

Dynamics of coarse woody debris and decomposition rates in an old-growth forest in lower tropical China

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ABSTRACT

The biomass and decomposition of coarse woody debris (CWD, ≥ 10 cm in diameter) were studied in a monsoon evergreen broad-leaved old-growth forest in Dinghushan Nature Reserve, Southern China. The study examined the biomass of CWD from 1992 to 2008 and decomposition of three dominant tree species CWD (*Castanopsis chinensis*, *Cryptocarya concinna*, *Schima superba*) from 1999 to 2008. Changes in the wood density of three tree species' CWD were used to estimate the decay rates with a single exponential model. The results showed that the biomass of CWD in the old-growth forest was increasing from 17.41 tonnes ha^{-1} (t ha^{-1}) in 1992 to 38.54 t ha^{-1} in 2008, and a higher decay constant was observed for *C. concinna* (0.1570 – 19 years for 95% mass loss); the decay rates of *S. superba* and *C. chinensis* were 0.1486 (20 years for 95% mass loss) and 0.1095 (27 years for 95% mass loss), respectively. The difference in decay constant rates may be due to their substrate quality and decomposers. The content of carbon (C) in three species declined after 9 years of decay. Nitrogen (N) content increased in all species with decay. The C/N ratio in the three species declined during the decay process.

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1. Introduction

Coarse woody debris (CWD) is defined as standing and fallen dead trees larger than 10 cm in diameter that cannot be captured by littertraps, including sound and rotting snags, stumps, logs and large branches (Harmon et al., 1986; Idol et al., 2001). CWD is a substantial forest carbon (C) stock and a source of nutrients (Ganjegunte et al., 2004; Manies et al., 2005; Beets et al., 2008) in the forest ecosystem. The percentage of CWD to total aboveground biomass depends greatly on forest geographical location, forest management (Carmona et al., 2002; Stevenson et al., 2006; Yan et al., 2007; Woodall and Liknes, 2008), forest succession stages and disturbance (Harmon et al., 1986). CWD in natural forests and plantations are usually different in biomass (Agee and Huff, 1987; Grove, 2001; Yan et al., 2007). Currie and Nadelhoffer (2002) concluded that CWD biomass in coniferous plantations was lower than that in natural deciduous forests. Several studies also showed that old-growth forests, with least anthropogenic disturbances, usually contain higher CWD biomass than young or transition

forests (Grove, 2001; Carmona et al., 2002; Eaton and Lawrence, 2006; Yan et al., 2007). Previous studies conducted in the Dinghushan Biosphere Reserve of South China, an old-growth forest, showed that CWD in an old-growth forest was approximately 100 times higher than in a pioneer pine forest (Tang and Zhou, 2005). The CWD constitutes a significant proportion of dead mass and could play a significant ecological role in forest functioning. Critical ecological roles may include nutrient sources, carbon sink, substrate for seed germination, habitats for biological diversity and as soil stabilizers (Harmon et al., 1986; Means et al., 1992; Currie and Nadelhoffer, 2002; Woldendorp et al., 2004; Brais et al., 2005). The dominated role however, may vary depending on forest age. Thus CWD dynamics could influence soil fungi and fauna community formation (Harmon et al., 1986; Rubino and McCarthy, 2003), biodiversity conservation and even ecosystem stability of natural forests.

Decomposition dominates CWD dynamics and is one of the major pathways by which carbon fixed during photosynthesis is returned to the atmosphere or converted and stored as soil organic carbon (C). Recent studies show a widespread tree mortality rates in natural forests (Mantgem van and Stephenson, 2007; Mantgem van et al., 2009; Pennisi, 2009). Studying the influx of CWD may provide an alternative approach for tracking changes in natural forest ecosystems and for predicting the impacts on forests

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associated with shifts in climate and land use. However, because annual influx of CWD cannot be directly measured, it can only be estimated through the combination of CWD decomposition rates and regular surveys on CWD dynamics. In any case, understanding CWD decomposition rates is important to quantifying of the carbon and nutrient pools, especially in old-growth forests.

The monsoon evergreen broad-leaved forest (MEBF) in Dinghushan Biosphere Reserve, South China is an old-growth forest of climax community that has been intensively monitored since 1978 (Wang and Ma, 1982; Tu, 1984; Zhang et al., 1997; Tang et al., 2003; Tang and Zhou, 2005; Yan et al., 2006; Zhou et al., 2006, 2008). As a part of comprehensive monitoring, CWD stock has been regularly surveyed since 1992 and the CWD decomposition experiment has been conducted since 1999; this long-term monitoring is a substantial advantage for this study. The objectives of this study were to (1) estimate the annual influx of CWD from the aboveground biomass in an old-growth forest, (2) estimate CWD decomposition rates of the dominant species through CWD decomposition experiments.

2. Materials and methods

2.1. Study site

The study area, covering 1156 ha, was located in the Dinghushan Biosphere Reserve (23°09′–23°11′N, 112°30′–112°33′E), Guangdong Province, and Southern China (Fig. 1). The Reserve was established in 1950 to protect the only remnant of undisturbed natural monsoon evergreen broad-leaved forest (MEBF) in the subtropics, and was accepted as the first MAB Reserve in China in 1978. It had 2054 recorded native species of higher plants. The elevation ranged from 14 m to 1000 m above sea level. The mean annual precipitation was 1956 mm, of which about 80% occurred during the wet season (April–September). Mean annual air temperature and relative humidity were 21.5 °C and 80%, respectively. The region was characterized by a typical subtropical monsoon climate. Monthly mean air temperature and precipitation for the period 1992–2008 for the Dinghushan Biosphere Reserve were shown in Fig. 2. The bedrock was typically sandstone and shale (Zhou et al., 2006). The study area was located in the monsoon evergreen broad-leaved forest, dominated by *C. chinensis*, *C. concinna*, and *S. superb*, with forest coverage of 78.7% and a forest canopy density of 93% (Zhou et al., 2005). The forest at this site was intact and had not experienced any anthropogenic disturbance during the last 400 years (Zhou et al., 2006). The forest had five (5) clearly defined canopy layers, including three sublayers comprising trees, shrubs and herbs, respectively. Tree height in the first sublayer was 16–25 m. Major tree species in this layer were *Castanopsis chinensis* and *Schima superb*. Arbor species

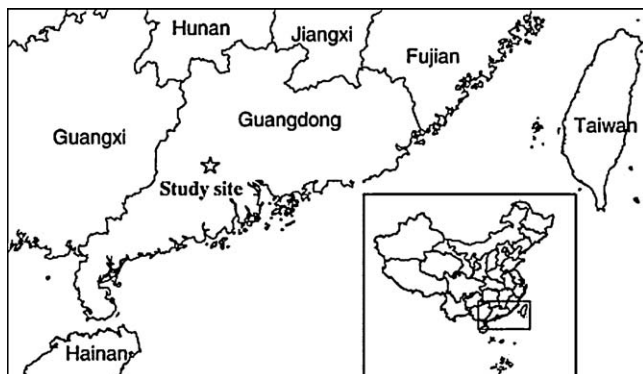


Fig. 1. Location of the Dinghushan study area within Guangdong Province of southern China.

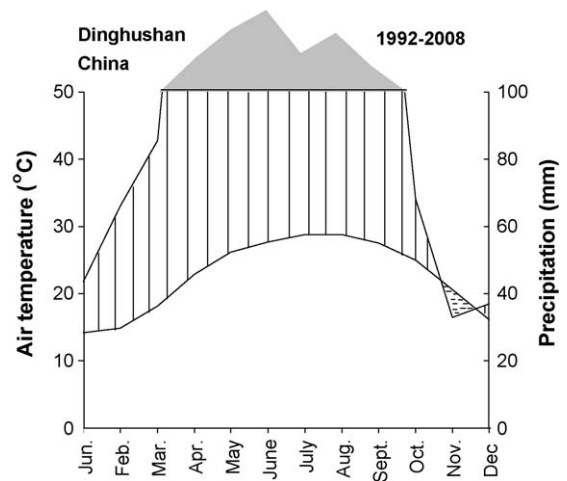


Fig. 2. Climate diagram according to Walter (1979) for Dinghushan, China (Meteorological station 23°10′N, 112°33′E, 150 m a.s.l.). The grey portion indicates precipitation was over 100 mm and the scale is 1:10 for precipitation. The average precipitation in June, July and August was 340.2, 274.0, and 212.0 mm, respectively.

accounted for 63% of the total species in MEBF. The average height of shrub layer was 1.2–9 m, dominated by *Aporosa yuannanensis*, *Blastus cochinchinensis*, and *Psychotria rubra*. The bottom layer, and was dominated by *Hemigramma decurrens*.

2.2. CWD biomass measurements

CWD biomass was investigated across MEBF in 10–0.1 ha plots during the dry season from 1992 to 2008. Within each plot, CWD was measured using a fixed area plot sampling method (Harmon and Sexton, 1996; Yan et al., 2007). Types of CWD were sampled according to the protocol of Harmon and Sexton (1996). We recorded each CWD inventoried in the field: species, length, types, diameter, and decay class. A decay class of each piece of CWD was assigned, ranging from 1 to 3 according to the methods of Sollins (1982) and Tang and Zhou (2005). We calculated CWD biomass (tonnes ha⁻¹, abbreviated here as t ha⁻¹) using equations described by Wen et al. (1998) and Harmon and Sexton (1996).

2.3. CWD sampling

We considered felled dead wood and standing dead trees with a diameter ≥ 10 cm as CWD. The tree species selected for study were *Castanopsis chinensis*, *Cryptocarya concinna*, and *Schima superba*. This choice was partly influenced by the availability of previously sampled dead standing and fallen trees for which there was earlier data, including dates of windfall and species (Wei et al., 1997; Wen et al., 1998; Tang and Zhou, 2005). When a tree fell and/or died, a forest worker would note the date and species, and placed a sign on the tree. CWD samples were taken from trees in the 10–0.1 ha plots that were uprooted in large storms and landslides, mostly occurring in 1999, 2003, 2005 and 2007. Soon after the tree died or fell, five to seven 50-cm-long samples (depending on the total length of a CWD sample tree) were taken from the basal part of the tree all the way to the treetop, approximately every 2–3 m. Before being placed in the permanent site, the samples were weighed, measured and tagged. In order to simplify the environmental and essential texture factors, all the CWD samples were selected from trees that died at the age of 25–35 years. Our permanent site for CWD study was established in 1999 with an area of 20 m \times 20 m with three replicate plots for each species, and in 2007, it was extended to 40 m \times 40 m. To reduce the disturbance from wild boars, the permanent site was protected by an enclosure. The three

plots were distributed in a nearly flat location with the same understory and overstory canopy so that the microclimate for decay was similar. The plots were designed so that 15–21 CWD samples were placed there per year. By 2007 there were a total of 205 CWD samples with known ages among the three plots (Wen et al., 1998; Tang and Zhou, 2005). All the CWD were allowed to naturally decay on the permanent site. In December of 2008, CWD samples were collected at the permanent site representing 1, 3, 5, and 9 years of decay after the tree had fallen or died. At the collection time, each cross-section of CWD was cut into approximately 2 cm diameter thick pieces and sealed in plastic bags to preserve original moisture content and hence volume before transferring to the laboratory (Grove, 2001). CWD sub-samples were oven-dried at 70 °C for about one week to a constant weight, and then the volumes were determined gravimetrically by water displacement. Finally, the CWD density ($\text{g dry mass cm}^{-3}$) was estimated as the ratio of dry mass to volume.

2.4. Decay rate constant (k)

A single exponential decay model (Eq. (1)) was used to determine the decay rate constant (k) (Olson, 1963).

$$X_t = X_0 e^{-kt} \quad (1)$$

where X_t is the density of CWD at time t , X_0 is the initial density of substrate, and t is the time.

The time to lose 95% of the density was estimated from the decay constant:

$$T_{0.95} = -\frac{\ln(0.05)}{k} = \frac{3}{k} \quad (2)$$

2.5. Nutrient contents

Dried cross-sections were crushed to pass through a No. 100 mesh for nutrient analysis. Total carbon (C) was determined by potassium dichromate oxidation; total nitrogen (N) and phosphorus (P) were measured by the kjeldahl N law and Mo anti-antimony colorimetry, respectively; the contents of potassium (K), sodium (Na), calcium (Ca) and magnesium (Mg) were determined by a scanning CCD plasma emission spectrometer (Optima 2000 DV) after being wet digested using concentrated H_2SO_4 and HClO_4 (Dong, 1999).

2.6. Statistical analysis

All statistics were carried out using SPSS 11.5. A single exponential regression and a one-way ANOVA were used to test for the effect of decay time on C, N and other nutrient contents and the effect of decay time on CWD density. The means were compared using Duncan's t -test. All significant results were reported at $P < 0.05$.

3. Results

3.1. CWD biomass dynamics

Average annual increment of CWD biomass in the period of 1992–2008 was 1.32 t ha^{-1} . The biomass increased to 38.54 t ha^{-1} in 2008, the amount was roughly equivalent to 14.54% of the total vegetation biomass (Fig. 3). The annual influx of CWD biomass rose from 1.12 t ha^{-1} in 1992–1999 to 1.47 t ha^{-1} in 1999–2008 and to 3.16 t ha^{-1} in 2004–2008, although the total vegetation biomass declined in 1999–2008 (Fig. 3). The dominant species of *C. chinensis*, *C. concinna* and *S. superba* accounted for 36%, 17% and 30% of the

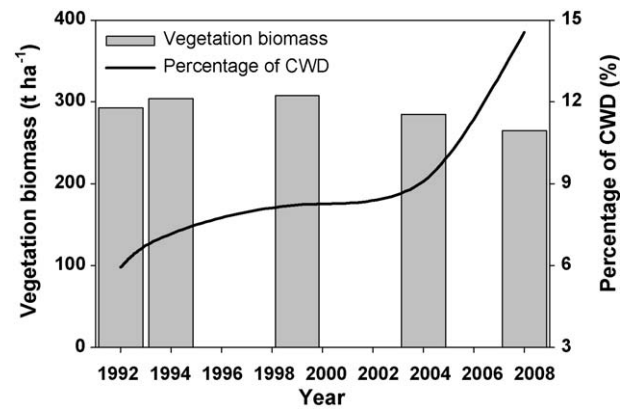


Fig. 3. The relationship between vegetation biomass and CWD biomass from 1992 to 2008. Sources of vegetation biomass data are Wen et al. (1997) and the unpublished Dinghushan long-term ecological monitoring database.

CWD biomass in the study region in 2008, respectively (Table 1). C stock of CWD was varied across different decay class, and in 2008 the C stock of class II accounted for 64.3% of the total C stock of CWD, and classes I and III accounted for 27.5% and 8.2%, respectively (Table 2). Stocks of C and nutrients in CWD increased from 1992 to 2008 (Table 3), with C stock in CWD ranging from 7.64 to 19.66 t ha^{-1} , and nutrients stock in CWD (all units in kg ha^{-1}) ranging from 47.01 to 104.06 for N, 2.56 to 5.78 for P, 34.47 to 76.31 for K, 57.63 to 127.18 for Ca, 4.56 to 10.02 for Mg, and 2.84 to 6.17 for Na. The carbon stock in 2008 was 157% of the value in 1992. Annual nutrient inputs ($\text{kg ha}^{-1} \text{ year}^{-1}$) for 1992–2008 were 3.57 for N, 0.20 for P, 2.62 for K, 4.35 for Ca, 0.34 for Mg, and 0.21 for Na.

3.2. Decay rate constants (k)

As this study's CWD samples were maintained in the field plots, the difference of microclimate between the plots was negligible. Decay rate constants (k) and the corresponding times taken for CWD to lose 95% of initial density are given in Table 4. The decay rate constants of $K = 0.1095, 0.1486, 0.1570$ indicated that the times for 95% decay ($t_{0.95}$) for *C. chinensis*, *S. superba*, and *C. concinna* were 27, 20, and 19 years, respectively. *C. concinna* decomposed faster than *S. superba* and *C. chinensis*. The decay rate constant for *C. chinensis* was lower than the constant for *S. superba*. There was a curvilinear correlation between woody density and decay time of CWD (Fig. 4). *S. superba* lost 71.6% (S.E. = 0.02, $P < 0.05$) of the original density after 9 years while *C. chinensis* and *C. concinna* had a 59.2% (S.E. = 0.02, $P < 0.05$) and 70.4% (S.E. = 0.02, $P < 0.05$) loss after 9 years, respectively (Table 4). The decay rate

Table 1

Characteristics of the monsoon evergreen broad-leaved forest selected for this study.

Dominant species	CWD biomass (t C ha^{-1})	Percentage (%)
<i>C. chinensis</i>	7.08	36
<i>C. concinna</i>	3.34	17
<i>S. superba</i>	5.90	30

Table 2

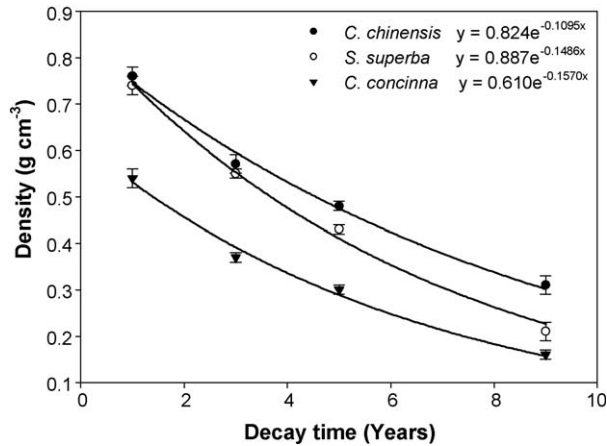
CWD biomass of different decay classes in the monsoon evergreen broad-leaved forest. Decay classes I, II and III represent different time periods of decay. I, II and III indicate primary decay, intermediate decay and advanced decay, respectively.

Decay class	CWD biomass (t C ha^{-1})	Percentage (%)
I	5.41	27.5
II	12.64	64.3
III	1.61	8.2

Table 3

Biomass, C and nutrients stock of CWD from 1992 to 2008 in an old-growth forest in lower tropical China.

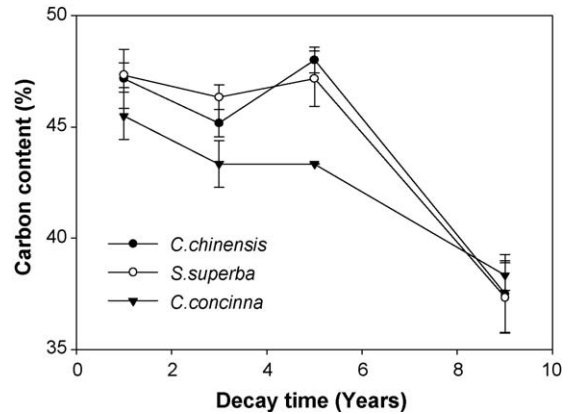
Year	Biomass (t ha ⁻¹)	C (t ha ⁻¹)	N (kg ha ⁻¹)	P (kg ha ⁻¹)	K (kg ha ⁻¹)	Ca (kg ha ⁻¹)	Na (kg ha ⁻¹)	Mg (kg ha ⁻¹)
1992	17.41	7.64	47.01	2.56	34.47	57.63	2.84	4.56
1994	21.79	9.56	58.83	3.21	43.14	72.12	3.56	5.70
1999	25.28	11.09	68.26	3.73	50.04	86.68	4.13	6.62
2004	25.89	11.36	69.90	3.82	51.25	85.69	4.23	6.78
2008	38.54	19.66	104.06	5.78	76.31	127.18	6.17	10.02

**Fig. 4.** CWD wood density remaining of the three species: *C. chinensis*, *C. concinna*, *S. superba* after 1, 3, 5, and 9 years of decay. Error bars represent the standard error about the mean.

constant average across all species was 0.1384, which means that it took on average 22 years for CWD to lose 95% of its mass. The remaining density of CWD significantly varied among the decay times ($P < 0.001$).

3.3. C and N contents and the C/N ratio

C content in the three species' CWD after 1 year of decay did not differ significantly. C content in *C. chinensis* was 49.67% (S.E. = 1.7%) while C content in *C. concinna* was 47.27% (S.E. = 1.4%). After 3 years of decay the loss of C content was greater in *C. concinna* (7.7%) (S.E. = 1.4%). However, *S. superba* showed a greater range (48.79–37.75%) (S.E. = 1.5%) in C content than the other two species (Fig. 5). The results showed that the loss of C content after 9 years of decay in *C. concinna*, *S. superba* and *C. chinensis* resulted in C contents of 18.34%, 22.63% and 22%, respectively. The C contents of CWD significantly varied between 9 years and 1, 3, 5 years, respectively ($P < 0.05$). N content increased significantly after 9 years of decay

**Fig. 5.** Carbon content of the three species: *C. chinensis*, *C. concinna*, *S. superba* after 1, 3, 5 and 9 years of decay. Error bars represent the standard error about the mean.

except for *C. concinna* (Fig. 6). *C. concinna* had a higher increase (7.7%) (S.E. = 0.03%) after 3 years of decay while *C. chinensis* increased faster (7.5% and 65.9%) (S.E. = 0.03%) after 5 and 9 years of decay (Fig. 6). The C/N ratio declined in the three species over the first 3 years of decay and this decline proceeded to 9 years (Fig. 7).

3.4. Other nutrient (K, Ca, P, Na, Mg) contents

K contents increased after 3 years of decay but then decreased after 9 years of decay to lower values than after 1 year of decay (Fig. 8A). The contents of Ca increased in *C. chinensis*, *C. concinna* and *S. superba* by 178%, 219% and 209% after 9 years of decay, respectively (Fig. 8B). The contents of P increased during the period of decay (Fig. 8C). Sodium contents increased in the first 3 years and then decreased, but the general trend of increasing nutrient content over the entire decay process was increasing (Fig. 8D). Magnesium contents increased in *C. chinensis* but decreased in *C. concinna* after 3 years of decay. Contents of Mg in *S. superba* increased during the 9 years of decay and contained the greatest Mg contents among the species (Fig. 8E).

Table 4Density (g cm^{-3}), percentage loss, carbon-to-nitrogen ratio, and time to lose 95% of the density in *C. chinensis*, *C. concinna*, and *S. superba* for 1, 3, 5, and 9 years of decay. Standard error is provided in parentheses. Values in a column followed by the same letter do not differ significantly ($P < 0.001$).

Species	Years of decay (year)	Density (g cm^{-3})	Percentage loss (%)	C/N ratio	$t_{0.95}$ (year)
<i>C. chinensis</i>	1	0.76 a (0.02)	0	365 (21)	27
	3	0.57 b (0.02)	25.0	234 (8)	
	5	0.48 c (0.02)	36.8	171 (10)	
	9	0.31 d (0.02)	59.2	94 (3)	
<i>C. concinna</i>	1	0.54 a (0.02)	0	333 (28)	19
	3	0.37 b (0.01)	31.5	166 (18)	
	5	0.30 c (0.02)	44.4	110 (5)	
	9	0.16 d (0.02)	70.4	92 (4)	
<i>S. superba</i>	1	0.74 a (0.01)	0	361 (27)	20
	3	0.55 b (0.01)	25.7	263 (45)	
	5	0.43 c (0.01)	41.9	171 (20)	
	9	0.21 d (0.04)	71.6	111 (7)	

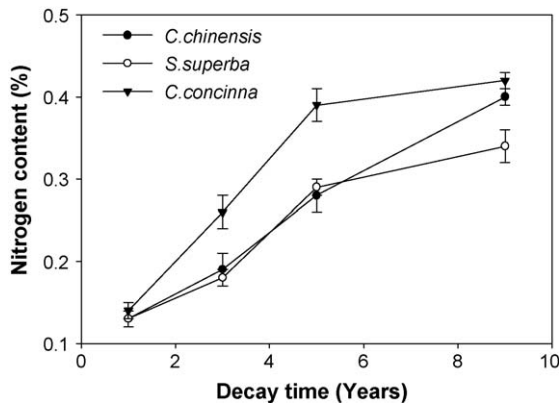


Fig. 6. Nitrogen content of the three species: *C. chinensis*, *C. concinna*, *S. superba* after 1, 3, 5 and 9 years of decay. Error bars represent the standard error about the mean.

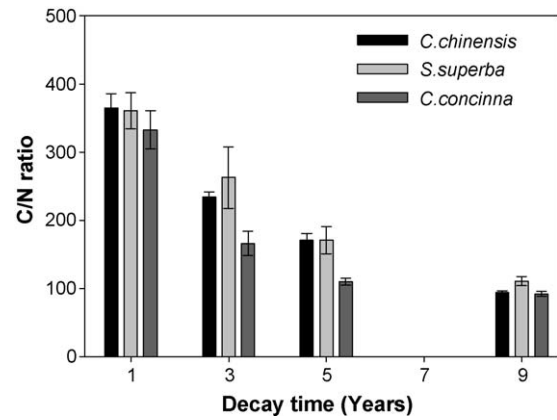


Fig. 7. C/N ratio of the three species: *C. chinensis*, *C. concinna*, *S. superba* after 1, 3, 5 and 9 years of decay. Error bars represent the standard error about the mean.

4. Discussions

4.1. CWD biomass dynamics

CWD biomass at the Dinghushan study site was higher than those in the north temperate forest (Gough et al., 2007) and in the lowland tropical rainforest in Australian (Grove, 2001), but was lower than that in an evergreen broad-leaved forest in Chile (Carmona et al., 2002) and in Eastern China (Yan et al., 2007). Biomass of CWD is partially affected by climatic variables such as temperature and humidity (Woodall and Liknes, 2008), which regulate the decay rate. Differences in CWD biomass are therefore dependant on the decay rates and the initial substrate mass (Baker et al., 2007). We observed a comparatively higher decay rates in our study site. Based on these observations and findings from other studies (Mantgem van et al., 2009; Pennisi, 2009) the current

global warming due to climate forcing may lead to accelerated decomposition rates of CWD and increased CO₂ input into the atmosphere.

Forest succession has a significant influence on the biomass of CWD, and CWD can be an indicator reflecting forest management history (Yan et al., 2007). Our results suggest that the increasing biomass of CWD in this old-growth forest was due to the natural disturbances (e.g., typhoon and landslides in South China), mortality rate and air warming. Mortality rates in the old-growth forest in Dinghushan went from 2.1% year⁻¹ in 1992–1994 to 2.4% year⁻¹ in 1994–1999 (Wen et al., 1998; Tang et al., 2003), while in 1999–2008 the value was jumped to 6.4% year⁻¹. This jump in mortality rates was caused by a cohort of old, tall, large diameter trees that died and fell (i.e. two *C. chinensis* with diameter breast height >70 cm, length >10 m died and fell in 2008 at the study site), crushing smaller trees. The pervasive increase in CWD

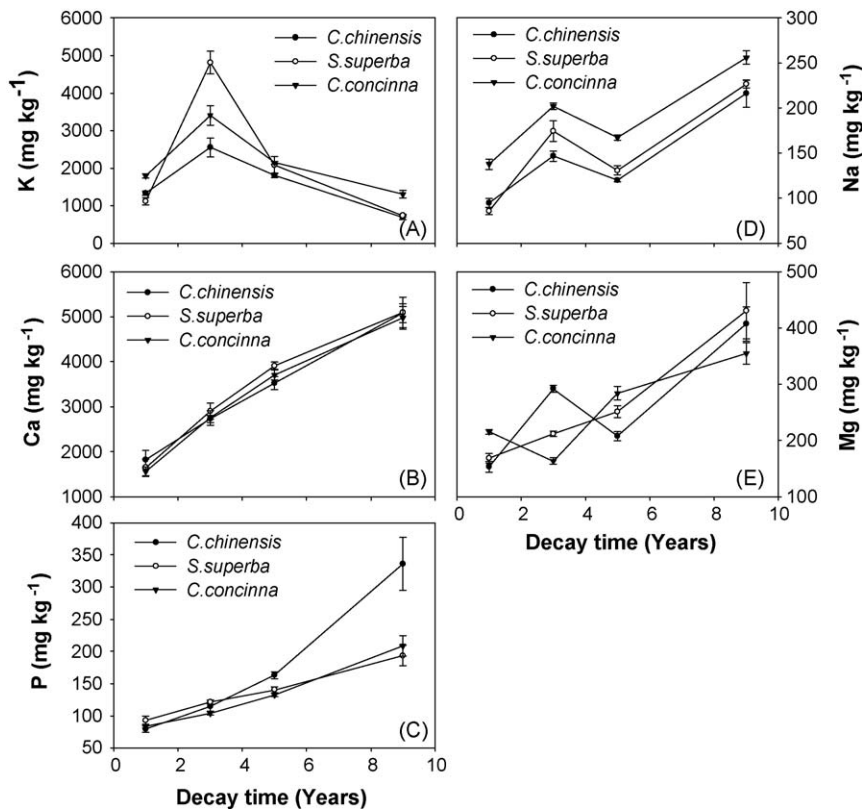


Fig. 8. Contents and standard errors of potassium (A), calcium (B), phosphorus (C), sodium (D) and magnesium (E) after 1, 3, 5, and 9 years of decay.

biomass in the old-growth forest of the Dinghushan region was similar with that reported by Mantgem van et al. (2009). A few recent studies suggested that the warming of temperature likely caused the trees' increased death rate (Mantgem van et al., 2009; Pennisi, 2009). The increasing trend of CWD biomass can explain the accumulation of carbon in soils in old-growth forests (Zhou et al., 2006). The results in our study can also lead us to believe that maintaining the health and preserving biodiversity of forest ecosystem should include the maintenance of CWD.

4.2. Decay rate constants (k)

The decomposition of CWD is complex and controlled by different factors such as the type of wood, humidity of wood, mean annual temperature and decomposers (Harmon et al., 1986; Mackensen et al., 2003; Bond-Lamberty et al., 2003; Garrett et al., 2007, 2008; Beets et al., 2008). In a mixed hardwood forest in North Carolina, Mattson et al. (1987) found a 10-fold variation in decay rates among species. Eaton and Lawrence (2006) recorded the average decay rate constant was 0.278 in secondary forests in Southern Mexico, which is higher than our study findings. Mackensen et al. (2003) suggested that the decay time to lose 95% mass for native Australian species ranges from 7 years in *Eucalyptus regnans* to 375 years in *E. camaldulensis*. IPCC (2003) defined a 10-year default for all litter. Differences in decay rates are likely due to CWD substrate quality differences (Harmon et al., 1986; Ganjegunte et al., 2004; Guo et al., 2006; Garrett et al., 2007; Beets et al., 2008), the humidity and temperature (Chambers et al., 2001; Mackensen et al., 2003; Bond-Lamberty et al., 2003; Garrett et al., 2008), the diversity of microbes (Harmon et al., 1994; Beets et al., 2008), and the contact with soil (Ganjegunte et al., 2004; Garrett et al., 2008).

Among the different species, *C. concinna* decomposed faster than *C. chinensis* and *S. superba*. Differences in decay of the three species have been attributed to substrate quality and decomposer organisms (Swift et al., 1979; Ganjegunte et al., 2004; Garrett et al., 2007, 2008; Beets et al., 2008). Tang and Zhou (2005) reported the decay rate constant in Dinghushan Reserve was 0.031, implying that it would take 32 years to lose 95% mass. Applying all diameters (i.e. <10 cm) and types of species to estimate the decay rate would underestimate the decay rate of the dominant downed wood and we suggest that more research is needed to illuminate an all-species decay rate in Dinghushan. Lv et al. (2006) reported that the decay rate of *C. concinna* (5–10 cm in diameter) was 0.2225, which is higher than our study on *C. concinna* ($k = 0.1570$). The relative larger diameter (≥ 10 cm) in this study may result in the difference (Mackensen et al., 2003).

4.3. C and nutrient contents

As a part of the organic matter pool on the forest floor, CWD stores significant amounts of C ($19.66 \text{ t C ha}^{-1}$) in the Dinghushan old-growth forest. Forest floor C and N stocks are largely composed of CWD (Guo et al., 2006). Da Costa (1979) reported that *P. radiata* had a short turnover time which was less than 10 years. The relatively lower turnover of CWD (<22 years) resulted in a relatively slow release of C and N. Hence, CWD in MEBF is an important long-term C sink and N source due to the decay rate. CWD potentially affects soil cycling through the dissolving of organic C which would lead to N immobilization (Mattson et al., 1987; Fierer et al., 2001; Spears et al., 2003; Hafner and Groffman, 2005). N and P stocks in CWD were similar to those reported in other studies (Idol et al., 2001; Currie and Nadelhoffer, 2002) while higher than the research studied in a natural mixed deciduous forest in Korea (Kim et al., 2006). The results suggested that the ecological value of CWD for C and nutrients cycling was relatively important.

The loss of C from three species after 3 years followed the same trend as mass loss. We found an increase in C content after 5 years of decay; however, this did not persist. A small increase in C content with decay had also been tested in some studies (Creed et al., 2004; Garrett et al., 2008). N content increased after 9 years of decay, possibly due to fungal and bacteria fixation of N as well as rainfall input (Graham and Cromack, 1982; Garrett et al., 2008). The decrease of C content and increase of N content resulted in a declining C:N ratio with the decay process; the C:N ratio could be a potential indicator of the decay rate.

The only element that showed a decrease with biomass stock in past research was K, which is known to be easily mobile. The decrease in K content may be attributed to leaching, and the rate of leaching is faster than the rate of mass loss (Preston et al., 1998; Krankina et al., 1999; Ganjegunte et al., 2004).

Mass loss of CWD was related to the initial content of N and P in previous studies (Hoorens et al., 2003; Berg et al., 2007). We tested the effect of each single nutrient on CWD decomposition and found that most nutrients had a positive relation to decay times. This might be due to different rates of CWD decay between nutrients loss. An increase of most nutrients' content with decay suggested that nutrient content change with CWD mass loss (Krankina et al., 1999).

5. Conclusions

The study at Dinghushan Nature Reserve has added to the knowledge of CWD biomass and decay rates for calculating the C stock and turnover time in natural forests in China. Forest age could affect the stocks of CWD (Grove, 2001; Carmona et al., 2002; Eaton and Lawrence, 2006; Yan et al., 2007) and consequently influence the decay process of CWD. Although our study only studied CWD in the old-growth forest and did not compare the biomass and decomposition rates in different successional forests, we did find CWD biomass increasing with time, and different CWD species had varied decay rates in similar microclimatic conditions. Our research suggested that the time for most CWD to disappear ($t_{0.95}$) exceeds 19–27 years in Dinghushan Nature Reserve. The decay rate constants for the three dominant species at Dinghushan were lower than that previously reported in IPCC (decay period of 10 years). The natural condition and the substrate quality of CWD were the main factor affecting the decay rate of CWD. The increasing inputs of CWD enquired us to be aware of the importance of the interaction between CWD, C and nutrient storage for use in forest ecosystem health management in the future. CWD is a C sink and a nutrient source indicating that CWD could partly offset soil C loss. CWD's relatively slow decomposition rate means that it could store C and other nutrients for a long time in forest ecosystems (Guo et al., 2006). Therefore, long-term decay results are needed to validate the behavior of CWD in the forest ecosystem.

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References

- Agee, J.K., Huff, M.H., 1987. Fuel succession in western hemlock/Douglas-fir forest. *Canadian Journal of Forest Research* 17, 697–704.
- Baker, T.R., Honorio Coronado, E.N., Phillips, O.L., Martin, J., van der, H.G.M.F., Garcia, M., Espino, J.S., 2007. Low stocks of coarse woody debris in a southwest Amazonian forest. *Oecologia* 152, 495–504.

- Beets, P.N., Hood, I.A., Kimberley, M.O., Oliver, G.R., Pearce, S.H., Gardner, J.F., 2008. Coarse woody debris decay rates for seven indigenous tree species in the central North Island of New Zealand. *Forest Ecology and Management* 256, 548–557.
- Berg, B., Steffen, K., McClaugherty, C., 2007. Litter decomposition rate is dependent on litter Mn concentrations. *Biogeochemistry* 82, 29–39.
- Brais, S., Sadi, F., Bergeron, Y., Grenier, Y., 2005. Coarse woody debris dynamics in a post-fire jack pine chronosequence and its relation with site productivity. *Forest Ecology and Management* 220, 216–226.
- Bond-Lamberty, B., Wang, C., Gower, S.T., 2003. Annual carbon flux from woody debris for a boreal black spruce fire chronosequence. *Journal of Geophysical Research* 108 (D23), 8220–8228.
- Carmona, M.R., Armesto, J.J., Aravena, J.C., Pérez, C.A., 2002. Coarse woody debris biomass in successional and primary temperate forests in Chiloé Island, Chile. *Forest Ecology and Management* 164, 265–275.
- Chambers, J., Schimel, J.P., Nobre, A.D., 2001. Respiration from coarse woody litter in central Amazon forests. *Biogeochemistry* 52, 115–131.
- Creed, I.F., Webster, K.L., Morrison, D.L., 2004. A comparison of techniques for measuring density and concentrations of carbon and nitrogen in coarse woody debris at different stages of decay. *Canadian Journal of Forest Research* 34, 744–753.
- Currie, W.S., Nadelhoffer, K.J., 2002. The imprint of land use history: patterns of carbon and nitrogen in downed woody debris at the Harvard forest. *Ecosystems* 5, 446–460.
- Da Costa, E.W.B., 1979. Comparative decay resistance of Australian timbers in accelerated laboratory tests. *Australian Forest Research* 9, 119–135.
- Dong, M., 1999. Survey, Observation and Analysis of Terrestrial Bio-communities. Standard Press of China, Beijing, pp. 152–154 (in Chinese).
- Eaton, J.M., Lawrence, D., 2006. Woody debris stock and flux during succession in a dry tropical forest. *Forest Ecology and Management* 232, 46–55.
- Fierer, N., Schimel, J.P., Cates, R.G., Zou, J., 2001. Influence of balsam poplar tannin fractions on carbon and nitrogen dynamics in Alaskan taiga floodplain soils. *Soil Biology and Biochemistry* 33, 1827–1839.
- Ganjegunte, G.K., Condron, L.M., Clinton, P.W., Davis, M.R., Mahieu, N., 2004. Decomposition and nutrient release from radiata pine (*Pinus radiata*) coarse woody debris. *Forest Ecology and Management* 187, 197–211.
- Garrett, L.G., Davis, M.R., Oliver, G.R., 2007. Decomposition of coarse woody debris and methods for determining decay rates. *New Zealand Journal of Forestry Science* 37, 227–240.
- Garrett, L.G., Oliver, G.R., Pearce, S.H., Davis, M.R., 2008. Decomposition of *Pinus radiata* coarse woody debris in New Zealand. *Forest Ecology and Management* 255, 3839–3845.
- Graham, R.L., Cromack Jr., K., 1982. Mass, nutrient content and decay rate of dead boles in rain forests of Olympic National Park. *Canadian Journal of Forest Research* 12, 511–521.
- Gough, C.W., Vogel, C.S., Kazanski, C., Nagel, L., Flower, C.E., Curtis, P.S., 2007. Coarse woody debris and the carbon balance of a north temperate forest. *Forest Ecology and Management* 244, 60–67.
- Grove, S.J., 2001. Extent and composition of dead wood in Australia lowland tropical rainforest with different management history. *Forest Ecology and Management* 154, 35–53.
- Guo, L.B., Bek, E., Gifford, R.M., 2006. Woody debris in a 16-year old *Pinus radiata* plantation in Australia: mass, carbon and nitrogen stocks, and turnover. *Forest Ecology and Management* 228, 145–151.
- Hafner, S.D., Groffman, P.M., 2005. Soil nitrogen cycling under litter and coarse woody debris in a mixed forest in New York State. *Soil Biology and Biochemistry* 37, 2159–2162.
- Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack Jr., K., Cummins, K.W., 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* 15, 133–301.
- Harmon, M.E., Sexton, J., 1996. Guidelines for Measurements of Woody Detritus in Forest Ecosystems. US LTER Publication No. 200S LTER network office, University of Washington, Seattle, WA, USA, pp. 1–34.
- Harmon, M.E., Sexton, J., Caldwell, B.A., 1994. Fungal sporocarp mediated losses of Ca, Fe, K, Mg, Mn, N, P, and Zn from conifer logs in the early stages of decomposition. *Canadian Journal of Forest Research* 24, 1883–1893.
- Hoorens, B., Aerts, R., Stroetenga, M., 2003. Does initial litter chemistry explain litter mixture effects on decomposition? *Oecologia* 137, 578–586.
- Idol, T.W., Figler, R.A., Pope, P.E., Ponder Jr., F., 2001. Characterization of coarse woody debris across a 100-year chronosequence of upland oak-hickory forests. *Forest Ecology and Management* 149, 153–161.
- IPCC, 2003. Good Practice Guidance for Land Use, Land-Use Change and Forestry. IPCC National Greenhouse Gas Inventories Programme, Technical Support Unit, Hayama, Japan, pp. 3, 178.
- Kim, R.H., Son, Y., Lim, J.H., Lee, I.K., Seo, K.W., Koo, J.W., Noh, N.J., Ryu, S.R., Hong, S.K., Ihm, B.S., 2006. Coarse woody debris mass and nutrients in forest ecosystems of Korea. *Ecological Research* 21, 819–827.
- Krankina, O.N., Harmon, M.E., Griazkin, A.V., 1999. Nutrient stores and dynamics of woody detritus in a boreal forest: modeling potential implications at the stand level. *Canadian Journal of Forest Research* 29, 20–32.
- Lv, M.H., Zhou, G.Y., Zhang, D.Q., 2006. Decomposition of *Cryptocarya concinna* coarse woody debris (CWD) in Dinghushan. *Journal of Guangxi Botany* 26 (5), 523–529 (in Chinese, with English abstract).
- Mackensen, J., Bauhus, J., Webber, E., 2003. Decomposition rates of coarse woody debris—a review with particular emphasis on Australian tree species. *Australian Journal of Botany* 51 (1), 27–37.
- Manies, K.L., Harden, J.W., Bond-Lamberty, B.P., O'Neill, K.P., 2005. Woody debris along an upland chronosequence in Boreal Manitoba and its impact on long-term carbon storage. *Canadian Journal of Forest Research* 35, 472–482.
- Mantgem van, P.J., Stephenson, N.L., 2007. Apparent climatically induced increase of tree mortality rates in a temperate forest. *Ecology Letters* 10, 909–916.
- Mantgem van, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fulé, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., Veblen, T.T., 2009. Widespread increase of tree mortality rates in the Western United States. *Science* 323, 521–524.
- Mattson, K.G., Swank, W.T., Waide, J.B., 1987. Decomposition of woody debris in a regenerating, clear-cut forest in the southern Appalachians. *Canadian Journal of Forest Research* 17, 712–721.
- Means, J.E., MacMillan, P.C., Cromack Jr., K., 1992. Biomass and nutrient content of Douglas-fir logs and other detrital pools in an old growth forest, Oregon. *Canadian Journal of Forest Research* 22, 1536–1546.
- Olson, J.S., 1963. Energy storage and the balance of producers and decomposers in ecological systems. *Ecology* 44, 322–331.
- Pennisi, E., 2009. Western U.S. forests suffer death by degrees. *Science* 323, 447.
- Preston, C.M., Trofymow, J.A., Niu, J., Fyfe, C.A., 1998. ¹³C PMAS-NMR spectroscopy and chemical analysis of coarse woody debris in coastal forests of Vancouver Island. *Forest Ecology and Management* 111, 51–68.
- Rubino, D.L., McCarthy, B.C., 2003. Composition and ecology of macrofungal and myxomycete communities on oak woody debris in a mixed-oak forest of Ohio. *Canadian Journal of Forest Research* 33, 2151–2163.
- Sollins, P., 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. *Canadian Journal of Forest Research* 12, 18–28.
- Spears, J.D.H., Holub, S.M., Harmon, M.E., Lajtha, K., 2003. The influence of decomposing logs on soil biology and nutrient cycling in an old-growth mixed coniferous forest in Oregon, USA. *Canadian Journal of Forest Research* 33, 2193–2201.
- Stevenson, S.K., Jull, W.J., Rogers, B.J., 2006. Abundance and attributes of wildlife trees and coarse woody debris at three silvicultural systems study areas in the Interior Cedar-Hemlock Zone, British Columbia. *Forest Ecology and Management* 233, 176–191.
- Swift, M.J., Heal, O.W., Anderson, J.M., 1979. Decomposition in Terrestrial Ecosystems. Blackwell Scientific Publications, Oxford, p. 372.
- Tang, X.L., Zhou, G.Y., 2005. Coarse woody debris biomass and its potential contribution to the carbon cycle in successional subtropical forests of Southern China. *Acta Phytocologica Sinica* 29 (4), 559–568 (in Chinese, with English abstract).
- Tang, X.L., Zhou, G.Y., Zhou, X., Wen, D.Z., Zhang, Q.M., Yin, G.C., 2003. Coarse woody debris in monsoon evergreen broad-leaved forests of Dinghushan Nature Reserve. *Acta Phytocologica Sinica* 27, 484–489 (in Chinese, with English abstract).
- Tu, M.Z., 1984. Litter production in Dinghushan Nature Reserve. *Tropical and Subtropical Forest Ecosystem Research* 2, 18–23 (in Chinese, with English abstract).
- Walter, H., 1979. *Vegetation of the Earth and Ecological Systems of the Geobiosphere*. Springer Verlag, New York, p. 274.
- Wang, B.S., Ma, M.J., 1982. The successions of the forest community in Dinghushan. *Tropical and Subtropical Forest Ecosystem Research* 1, 142–156 (in Chinese, with English abstract).
- Wei, P., Wen, D.Z., Huang, Z.L., Zhang, Q.M., Kong, G.H., 1997. The biomass and characteristic of the dead trees in monsoon evergreen broad-leaved forest in Dinghushan. *Acta Ecologica Sinica* 17 (5), 505–510 (in Chinese, with English abstract).
- Wen, D.Z., Wei, P., Kong, G.H., Zhang, Q.M., Huang, Z.L., 1997. Biomass study of the community of *Castanopsis chinensis* + *Schima superba* + *Cryptocarya concinna* in a southern China reserve. *Acta Ecologica Sinica* 17, 497–504 (in Chinese, with English abstract).
- Wen, D.Z., Zhang, D.Q., Wei, P., Kong, G.H., 1998. Vegetation biomass, coarse woody debris storage and litter dynamics of the community of *Castanopsis chinensis*, *Cryptocarya concinna*. *Tropical and Subtropical Forest Ecosystem Research* 9, 203–208 (in Chinese, with English abstract).
- Woldendorp, G., Keenan, R.J., Barry, S., Spencer, R.D., 2004. Analysis of sampling methods for coarse woody debris. *Forest Ecology and Management* 198, 133–148.
- Woodall, C.W., Liknes, G.C., 2008. Relationships between forest fine and coarse woody debris carbon stocks across latitudinal gradients in the United States as an indicator of climate change effects. *Ecological Indicators* 8, 686–690.
- Yan, E.R., Wang, X.H., Huang, J.J., Zeng, F.R., Gong, L., 2007. Long-lasting legacy of forest succession and forest management: characteristics of coarse woody debris in an evergreen broad-leaved forest of Eastern China. *Forest Ecology and Management* 252, 98–107.
- Yan, J.H., Wang, Y.P., Zhou, G.Y., Zhang, D.Q., 2006. Estimates of soil respiration and net primary production of three forests at different succession stages in south China. *Global Change Biology* 12, 810–821.
- Zhang, D.Q., Yu, Q.F., Kong, G.H., Zhang, Y.C., 1997. Chemical properties of forest floor litter in Dinghushan monsoon evergreen broadleaved forest. *Acta Ecologica Sinica* 18 (1), 96–100.
- Zhou, C.Y., Zhou, G.Y., Yan, J.H., Wang, X., 2005. Long term comparative study of the hydrological characteristics of forests in different successional stages in the Dinghushan Biosphere Reserve, Guangdong Province, China. *Acta Ecologica Sinica* 29 (2), 208–217 (in Chinese, with English abstract).
- Zhou, G.Y., Guan, L.L., Wei, X.H., Tang, X.L., Liu, S.G., Liu, J.X., 2008. Factors influencing leaf litter decomposition: an intersite decomposition experiment across China. *Plant and Soil* 9, 179–185.
- Zhou, G.Y., Liu, S.G., Li, Z.A., Zhang, D.Q., Tang, X.L., Zhou, C.Y., Yan, J.H., Mo, J.M., 2006. Old-growth forests can accumulate carbon in soils. *Science* 314, 1417.