate of CWD in YMS was estimated from the total carbon weight of the dead wood in the forest, divided by the forest area (1.7 ha).

2.2.3. CWD decomposition rate.

2.2.3.1. Measurement of CWD decomposition rate. CWD decomposition consists mainly of mineralisation and fragmentation processes (Harmon et al., 1986). Because CO_2 exchange between the atmosphere and forest has been measured directly to estimate forest NEP in recent years, it is important to estimate the CO_2 evolution rate resulting from decomposition processes. CO_2 evolution from CWD is treated in the main as a mineralisation process. In general, the CWD mineralisation rate is estimated from the loss of wood density by a CWD item (Harmon et al., 1986). However, any weight loss by leaching will be included in the mineralisation rate estimated by this method. Moreover, decomposition experiments require several years to decades, and it is difficult to clarify the relationship between the CWD mineralisation rate and environmental factors because of interannual variation in these factors. Forest respiration, including soil, stem and root respiration, has been measured directly, clarifying its response to environmental factors, and used to evaluate and estimate NEP. CWD respiration can be similarly used to evaluate NEP. Thus, in this study, we measured CWD respiration directly and estimated the CWD decomposition rate only through the respiration process. Some other studies have used similar methods to estimate landscape R_{CWD} as CO_2 evolution (Yoneda, 1980; Chambers et al., 2001; Bond-Lamberty et al., 2003).

2.2.3.2. Measurement of CWD respiration rate. We obtained 91 samples from snags and logs in the forest, using a hand saw or chain saw. The samples varied with respect to diameter ($3 \leq D \leq 27$ cm), length ($10 \leq L \leq 70$ cm), species (12 different species), and wood density ($0.1 \leq \rho \leq 0.9$ g cm^{-3}, Table 1). To eliminate emission of CO_2 from the cut sample surfaces or microbial invasion into them, we sealed the cut surfaces with silicone sealant. Because the drying treatment was expected to affect the microbial condition of CWD, the dry weight of each sample was estimated from the sample volume and the density of a subsample of the same CWD sample. We assumed that the dry weight and wood density of these samples did not change during our measurements. During measurement, snag samples were leaned in a vertical position against a steel frame and kept isolated from the ground by a vinyl sheet spread under the frame. Log samples were laid on the ground. All measurements were conducted in situ (i.e. at the site of the sampled CWD item). The CWD respiration rate (R_{CWD}) was measured one to 36 times during each measurement period to obtain R_{CWD} under various environmental con-

Table 1. Outline of measurements and CWD samples

Measurement period	Dates	Number of species	Number of sample	Number of measurements	D (Mean ± SD) (cm)			L (Mean ± SD) (cm)			ρ (Mean ± SD) (g cm^{-3})		
1	2001/06/12	3	6	1	6.0	±	0.6	13.3	±	2.8	0.38	±	0.07
2	2001/07/16–24	8	27	7	6.4	±	1.1	13.4	±	0.9	0.43	±	0.10
3	2002/06/26	2	8	1	10.0	±	1.8	13.8	±	1.2	0.47	±	0.18
4	2002/01–2002/12	2	4	20–36[b]	10.8	±	1.7	14.4	±	1.0	0.48	±	0.20
5	2003/05/31	8	20	1	5.1	±	2.2	13.2	±	3.1	0.50	±	0.19
6[a]	2003/08–2003/12	1	12	5–10[b]	7.5	±	1.1	15.0	±	1.7	0.39	±	0.13
		1	14	5–10[b]	16.4	±	6.1	68.9	±	2.4	0.29	±	0.09

[a]Large and small samples were used in measurement 6.
[b]From minimum to maximum number of the measurements for each sample.

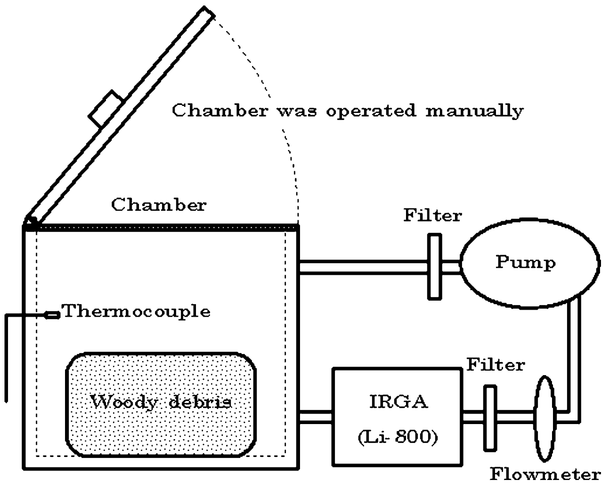

Fig. 1. Schematic diagram of the CWD respiration measurement system using a closed dynamic chamber with IRGA.

ditions and for CWD items with different characteristics (Table 1).

R_{CWD} was measured in a closed dynamic chamber with IRGA. The system was composed of an IRGA meter (LI-800, LI-COR, Inc., Lincoln, NE, USA), a chamber (made of acrylic resin; $20 \times 20 \times 20$ cm; 8000 cm^3), tubes, a pump (GS-3EA, Enomoto Micro Pump, Tokyo, Japan), filters, and a flow meter (Fig. 1). The temperature in the chamber was measured with a copper–constantan thermocouple. We enclosed a CWD sample in the chamber and measured the CO_2 concentration in the chamber for 5 min. The CO_2 concentration and temperature in the chamber (T_c) were recorded each second with a data logger (NR-1000, Keyence, Osaka, Japan). To avoid the effects of air disturbance caused by opening the chamber cover, data for the 60 s after the start and before the finish of each measurement were not used. The data were used to calculate the gradient of the CO_2 concentration increase as follows:

$$\mathrm{R_{CWD}} = \frac{1}{n}\left(\sum_{i=1}^{n}\frac{C_{CO_2}(t_i+\Delta t)-C_{CO_2}(t_i)}{\Delta t}\right) \times \frac{V-V_s}{V_{air}}\frac{273.2}{273.2+T_{cell}}\frac{M_{CO_2}}{10^3}\frac{10^3}{W}\,60^2, \quad (1)$$

where R_{CWD} is CWD respiration (mg CO_2 kg^{-1} h^{-1}), n is the number of time-intervals in the measurement period (120), t_i is the start time, Δt is the time-interval (60 s), $C_{co_2}(t)$ is the concentration of CO_2 at time t (ppm), V is the volume of the system (8.08l), V_s is the volume of CWD sample (l), V_{air} is the standard gas volume (22.41l), T_{cell} is the temperature in the measurement cell of the IRGA (°C), M_{co_2} is the molecular weight of CO_2 (44.01 g), and W is the dry weight of the CWD sample (g). T_c was averaged over each measurement period. The water content of the samples was calculated from the fresh weight at the time of measurement and the wood density of the sample, obtained at the time of sampling.

2.2.3.3. CWD respiration rate function. Jomura et al. (2005a) conducted continuous measurements of CWD respiration for 2 yr using an automated chamber system and found that a similar function to that used to determine soil respiration (Mielnick and Dugas, 2000) could explain changes in R_{CWD} as a function of the temperature and water content of the CWD:

$$R_{CWD} = a\exp(bT)(\theta - c)(d-\theta)^f, \quad (2)$$

where T is the temperature of the CWD at 3 cm depth in the sample and θ is the volumetric water content of the CWD, and a, b, c, d and f are constants. We used the temperature in the chamber (T_c) in this study. Water content of CWD can be evaluated gravimetrically (θ_{dw}), volumetrically (θ_v), or volumetrically on the basis of the volume of voids in the CWD (θ_{pore}). Because the density of CWD ranges from 0 to 1 g cm^{-3}, the maximum values of θ_{dw} and θ_v differ for different wood densities (Boddy, 1983). Thus, in this study we used θ_{pore}, which was calculated as follows:

$$\theta_{pore}(m^3m^{-3}) = V_{water}\left(V_{sample} - \mathrm{DW}_{sample}\rho_{wood}^{-1}\right)^{-1}, \quad (3)$$

where V_{water} is the water volume, V_{sample} is the sample volume, DW_{sample} is the sample dry weight, and ρ_{wood} is the density of the wood substrate (1.5 g cm^{-3}; Asano, 1982). Substrate characteristics, such as the diameter and density of the CWD, are reported to affect R_{CWD} (Yoneda, 1975; Chambers et al., 2001; Wang et al., 2002). Thus, we evaluated whether the effects of diameter (D) and wood density (ρ) on R_{CWD} could explain the R_{CWD} variation. We applied linear, logarithmic, exponential and power functions to these characteristics and selected those functions that yielded the maximum determination coefficient. We modelled R_{CWD} using environmental factors (T_c and θ_{pore}) and CWD characteristics (D and ρ). The parameters were fitted by the least-squares method (IMSL, Visual Numerics, Inc., Roman, CA, USA).

2.2.3.4. Estimation of forest-wide CWD respiration and the carbon budget. We estimated the annual R_{CWD} for a single CWD item ($R_{CWDitem}$) using the following equation:

$$R_{CWDitem}(gCy^{-1}) = \sum_{i=1}^{8760}\left(f(T_c(t),\theta_{pore}(t),D,\rho)M_C M_{CO_2}^{-1}10^{-6}\mathrm{DW}\right), \quad (4)$$

where M_C is the molecular weight of carbon and M_{co_2} is the molecular weight of CO_2. To calculate the respiration of each log CWD item, we used hourly data of the temperature and water content of a log sample ($D = 27$ cm, $\rho = 0.65$ g cm^{-3}) measured in 2003 (Jomura et al., 2005a). Because the water content of woody material differs if the material is in contact with the ground (Jomura et al., 2005b), we measured the water content of a snag ($D = 20$ cm, $\rho = 0.25$ g cm^{-3}, measurement height = 2.0 m) as well, using time-domain reflectometry (Hydra Probe, Stevens Water Monitoring System, Inc., Beaverton, OR, USA) from July to December 2003 and used these data to develop a function for converting the water content of logs to that of snags.

The annual R_{CWD} for the forest ($R_{CWDforest}$) was estimated by summing all values of $R_{CWDitem}$ and dividing the total by the study area (1.7 ha):

$$R_{CWDforest}(tC\ ha^{-1}y^{-1}) = \left(\sum_{i=1}^{n} R_{each\ CWD}\,(i)\right) Area^{-1}10^{-3}, \tag{5}$$

where n is the number of CWD items in the forest and *Area* is the study area (ha).

Using the estimates of the input and respiration rates of CWD described above (Sections 2.2.2. and 2.2.3.), we evaluated the annual contribution of the forest R_{CWD} to the annual forest R_h and that of the CWD carbon budget to the forest carbon cycle and forest NEP.

3. Results

3.1. CWD accumulation and input rate in YMS

Mean wood density of CWD apparently decreased from decay class 1 to 4, and then increased again from decay class 4 to 5 (Fig. 2). This increase reflected the accumulation of resin in the heartwood of *P. densiflora,* which was the species that dominated snags and logs of decay class 5 (Fig. 3). In addition, differences in the amount of accumulation of resin among CWD items led to considerable variation in the mean wood density of items in decay class 5. Both snags and logs in decay classes 1–3 included many of the current living tree species, but CWD decay classes 4 and 5 were dominated by *P. densiflora* (Fig. 3).

The CWD accumulation in YMS in 2003 was 9.30 tC ha^{-1} (Table 2), which is equivalent to 21% of the 1999 living wood biomass (44.54 tC ha^{-1}; Goto et al., 2003). CWD consisting of *P. densiflora* that had died by pine wilt disease approximately 30 yr before this study was conducted accounted for 89% of the total CWD biomass in 2003. Snags constituted 60% of the total CWD biomass. The total projected area of CWD was 180.89 m^2 ha^{-1}, or 1.8% of the total forest floor area (Table 2).

The CWD input rate varied annually (Table 3), and the 5-yr mean input rate was 0.61 tC ha^{-1} yr^{-1} (range, 0.29–0.89 tC ha^{-1} yr^{-1}). Snags comprised 89% of the total CWD input mass. Deciduous and evergreen broad-leaved species, comprising pioneer species such as *Alnus pendula* and *Rhus trichocarpa,* accounted for 89% of the total input mass. *Pinus densiflora* contributed only 10% of CWD input. The snag and total CWD input rates varied among years by a factor of about 3, whereas the log input rate varied by a factor of about 30 because a large increase in the log input rate occurred in 2004, when several strong typhoons hit Japan.

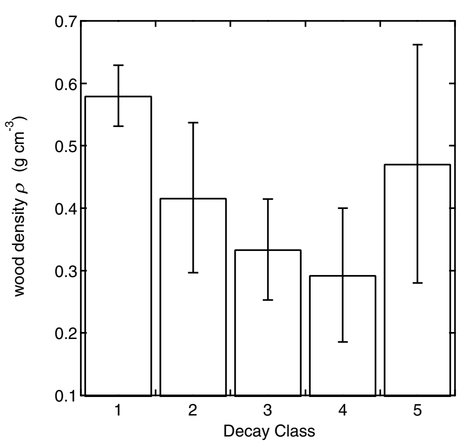

Fig. 2. Mean wood density of CWD in each decay class. The bars showed standard deviations.

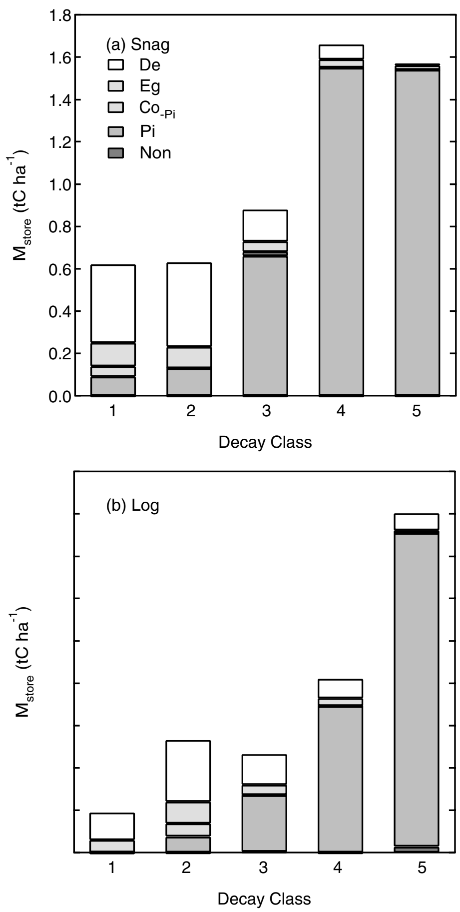

Fig. 3. Mass of CWD in each decay class (De, deciduous broad-leaved; Eg, evergreen broad-leaved; Co$_{-pi}$, coniferous excluding *Pinus densiflora*; Pi, *Pinus densiflora*; Non, not distinguishable).

Table 2. Biomass and projected area of CWD in 2003

	Biomass ($tC\ ha^{-1}$)	Projected area ($m^2\ ha^{-1}$)
Total	9.30	180.89
Snag	5.61	11.18
Log	3.69	169.72

Table 3. Annual mean input of CWD from 1999 to 2004 (October–September)

	Total ($tC\ ha^{-1}\ yr^{-1}$)	Snag ($tC\ ha^{-1}\ yr^{-1}$)	Log ($tC\ ha^{-1}\ yr^{-1}$)
1999–2000	0.65	0.63	0.02
2000–2001	0.29	0.24	0.04
2001–2003	0.61	0.60	0.01
2003–2004	0.89	0.61	0.29
1999–2004	0.61	0.54	0.07

3.2. CWD respiration rate function

The R_{CWD} of 91 samples, including seven snag samples, was measured in various seasons and under different environmental conditions (Table 1). R_{CWD} varied considerably, from 0.1 to 148.6 mg CO_2 kg^{-1} h^{-1}. R_{CWD} increased exponentially in response to increasing temperature (Fig. 4a), similar to many previous respiration results (e.g. Kirschbaum, 1995). R_{CWD} was low when θ_{pore} was either low or high, but it was high at intermediate values of θ_{pore} (Fig. 4b). Moreover, R_{CWD} decreased exponentially as diameter increased, and also decreased linearly with increasing wood density (Fig. 4c, d). These variations in R_{CWD} in relation to changes in T_c, θ_{pore}, D and ρ can be described by the following function:

$$R_{CWD} = 0.468 \exp(0.045T_c)(\theta_{pore} + 0.073)(0.867 - \theta_{pore})^{0.551} (-7.131 \log D + 28.096)(-20.177\rho + 15.670)r^2 = 0.54. \quad (6)$$

The respiration of both snag samples (R_{snag}) and log samples (R_{log}) varied similarly with water content (Fig. 4b), but the range in water content clearly differed between snag and log samples. θ_{pore} of snag samples ranged from about 0.0 to 0.3 $m^3\ m^{-3}$, whereas θ_{pore} of log samples varied from 0.02 to 0.82 $m^3\ m^{-3}$. Therefore, we estimated R_{snag} and R_{log} using the same function estimated by the results of R_{snag} and R_{log} but with the respective data for θ_{pore}.

Because the water content of snags and logs was markedly different, intensive measurements of the water content of snags and logs were conducted. The θ_{pore} value of snags and logs (θ_{pore_snag} and θ_{pore_log}, respectively) varied with precipitation, and each showed a similar sawtooth waveform (Fig. 5a). However, θ_{pore_snag} values were about one-fifth the magnitude of θ_{pore_log} values (Fig. 5b). The relationship between θ_{pore_snag} and θ_{pore_log} was described by the following equation:

$$\theta_{pore\_log} = -0.035 + 0.191\theta_{pore\_snag}\ r^2 = 0.50. \quad (7)$$

We used this relationship to estimate θ_{pore_snag} from θ_{pore_log}. In 2003, the hourly temperature at 3 cm depth in the log ($D =$ 27 cm, $\rho = 0.65$ g cm^{-3}) showed a clear seasonal change (Fig. 6a). The maximum and minimum temperatures that year were 31.2 °C and 0.0 °C. The hourly water content of the log changed with precipitation but did not change seasonally, despite a slight increase in precipitation in the rainy and typhoon seasons (Fig. 6a).

When we estimated the R_{CWD} of representative samples over the course of a year using eq. (6), it changed seasonally with temperature; the estimated values in summer were about eight times larger than those in winter for all samples (Fig. 6b, c, d). R_{CWD} fluctuated throughout the year with water content changes related to changes in precipitation. The difference in θ_{pore_snag} and θ_{pore_log} resulted in R_{snag} being about half of R_{log}. Thus, the effect of the difference in the spatial orientation of the CWD item on water content was stronger than that caused by wetting and drying related to precipitation (Fig. 6d).

3.3. CWD carbon budget in the forest

The annual R_{CWD} for the forest was estimated to be 0.50 tC ha^{-1} yr^{-1} (Table 4, Fig. 7), with 34% of the total respiration being from snags and 66% from logs. Given these results, the mean decomposition rate constants of snags (k_{snag}) and logs (k_{log}) were calculated as 0.031 and 0.094 yr^{-1}, respectively, and the mean residence time as 33.0 and 11.2 yr, respectively. On a total projected area basis, R_{CWD} was 2.8 kgC m^{-2} yr^{-1}; R_{snag} was 15.2 kgC m^{-2} yr^{-1}, and R_{log} was 1.9 kgC m^{-2} yr^{-1} (Table 4). Because respiration from SOM and leaf litter in the forest has been estimated to be from 0.21 to 0.35 kgC m^{-2} yr^{-1} (Tamai et al. 2005), R_{snag} and R_{log} were, respectively, approximately 54 and seven times the soil respiration. The high contribution of snags is a consequence of the low estimated value of their projected area. The annual mean input of CWD was estimated to be 0.61 tC ha^{-1} yr^{-1}, and the respiration rate was estimated to be 0.50 tC ha^{-1} yr^{-1}; most of the difference between these two fluxes, 0.11 tC ha^{-1} yr^{-1}, was probably sequestered as CWD in the forest from 1999 to 2004 (Fig. 7), but leaching may account for some of the difference.

4. Discussion

4.1. Annual CWD respiration rate

R_{CWD} in the forest was estimated to be 0.50 tC ha^{-1} yr^{-1}. Soil respiration (R_s) in the forest has been estimated to be 4.2–7.1 tC ha^{-1} yr^{-1} (Tamai et al., 2005) or, with the contribution of root respiration, about 37.2% (Dannoura et al., 2006). Thus, heterotrophic respiration (R_h) from leaf litter and SOM only was

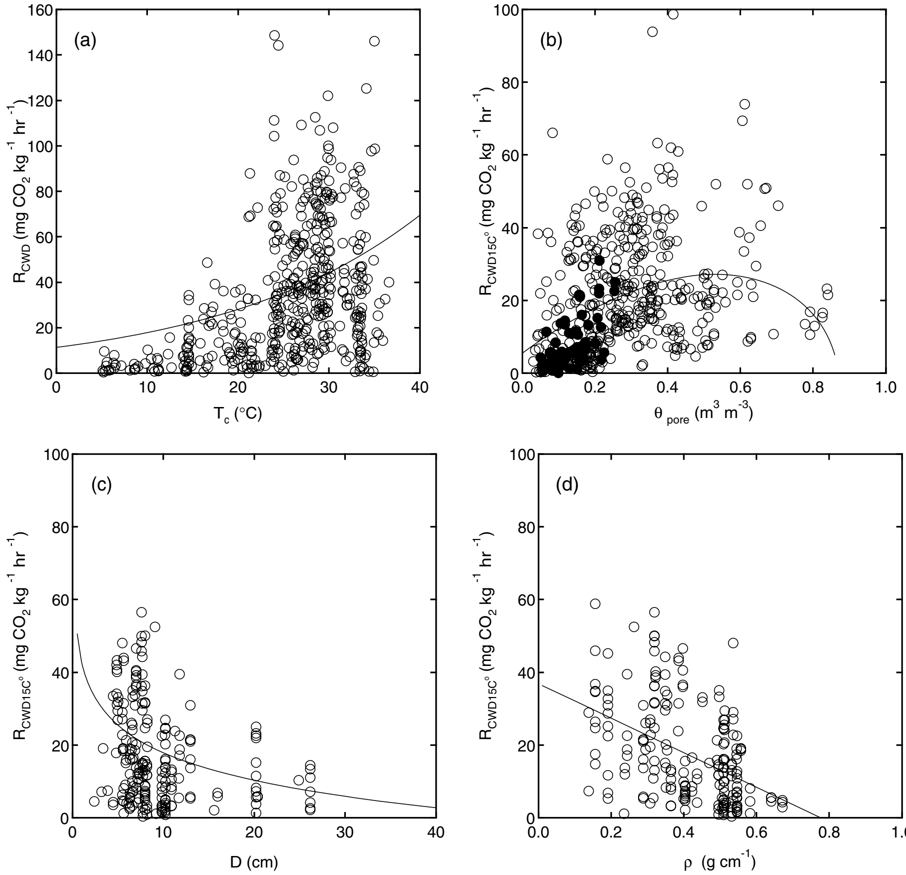

Fig. 4. (a) Relationship between R_{CWD} and T_{c}. The line shown is eq. (6) (see the text) with $\theta_{\mathrm{pore}} = 0.2$ m^3 m^{-3}, $D = 10$ cm and $\rho = 0.4$ g cm^{-3}. (b) Relationship between θ_{pore} and $R_{\mathrm{CWD15^\circ C}}$, standardized using the Q_{10} value obtained from eq. (6). The line shown is eq. (6) with $T_{\mathrm{c}} = 15$ °C, $D = 10$ cm and $\rho = 0.4$ g cm^{-3}. (c) Relationship between $R_{\mathrm{CWD15^\circ C}}$ and D for only those CWD samples with $0.2 > \rho \geq 0.6$ g cm^{-3} and $0.1 > \theta_{\mathrm{pore}} \geq 0.3$ m^3 m^{-3}. The line shown is eq. (7) with $T_{\mathrm{c}} = 15$ °C, $\theta_{\mathrm{pore}} = 0.2$ m^3 m^{-3} and $\rho = 0.4$ g cm^{-3}. (d) Relationship between $R_{\mathrm{CWD15^\circ C}}$ and ρ for only those CWD samples with $5 > D \geq 15$ cm and $0.1 > \theta_{\mathrm{pore}} \geq 0.3$ m^3 m^{-3}. The line shown is eq. (7) with $T_{\mathrm{c}} = 15$ °C, $\theta_{\mathrm{pore}} = 0.2$ m^3 m^{-3} and $D = 10$ cm.

estimated to be 2.6–4.5 tC ha^{-1} yr^{-1}. Forest R_h including R_{CWD} was estimated to be 3.1–5.0 tC ha^{-1} yr^{-1}; thus, R_{CWD} accounted for 10%–16% of the total forest R_h. Thus, as a forest CO_2 source, R_{CWD} was comparable to leaf litter and SOM, and it is thus an important component of the forest carbon cycle in this temperate broad-leaved secondary forest in Japan.

The R_{CWD} of snags (R_{snag}) was estimated to account for 34% of the total R_{CWD} of the forest. Snag samples evolved CO_2 very similarly to logs in relation to water content (Fig. 4b). Moreover, snags underwent wetting and drying in response to variations in precipitation (Fig. 5a). Because the response of microbial activity to wetting is rapid (Borken et al., 1999; Jomura et al., 2005a), wetting by precipitation was assumed to stimulate microbial activity in snags. Although the mass of snags accounted for 60% of the total CWD mass, however, carbon emission from snags was only 34% of the total, mainly because the water content of snags was consistently lower than that of logs. In fact, the water content of snags was less than 0.3 m^3 m^{-3}, about 20% of the water content of logs (Fig. 5b). The results of the regression of the R_{CWD} response against water content showed that the optimal water content for maximal R_{CWD} was about 0.5 m^3 m^{-3} (Fig. 4b). Therefore, we assumed that the carbon emission from snags was limited by their lower water content. Thus, the spatial variation in water content caused by CWD orientation (i.e. whether a CWD item was a snag or a log) markedly affected the landscape R_{CWD}.

The mean decomposition rate constants of snags (k_{snag}) and logs (k_{log}) were estimated from the mineralisation rate to be 0.031 and 0.094 yr^{-1}, resulting in a mean residence time of snags and logs of 33.0 and 11.2 yr, respectively. These k_{snag} and k_{log} values are consistent with the results of weight-loss measurements of block specimens of *P. densiflora* set above and on the ground in the forest (Jomura et al., 2005b), indicating that the estimate of the mineralisation rate from the R_{CWD} measurements in this study was adequate. Our k_{snag} values were lower than the values reported in a review of data from temperate forests in

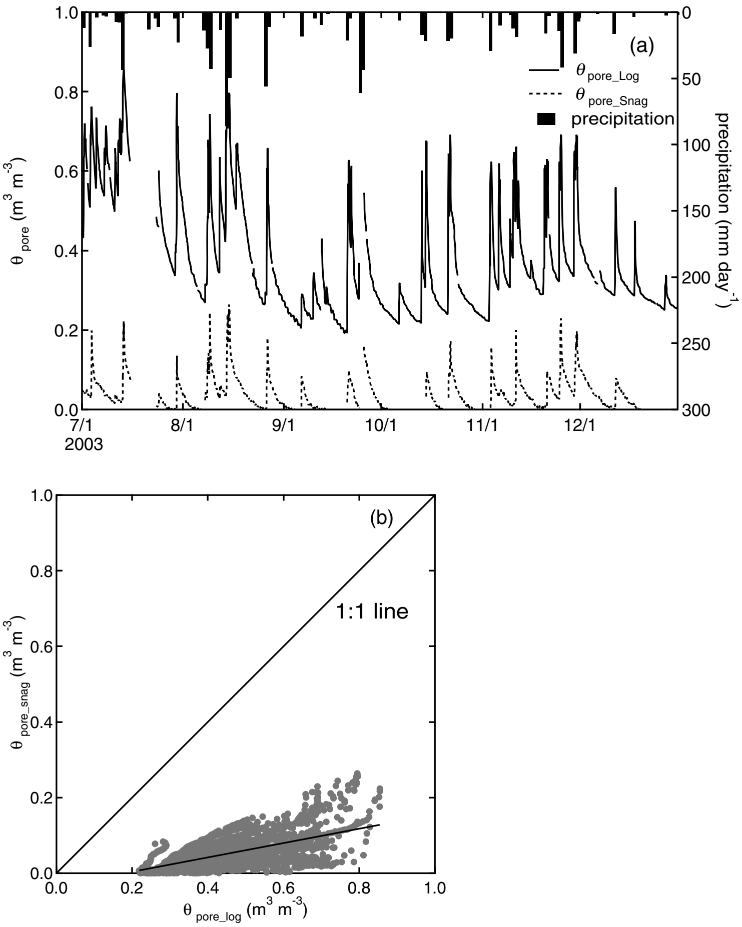

Fig. 5. (a) Changes in θ_{pore} with time for a snag and a log. (b) Relationship between θ_{pore} of snags and logs.

the north-western United States (Harmon et al., 1986), whereas our k_{log} values were larger. There are several possible reasons for these differences. At our study site, the hourly maximum air temperature in August reached 34.8 °C (see Section 2.1.), and precipitation was high in summer; early summer is the rainy season, and typhoons occur in summer and fall. This hot, moist summer climate likely induced rapid decomposition of CWD, despite the characterization of the study region as having a temperate climate. Moreover, the decomposition rate of CWD is affected by the size of CWD items (Erickson et al., 1985; Marra and Edmonds, 1994). R_{CWD} was correlated with the diameter of CWD (Fig. 4c). At this site, the maximum diameters of living and dead trees were relatively small, 55 and 40 cm, respectively. The decomposition rate of CWD generally increases as diameter decreases (Næset, 1999; Chambers et al., 2000; Mackensen et al., 2003), which is supported by the results of our experiments. The relatively small size of CWD items at our site might also have induced rapid decomposition. On the other hand, a recalcitrant substrate such as lignin, which is found in litter, slows the decomposition rate (Melillo, 1982). The CWD in our forest consisted mainly of *P. densiflora,* whose heartwood contains much resin. The resinous heartwood seemed to decompose slowly, suggesting that substrate did not cause rapid decomposition of CWD.

The R_{CWD} of logs (R_{log}) and the R_{h} of fine litter and SOM in the forest were estimated to be 0.33 and 2.6–4.5 tC ha^{-1} yr^{-1}, respectively. However, the projected area of logs covered only 1.7% of the total soil surface. Thus, on a projected area basis, R_{log} was four to seven times R_{h} from litter and SOM, indicating that logs are important sources of carbon in the forest and that the distribution of respired carbon in the soil surface layer is very heterogeneous. Moreover, Manies et al. (2005) estimated that 10%–60% of deep-soil carbon is derived from wood biomass. Thus, the past frequency and distribution of logs on the forest floor apparently affects the spatial heterogeneity of soil respiration.

4.2. *CWD input rate*

The mean input mass of CWD from 1999 to 2004 was 0.61 tC ha^{-1} yr^{-1}. Litter input from 1999 to 2001 was 2.23 tC ha^{-1} yr^{-1} (Goto et al., 2003). Taken together, these results show that CWD input accounted for 22% of the total input of dead organic matter. The ratio of CWD input to total input has been reported

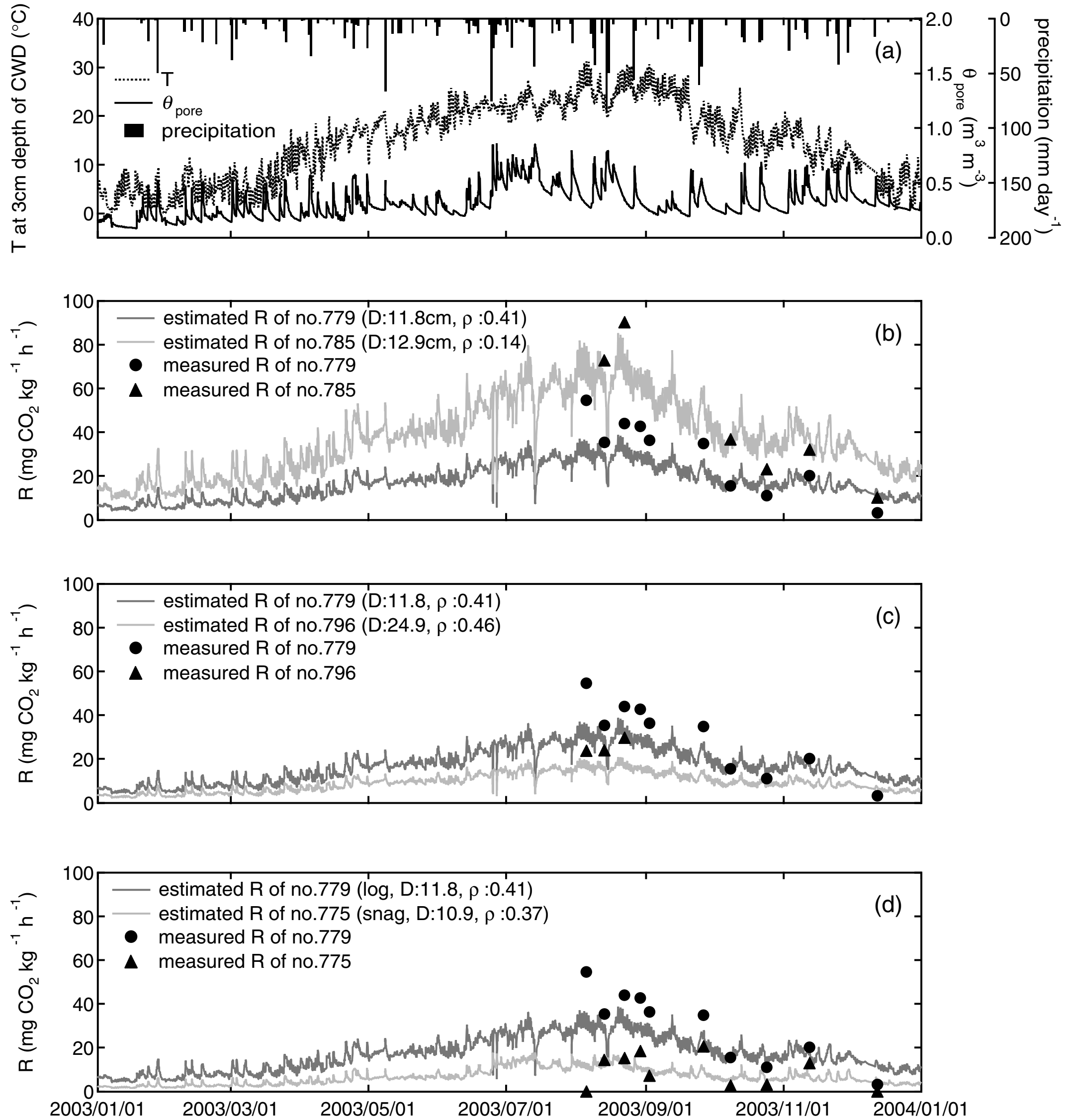

Fig. 6. Seasonal changes in T at 3 cm depth in CWD, θ_{pore} precipitation and R_{CWD} of representative samples, as estimated by eqs. (4) and (7). The dots represent actual R_{CWD} sample measurements. Samples with different values for ρ (b), D (c) and CWD state (snag or log; d) are compared.

to be 3%–73% (Laiho and Prescott, 2004) or 35%–55% in Japan (Ando et al., 1977). Thus, the ratio in our forest was lower than ratios reported by other studies in Japan. The tree size in YMS was relatively small (mean DBH, 7.4 cm; canopy height, 12 m; see Section 2.1.), probably owing to the poor soil and the fact that the forest was a secondary one regenerating from damage caused by pine wilt disease. Moreover, the mortality rate of the pioneer species, such as *Alnus pendula* Matsum. and *Rhus trichocarpa* Miq., that populated the forest after the pine wilt disease was relatively high (Goto et al., 2004). In 1999, the mean diameter of these species (7.6 cm) was smaller than the overall mean DBH. Thus, these factors may explain the small ratio of CWD input in YMS.

Most of the CWD occurred as snags, accounting for 89% of the total input. The decomposition rates of snags and logs were very different, mainly because the differences in spatial orientation caused spatial variation in water content, as mentioned above. It has been suggested that drying of wood reduces the activity of decay organisms in snags (Harmon et al., 1986; Yatskov et al., 2003). Moreover, the longevity of snags may be an important factor affecting the carbon budget of CWD (Harmon et al., 1986; Garber et al., 2005). Thus, the spatial orientation of a CWD item at the time of death and the length of time that a snag stands before it becomes a log should be monitored to evaluate the carbon budget of CWD and the carbon cycle of a forest.

Table 4. Annual R_{CWD} in the forest and on a projected area basis

	R_{CWD} in the forest ($tC\ ha^{-1}\ yr^{-1}$)	R_{CWD} on a projected area basis ($kgC\ m^2\ yr^{-1}$)
Total	0.50	2.76
Snag	0.17	15.21
Log	0.33	1.94

Interannual variation in CWD input mass, from 50% to 150% of the mean CWD input, was observed during the 5-yr monitoring of tree mortality. The fine litter input varied over 3 yr from 98% to 102% of the mean fine litter input (Goto et al., 2003). Thus, CWD input showed somewhat greater interannual variation than fine litter input. This variation differed markedly between snags (50%–120%) and logs (14%–414%), with the variation in logs being particularly large. We attributed this difference to the high input of logs in 2004, when several large typhoons struck Japan. The heavy rains and strong winds presumably caused this high input of logs. Because the frequency of major disturbances such as typhoons is low, long-term monitoring of CWD input mass and the spatial orientation of CWD items is necessary to obtain a representative mean value of CWD input and to estimate the effect of such disturbances on the forest carbon cycle.

4.3. Carbon budget of CWD

The pine wilt disease episode that occurred about 30 yr before our study generated much *P. densiflora* CWD in YMS; in 2003, 68% of the total R_{CWD} evolved from this CWD. Thus, most of the estimated R_{CWD} was released from CWD that was input several decades before. However, R_{CWD} was not larger than the CWD input, and about 0.11 $tC\ ha^{-1}\ yr^{-1}$ was probably sequestered as CWD in our forest. This non-equivalence was mainly caused by the lag-time of decomposition of the dead wood of the pioneer species. The mortality of the species that grew after the pine wilt disease episode was also high from 1995 to 1999 (Goto et al., 2004), but most dead wood of these species was assumed to be standing, with the result that CO_2 evolution from these species did not largely contribute to the total R_{CWD}. Thus, in a secondary forest, such as YMS, an equivalence between input and the decomposition rate of CWD cannot be assumed. These results suggested that the timing and mass of the transformation of snags to logs strongly affect the R_{CWD} and the carbon balance of CWD. The difference between the input and decomposition rates of CWD affects the NEP of the forest. In YMS, CWD probably sequestered 0.11 $tC\ ha^{-1}\ yr^{-1}$ or 7% of NEP (1.59 $tC\ ha^{-1}\ yr^{-1}$, Kominami et al., submitted to this special issue), as estimated from tower and biometric measurements.

5. Conclusion

The annual landscape R_{CWD} was estimated by integrating the annual R_{CWD} values with the spatial distribution of CWD accumulation in the forest. The spatial distribution of CWD as snags or logs markedly affected the landscape R_h. The annual R_{CWD} of snags was low because of their low water content, related to their limited contact with the ground. The spatial distribution of logs on the forest floor thus was the most important factor contributing to the spatial heterogeneity of R_h. Moreover, annual variation of input caused by disturbances or forest succession is likely to result in annual changes in CWD accumulation. Quantification of these spatiotemporal variations in CWD input, decomposition and accumulation are important for evaluation of the CWD carbon budget and evaluation of NEP in the carbon cycle of forests.

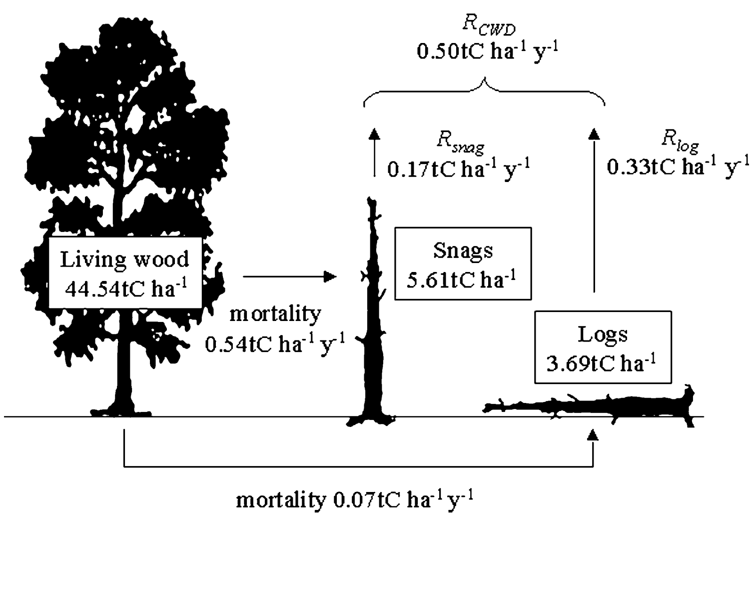

Fig. 7. Carbon cycle of CWD in a temperate deciduous broad-leaved forest.

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