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Long-lasting legacy of forest succession and forest management: Characteristics of coarse woody debris in an evergreen broad-leaved forest of Eastern China

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Abstract

Coarse woody debris (CWD) is an important structural and functional component in evergreen broad-leaved forests in Eastern China. In this study, we determine the temporal patterns of CWD in Tiantong National Forest Park by examining the CWD volume and mass in different decay classes and size classes along a chronosequence of secondary forest succession. The volume and mass of CWD followed the general ''U-shaped'' temporal trend: highest in the late-successional forest (97.73 m^3/ha, 42.41 Mg/ha), lowest in the middle successional forest (6.13 m^3/ha, 2.84 Mg/ha) and intermediate in the early successional forest (46.12 m^3/ha, 19.36 Mg/ha). The late-successional forest had larger amount of logs and stumps than the other two forests. In contrast, snags biomass and volume did not differ among these three forests. CWD in decay classes III and V was greater in late-successional forest than that in the other two forests, while CWD in decay classes II and IV did not differ among the three successional forests. CWD in class I was significantly higher in the early-successional forest than that in the middle successional forest. In the early and middle successional forests, CWD in early decay class was dominated by *Pinus massoniana* and followed by *Schima superba*. In the late-successional forest, CWD in early decay class was dominated by *Castanopsis fargesii* while CWD in late decay class was dominated by *P. massoniana* and *S. superba*. While forest succession had a large influence on the amount of CWD in different decay class, it had no effect on CWD distribution among different size classes. Our results suggested that both anthropogenic and natural disturbances have left a long-lasting legacy on the distribution of CWD among three forests.

Keywords: Coarse woody debris; Eastern China; Evergreen broad-leaved forest; Forest management; Forest succession

1. Introduction

Coarse woody debris (CWD) is dead woody material in various stages of decomposition, including sound and rotting logs, snags, stumps and large branches (Harmon and Sexton, 1996). It is an important functional and structural component of forested ecosystems and plays a substantial role in nutrient cycling, long-term carbon storage, tree regeneration and the maintenance of environmental heterogeneity and biological diversity (Harmon et al., 1986; Harmon and Sexton, 1996; Stevens, 1997; Sturtevant et al., 1997; Currie and Nadelhoffer, 2002). During the past decades, numerous studies have attempted to relate CWD characteristics with forest succession (Idol et al., 2001; Carmona et al., 2002; Woodall and Nagel, 2006), community composition (Sturtevant et al., 1997; Pedlar et al., 2002; Santiago, 2000; Motta et al., 2006), nutrient cycling (Raija and Prescott, 1999; Chambers et al., 2001; Fisk et al., 2002; Currie and Nadelhoffer, 2002) and forest management (Lee et al., 1997; Siitonen et al., 2000; Grove, 2001; Tinker and Knight, 2001; Shawn et al., 2002; Webster and Jenkins, 2005; Montes and Cañellas, 2006).

A general understanding of the CWD quantity and quality is crucial for the assessment of multiple functions of CWD in forest ecosystems. Some CWD characteristics, such as amount and type (i.e. logs, snag, and stumps), size classes, decay state and nutrients stocks, are often used to reflect stand structure, ecosystem function and forest management history (Lee et al., 1997; Siitonen et al., 2000; Pedlar et al., 2002; Ekbom et al., 2006). Currie and Nadelhoffer (2002) compared CWD in natural deciduous forests with that in coniferous plantations and

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showed that almost all classes of CWD existed in the deciduous forests. In contrast, the majority of biomass in the coniferous plantations was accumulated in the lowest size classes. In temperate forests of southern South America, recently disturbed and old-growth forests had the largest CWD biomass (Carmona et al., 2002). Early- and mid-successional stands had the lowest value. In addition, carbon stored in logs and snags was nearly 10 times higher in old-growth and primary forests than in young-successional forests (Carmona et al., 2002).

Despite the ecological relevance of CWD characteristics in forest ecosystem, there is no such quantitative information in evergreen broad-leaved forests in Eastern China. Evergreen broad-leaved forests (EBLFs), the zonal vegetation type in subtropical areas, have been changing to include more areas dominated by secondary forests, shrubs and plantations. One major forest management practice in this area is to harvest CWD from forest for firewood or to improve landscape view, which has altered the total amount and distribution pattern of CWD in this ecosystem. Knowledge of CWD attributes and dynamics will help forest managers understand the impact of current management practices on the CWD cycle and facilitate the incorporation of this important resource into future plans for more productive, diverse, and healthy forest ecosystems (Sturtevant et al., 1997).

This study aimed to understand CWD characteristics and the associated relationships with forest management and forest succession in an EBLF in Eastern China. Our specific objectives were to: (1) compare CWD characteristics (volume, mass, size and decay state) in a successional chronosequence of EBLF; (2) examine whether CWD mass (or volume) along a chronosequence in EBLF displayed the general ‘‘U-shaped’’ temporal trend observed in other forest systems; (3) determine factors affecting the distribution pattern of CWD in EBLF.

2. Materials and methods

2.1. Study site

This study was carried out in Tiantong National Forest Park (29°52′N, 121°39′E, 200 m a.s.l.), Zhejiang Province, China. The climate of this region is subtropical monsoon with mean annual temperature and precipitation of 16.2 °C and 1374.7 mm. The substrate parent materials are mesozoic sediments and acidic intrusive rocks, including quartzite and granite. The soil texture is mainly medium-heavy loam, and soil pH ranges from 4.4 to 5.1 (Song and Wang, 1995). The mature forests around a Buddhist temple in the centre of the park are considered as climax monsoon EBLF because this area has been protected from clear-cutting (Song and Wang, 1995). The canopy of this forest is dominated by *Castanopsis fargesii* Franch. Outside of this area are early- and mid-successional forests that are dominated by *Pinus massoniana* Lamb and *Schima superba* Gardn. et Champ, respectively (Song and Wang, 1995).

Table 1
Description of study sites, indicating position in the successional chronosequence, major disturbance regimes, and other characteristics in Tiantong National Forest Park, Eastern China

Site code	Plot size	Forest type	Dominant tree species	Tree species richness	Canopy height (m)	Stand age (year)[a]	Position in chronosequence	Forest management history	Natural disturbance regimes
ES1	25 m × 30 m	Coniferous forest	*Pinus massoniana*	6	13	40	Early-succession	Firewood and snags extraction[b]	Attacked by pinewood nematode[c]
ES2	40 m × 40 m	Coniferous forest	*P. massoniana*	8	12	50	Early-succession	Firewood and snags extraction[b]	Attacked by pinewood nematode[c]
ES3	20 m × 45 m	Coniferous forest	*P. massoniana*	6	12	58	Early-succession	Firewood and snags extraction[b]	Attacked by pinewood nematode[c]
MS1	25 m × 25 m	SEBLF[d]	*Schima superba*	7	18	95	Intermediate	Selective logging, firewood harvest[e]	Landslide and typhoon[f]
MS2	30 m × 40 m	SEBLF	*S. superba*	8	19	101	Intermediate	Selective logging, firewood harvest[e]	Landslide and typhoon[f]
MS3	30 m × 40 m	SEBLF	*S. superba*	7	19	97	Intermediate	Selective logging, firewood harvest[e]	Landslide and typhoon[f]
LS1	25 m × 25 m	CEBLF[g]	*Castanopsis fargesii*	17	25	150	Late-succession	Protected[h]	Typhoon and gap-phase dynamics[i]
LS2	20 m × 40 m	CEBLF	*C. fargesii*	16	24	155	Late-succession	Protected[h]	Typhoon and gap-phase dynamics[i]
LS3	20 m × 40 m	CEBLF	*C. fargesii*	15	24	155	Late-succession	Protected[h]	Typhoon and gap-phase dynamics[i]

[a] Years since abandonment, cited from Song and Wang (1995).
[b] Including firewood extraction prior to abandonment and selective logging snags since abandonment.
[c] Attacked by pinewood nematode during the past decades.
[d] Secondary evergreen broad-leaved forest.
[e] Including firewood extraction that remove all dead woody materials and selective logging snags.
[f] Occasional landslide, typhoon and heavy rain are the typical disturbances at local site.
[g] Climax evergreen broad-leaved forest.
[h] Protected from human disturbances, and remove snags to improve landscape view.
[i] Typhoon is the major disturbance at regional scale with returning interval of 7–8 years.

Table 2
Qualitative classification system of different types of CWD in five decay classes

Types of CWD	Character	Decay class				
		I	II	III	IV	V
Snags	Leaves	Present	Absent	Absent	Absent	As logs
	Bark	Tight	Loose	Partly present	Absent	
	Crown, branches and twigs	All present	Only branches present	Only large branch stub present	Absent	
	Bole	Recently dead	Standing, firm	Standing, decayed	Heavily decayed, soft and block structure	
	Indirect measure	Cambium still fresh, died less than 1 year	Cambium decayed, knife blade penetrates a few millimeters	Knife blade penetrates less than 2 cm	Knife blade penetrates 2–5 cm	Knife blade penetrates all the way
Logs	Structure integrity	Sound	Sapwood slightly rotting, heartwood sound	Sapwood missing, heartwood mostly sound	Heartwood decayed	Soft
	Leaves	Present	Absent	Absent	Absent	Absent
	Branches	All twig present	Larger twig present	Larger branches present	Branch stubs present	Absent
	Bark	Present	Present	Often present	Often absent	Absent
	Bole shape	Round	Round	Round	Round to oval	Oval to flat
	Wood consistency	Solid	Solid	Semi-solid	Partly soft	Fragmented, powdery
	Color of wood	Original color	Original color	Original color to faded	Original color to faded	Heavily faded
	Portion of log on ground	Elevated on support point	Elevated on support point	Near or on ground	All of log on ground	All of log on ground
	Indirect measure	Cambium still fresh, died less than 1 year	Cambium decayed, knife blade penetrates a few millimeters	Knife blade penetrates less than 2 cm	Knife blade penetrates 2–5 cm	Knife blade penetrates all the way
Stumps	Indirect measure	Cambium still fresh, died less than 1 year	Cambium decayed, knife blade penetrates a few millimeters	Knife blade penetrates less than 2 cm	Knife blade penetrates 2–5 cm	Knife blade penetrates all the way

Note: Adapted from Sollins (1982), Maser et al. (1979), Carmona et al. (2002) and Rouvinen et al. (2002).

2.2. Experimental design, field sampling and laboratory methods

C. fargesii dominated forest (mature climax EBLF), *S. superba* dominated forest, and *P. massoniana* dominated forests were chosen to represent late, middle and early successional stages, respectively (Song and Wang, 1995). We randomly chose three study plots in each of the three forest types (plot details in Table 1). Each plot was located at least 50 m from forest edge and was separated from other plots by at least 20 m buffer strip surrounding it. Within each plot, CWD was measured using a fixed area plot sampling method (Harmon and Sexton, 1996). In the summer of 2003, three types of CWD were examined according to the protocol of (Harmon and Sexton, 1996): (1) logs (downed or leaning deadwood with their minimum diameter ≥10 cm at the widest point and length ≥1 m), (2) stumps (vertical deadwood ≤1 m in height and ≥10 cm at the widest point in diameter), and (3) snags. The dead trees with a gradient (departure from vertical direction) ≤45° and the diameter at the widest point ≥10 cm were classified as snags while those with a gradient >45° were classified as logs.

We recorded the following variables for each log, snag and stump inventoried in the field: species, length, types, diameter at both ends and at the midpoint (for stump, only the diameter at midpoint was recorded), decay class (details in Table 2), and whether the piece was hollow or solid. When applicable, lengths and diameters were taken at the point where the log extended outside the plot boundaries. Diameters of logs, snags and stumps were measured using 100 cm calipers; however, for some tall snags, diameter of the top end was visually estimated and calibrated with a snag top that was within manual reach (Harmon and Sexton, 1996). The length of logs was measured and the height of snags was measured with a meter stick. For snags taller than 4 m, a clinometer was used to estimate the height. Decay class of coarse woody debris (Table 2) was determined by the system proposed by Sollins (1982), Maser et al. (1979), Carmona et al. (2002) and Rouvinen et al. (2002).

To determine wood density, we cut small pieces of wood from CWD based on decay class and species. In total, we obtained approximately 30–35 fragments for each plot. Each fragment was dried at 70 °C to constant weight (approximately 1 week) and weighed. The volume of fragments was then determined using water displacement method. Finally wood density (g dry mass cm^{-3}) was estimated as the ratio of dry mass to volume.

2.3. Calculation of volume and biomass

The volume of each piece of logs and snags was calculated using Newton's formula (Harmon and Sexton, 1996). This formula uses the length and cross-sectional area at three points (i.e. top, end and middle) along the deadwood stem to generate a volume estimate. The volume was calculated as:

$$V = \frac{L(A_b + 4A_m + A_t)}{6}$$

where V is the volume (m^3), L the length, and A_b, A_m and A_t are the areas of the base, middle and top, respectively.

For stumps, Huber's formula (Harmon and Sexton, 1996) was used to estimate volume:

$$V = A_m L$$

where V is the volume (m^3), A_m the area at the midpoint, and L is the length.

After the volume was determined, CWD mass was obtained by multiplying the volume of each piece by the appropriate wood density determined previously for each.

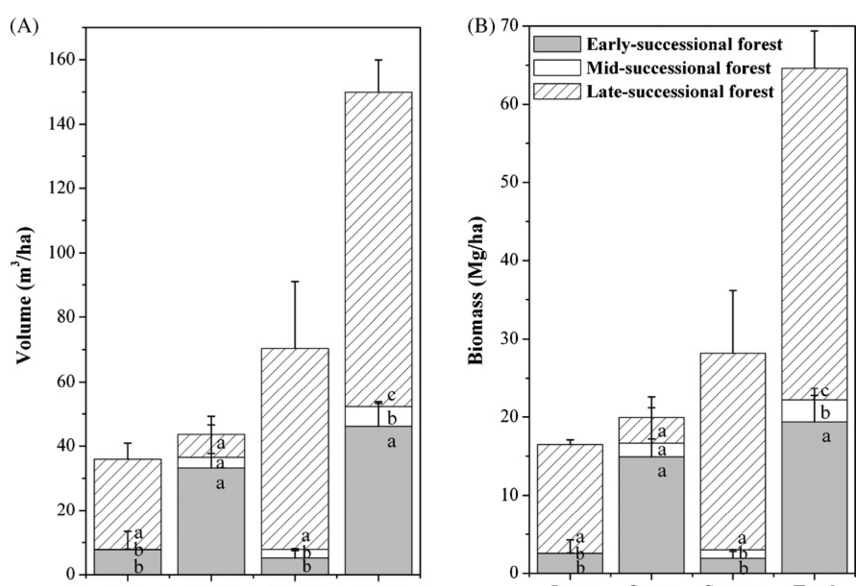

Fig. 1. Volume and biomass in different types and total amount of CWD along a successional chronosequence in an evergreen broad-leaved forest in Tiantong National Forest Park, Eastern China. Means and MS are presented. Different letters on one bar are significant at Tukey's adjusted $p < 0.05$.

2.4. Statistics

To determine whether volume (or mass) of CWD of different types, decay classes, and size classes differed among these three successional forests, successional stage was considered as a fixed factor and volume (or mass) of CWD was analyzed as a response variable using one-way analysis of variance (ANOVA). If there was a significant effect of successional stage, least-squares mean separation with Tukey's correction was used to test for differences among successional stages. Normality and homogeneity of variance of the residuals were tested and data were log-transformed if homogeneity of the variance was not met. All statistical tests were considered significant at the $p < 0.05$ level.

3. Results

3.1. Amount of CWD

There was significant effect of successional stage on total CWD volume ($F = 40.12$, $p < 0.001$) and biomass ($F = 28.43$, $p = 0.001$, Fig. 1). Late-successional forest (LS, hereafter) had the highest CWD volume and biomass (97.73 m^3/ha, 42.41 Mg/ha) while the mid-successional forest (MS, hereafter) had the lowest (6.13 m^3/ha, 2.84 Mg/ha) and early-successional forest (ES, hereafter) had the intermediate value (46.12 m^3/ha, 19.36 Mg/ha).

3.2. Type of CWD

CWD composition varied considerately among different successional forests (Fig. 1). Stumps were the major component of CWD in the LS forest, while snags were the dominant form of CWD in the MS and ES forests. Volume and mass of logs and stumps exhibited significant differences among different successional forests while snags did not differ (Table 3). The amount of stumps was significantly greater in the LS forest than that in the MS (volume: $p = 0.028$; biomass: $p = 0.024$) and ES forest (volume: $p = 0.033$; biomass: $p = 0.027$), while MS and ES forests did not differ (volume: $p = 0.988$; biomass: $p = 0.991$). Similarly, the LS forest had significantly larger amount of log volume and mass than did ES and MS forests (Fig. 1). In contrast, snags biomass and volume did not differ among these three forests (Fig. 1).

P. massoniana dominated the logs and snags biomass pool in the ES forest and the logs and stumps biomass pool in the MS forest (Table 4). In contrast, a low percentage of *P. massoniana* was observed for logs and snags in the LS forest.

Table 3
Results of one-way ANOVA's for volume and biomass of different types, decay classes and size classes of CWD in three forest successional stages, Tiantong National Forest Park, Eastern China

Characteristics of CWD		d.f.	Volume		Biomass	
			F	*p*	*F*	*p*
Types	Logs	2	10.92	0.010	48.74	<0.001
	Snags	2	3.71	0.089	3.34	0.106
	Stumps	2	8.06	0.020	8.82	0.016
Decay classes	I	2	6.14	0.035	5.63	0.042
	II	2	0.61	0.575	0.59	0.579
	III	2	9.83	0.013	30.91	0.001
	IV	2	5.03	0.052	4.39	0.067
	V	2	6.11	0.036	4.98	0.053
Size classes	10–20 cm	2	2.43	0.168	1.36	0.326
	20–30 cm	2	2.56	0.157	0.84	0.478
	>30 cm	2	5.13	0.050	3.97	0.08
Total	2	40.12	<0.001	28.43	0.001	

The *F*-values and *p*-values are presented for effects of successional stage.

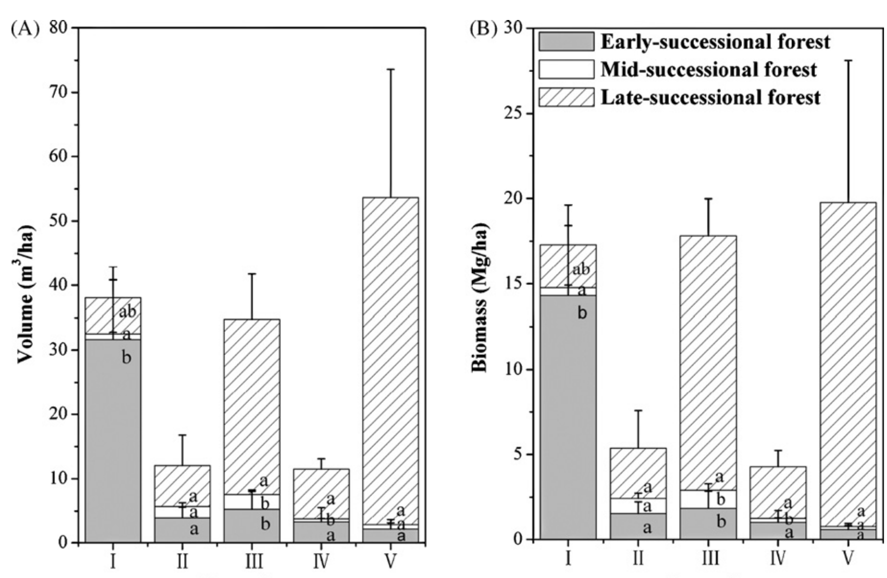

Fig. 2. Volume and biomass of CWD in each decay class along a successional chronosequence in an evergreen broad-leaved forest in Tiantong National Forest Park, Eastern China. Means and MS are presented. Different letters on one bar are significant at Tukey's adjusted $p < 0.05$.

Table 4
Percentage (%) of CWD in biomass (mean value ± S.E.) among species by decay class, type and size classes at different succession stages in the evergreen broad-leaved forests, Tiantong National Forest Park, Eastern China

Successional stage and species		Decay class					Type			Size class (cm)			Total
		1	2	3	4	5	Logs	Snags	Stumps	10–20	20–30	>30	
Early	*S. superba*	2.67 ± 1.67	1.0 ± 0	4.0 ± 4.0	0.67 ± 0.33	0.33 ± 0.33	2.33 ± 1.86	4.33 ± 3.84	1.0 ± 0	3.02.0 ± 0	0	4.0 ± 2.0	7.67 ± 3.48
	P. massoniana	62.0 ± 17.2	8.33 ± 6.36	5.33 ± 3.84	6.0 ± 4.51	4.0 ± 3.0	16.0 ± 12.5	61.9 ± 18.5	9.67 ± 5.93	28.67 ± 16.7	18.67 ± 10.4	40.0 ± 20.2	86.67 ± 3.18
	Castanopsis sclerophylla	1.0 ± 1.0	0	0	0	0	0	1.0 ± 1.0	0	1.0 ± 1.0	0	0	1.0 ± 1.0
	Lithocarpus glaber	0	2.0 ± 2.0	0	0	0	0	2.0 ± 2.0	0	0	2.0 ± 2.0	0	2.0 ± 2.0
	Elaeocarpus decipiens	0.33 ± 0.23	0	0	0	0	0	0	0.33 ± 0.33	0	0.33 ± 0.33	0	0.33 ± 0.33
	Myrica rubra	0	0	0	1.67 ± 1.67	0	0	0	5.0 ± 1.67	0	1.0 ± 1.0	0.67 ± 0.67	1.67 ± 1.67
	Cunninghamia lanceolata	0.33 ± 0.23	0	0.33 ± 0.33	0	0	0.33 ± 0.33	0	0.33 ± 0.33	0.33 ± 0.33	0.33 ± 0.33	0	0.67 ± 0.33
Middle	*S. superba*	6.0 ± 2.52	4.0 ± 1.73	2.0 ± 0.58	4.673.67 ±	2.67 ± 0.33	0.67 ± 0.33	1.67 ± 1.2	16.33 ± 8.09	12.67 ± 5.93	5.0 ± 3.61	0.67 ± 0.67	18.67 ± 8.97
	P. massoniana	13.33 ± 7.54	3.0 ± 1.53	8.0 ± 2.31	7.0 ± 1.15	2.33 ± 1.33	0.33 ± 0.33	10.33 ± 8.88	23.0 ± 2.31	4.0 ± 1.53	6.0 ± 2.0	24.0 ± 10.02	33.67 ± 10.68
	Castanopsis sclerophylla	0	5.0 ± 3.06	0.67 ± 0.33	0	0	0	5.0 ± 3.29	0	5.0 ± 3.06	0	0	5.0 ± 3.06
	Lithocarpus glaber	0	0	0.67 ± 0.33	0	0	0	0	1.33 ± 0.88	1.0 ± 1.0	0.33 ± 0.33	0	1.33 ± 0.88
	Myrica rubra	0	0	0.33 ± 0.33	0	0	0	0	0.33 ± 0.33	0.33 ± 0.33	0	0	0.33 ± 0.33
	Cunninghamia lanceolata	1.33 ± 0.88	17.0 ± 8.54	22.0 ± 11.06	0	0		21.0 ± 11.13	20.0 ± 10.01	18.0 ± 7.55	0.67 ± 0.67	22.33 ± 11.3	41.0 ± 19.04
Late	*C. fargesii*	6.0 ± 2.52	8.33 ± 6.84	33.3 ± 11.4	1.0 ± 0.58	3.0 ± 2.0	29.0 ± 7.0	10.0 ± 3.8	14.0 ± 7.0	12.0 ± 9.0	15.0 ± 8.01	26.0 ± 1.5	52.0 ± 22.0
	S. superba	0	0	0.7 ± 0.7	3.67 ± 1.67	19.33 ± 13.5	1.0 ± 0	0	5.0 ± 2.0	0.67 ± 0.33	0.33 ± 0.33	4.7 ± 2.3	6.0 ± 2.0
	P. massoniana	0.33 ± 0.33	0.33 ± 0.33	0.7 ± 0.7	3.0 ± 2.08	18.33 ± 11.8	2.0 ± 1.0	0	38.0 ± 19.0	0.67 ± 0.33	0.67 ± 0.33	39.0 ± 20.19	40.0 ± 20.0
	Castanopsis sclerophylla	0	0	0	1.33 ± 0.67	0.67 ± 0.67	2.0 ± 0	0	0	0.33 ± 0.33	0.33 ± 0.33	0.33 ± 0.33	2.0 ± 0

3.3. Decay state of CWD

The distribution of CWD in different decay classes changed across forests in the successional chronosequence (Fig. 2). Decay classes III, IV and V were more abundant in the LS forest relative to that in ES and MS forests. Decay classes I and II were the most abundant decay classes in the ES forest.

CWD in decay classes III and V was greater in the LS forest than that in the other two forests (Fig. 2). In contrast, CWD in decay classes II and IV did not differ among the three successional forests. CWD in class I was significantly higher in the ES than that in the MS forest (Table 3).

In the ES and MS forests, CWD in early decay classes (e.g. I) was dominated by *P. massoniana*, followed by *S. superba*. In the LS forest, however, CWD in early decay classes was dominated by *C. fargesii* and CWD in advanced decay class (e.g. V) was dominated by *P. massoniana* and *S. superba* (Table 4).

3.4. Size classes of CWD

Different forest types had similar proportions of CWD between size classes (Fig. 3), with the exception of the volume of larger size class (>30 cm) CWD, which was greater in the LS forest than that in the MS forest ($p = 0.046$). Overall, the successional forest type had no significant effects on volume and mass of CWD size classes (Table 3).

4. Discussion

4.1. Amount of CWD along forest succession

To our knowledge, this study is the first report of CWD distribution along a successional chronosequence in evergreen broad-leaved forests in Eastern China. This study showed that total CWD mass was lowest in a MS forest, and highest in a LS forest.

The early-successional forest is an approximately 40-year-old forest that developed following a clear-cutting (Song and Wang, 1995). Snags composed the majority of the CWD input. The majority of the snag production was due to the mortality of pine, which has been severely attacked by many pest infestations (e.g. pinewood nematodes such as *Asemum amurense*, *Shirahoshizo patruelis*, *Monochamus alternatus*, *Chalcophora japonica* and *Spondylis buprestoides*, unpublished data) in the past decade.

As succession progressed, amounts of CWD leveled off in the MS forest. It may be explained by three reasons. First, since *P. massoniana* is not abundant, there are much fewer pine snags in the MS forest. Second, *S. superba*, the dominant species in MS forest, has higher substrate quality (e.g. lower C/N compared to *P. massoniana*, unpublished data), which contributes to a faster decay rate for CWD. Third, local people harvested more logs from MS forest because it is easier to access than the ES and LS forests.

As expected, CWD biomass appeared to be the highest in LS forest due to high tree mortality. Overall, CWD amounts followed the general ‘‘U-shaped’’ temporal trend observed in

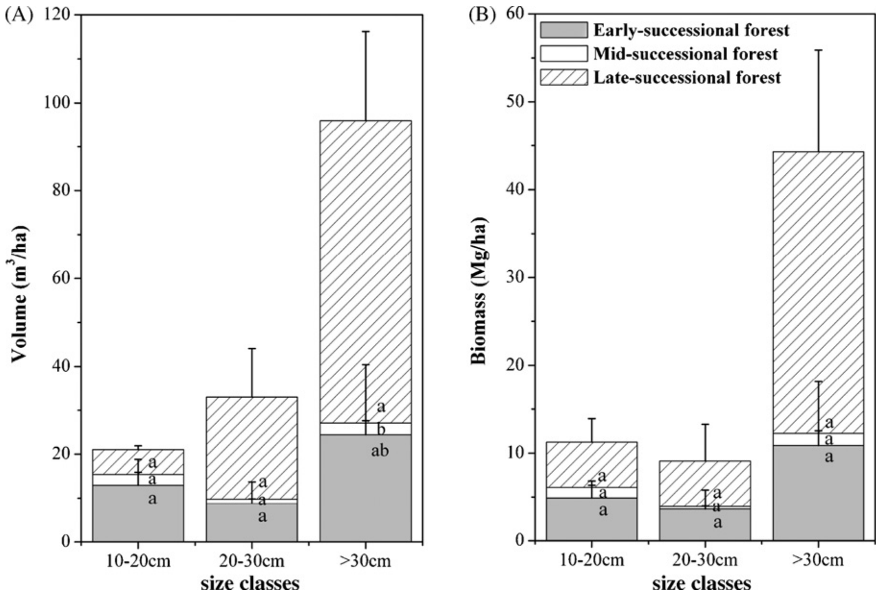

Fig. 3. Volume and biomass of CWD in each size class along a successional chronosequence in an evergreen broad-leaved forest in Tiantong National Forest Park, Eastern China. Means and MS are presented. Different letters on one bar are significant at Tukey's adjusted $p < 0.05$.

other forest systems (Sturtevant et al., 1997; Duvall and Grigal, 1999; Carmona et al., 2002; Ranius et al., 2003; Ekbom et al., 2006).

In forests of the Pacific northwest of North America, Harmon et al. (1986) and Spies et al. (1988) reported that recently disturbed stands had the highest woody residues biomass. They reported that CWD biomass declined over time due to decomposition, and finally increased in old-growth forests. In contrast, our study showed that the late-successional forest, instead of the early-successional forest, had the highest CWD. One reason is that the pre-existing (or freshly created) CWD amounts in the ES forest were small in our study area due to removal of logs after clear-cutting.

4.2. CWD as an indicator reflecting forest management history

In forest ecosystems, different CWD types (i.e. logs, snags and stumps) can be an indicator of origin and legacy of CWD. In addition, it can be used to reflect forest management and stand development history. For instance, a higher proportion of CWD due to stumps in a given site may suggest extensive anthropogenic disturbances, such as clear-cutting or selective logging, in the past.

Snags contributed the largest proportion of CWD biomass (~77%) in the ES forest, which is dominated by *P. massoniana*. This species was heavily attacked by pinewood nematode in the past decade and many pine trees died soon after the attack. Although current practice is to remove dead trees from the forests, there are still many snags due to the high pine mortality and limited labor in this region.

The amount of CWD mass due to logs was highest in the LS forest. In contrast, the MS and ES forests contained fewer amount of logs. The LS forest is near a Buddhist temple and therefore has been protected from cutting and removing firewood (Song and Wang, 1995). Consequently, there was a large accumulation of logs in LS forest.

In contrast to the ES forest, the highest percentage of CWD in the LS forest is due to stumps. The large amount of biomass due to stumps is mainly due to high tree mortality caused by natural events such as wind and natural senescence. The low percentage of CWD biomass due to logs can be attributed to decomposition, as decay class V accounted for 59.44% of CWD biomass in the LS forest. Since the LS forest is close to a Buddhist temple and considered as forest scenery, local forest practitioners often remove the dead trees from LS forest. As a result, snags are few in this mature forest.

In our study area, *P. massoniana* is a pioneer species that occupies the early stages of succession (Song and Wang, 1995). When secondary succession proceeds, this species is gradually replaced by *S. superba*, and *C. fargesii* (Ding and Song, 1998). Therefore, despite the disappearance of *P. massoniana* in mature forests due to species replacement, the stumps of *P. massoniana* have left a long-lasting legacy on the stand developmental history. For example, in the LS forest, we found that stumps of *P. massoniana* had significantly higher proportion biomass than other species (77.1% in total mass of stumps and 38.0% in total of CWD; Table 4). This is again confirmed by the high proportion of stumps of *P. massoniana* in MS forest, in which it accounted for 65% of total stump biomass and 23% of total CWD (Table 4).

After examining the distribution pattern of CWD in the forests of southern South America, Carmona et al. (2002) reported that a high proportion of woody residues was in advanced decomposition classes in the early stages of succession, while the majority was in the intermediate decomposition classes in older stands. In contrast, our study showed that CWD in decay classes III and V was more abundant in the LS forest, while CWD in class I was much greater in the ES forest (Fig. 2). The contradiction can partly be attributed to the differences in vegetation composition

Table 5
CWD amount and quality in subtropical China forests

Location	Forest type	Successional stage	Snags (Mg/ha)	Logs (Mg/ha)	Stumps (Mg/ha)	Large branches (Mg/ha)	Total (Mg/ha)	Reference
Ailao mountain (24°32′N, 101°01′E)[a]	Evergreen broad-leaved forest	Late-succession	8.83	84.45	–	5.18	98.45	Liu et al. (1995)
Wuyi mountain (27°33′N, 117°27′E)[a]	Evergreen broad-leaved forest	Early-succession	4.25	0.31	–	2.79	7.35	Li et al. (1996)
Dinghu mountain (23°09′N, 112°33′E)[a]	Evergreen broad-leaved forest	Late-succession	8.09	12.55	–	4.64	25.28	Tang et al. (2003)
Dinghu mountain (23°09′N, 112°33′E)[a]	Mixed coniferous and evergreen forest	Mid-succession	1.74	15.34	–	–	17.08	Tang and Zhou (2005)
Dinghu mountain (23°09′N, 112°33′E)[a]	Coniferous forest (*Pine massoniana*)	Early-succession	0.11	0.09	–	–	0.2	Tang and Zhou (2005)
Tiantong mountain (29°52′N, 121°39′E)	Evergreen broad-leaved forest	Late-succession	3.31	13.9	25.21	–	42.41	This study
Tiantong mountain (29°52′N, 121°39′E)	Evergreen broad-leaved forest	Mid-succession	1.73	0.03	1.08	–	2.84	This study
Tiantong mountain (29°52′N, 121°39′E)	Coniferous forest (*Pine massoniana*)	Early-succession	14.91	2.54	1.91	–	19.36	This study

Note: CWD definition and sampling methods are different in each study.
[a] Adopted the criteria of >2.5 cm in diameter.

and disturbance type. In our study area, CWD in the ES forest was mainly composed of snags of *P. massoniana*, which is caused by recent high pine mortality. Therefore most CWD was in the early stage of decay class.

Overall, our results suggested that both anthropogenic and natural disturbances had left a significant and long-lasting legacy on the distribution and abundance of coarse woody debris along a successional chronosequence in an evergreen broad-leaved forest of Eastern China.

4.3. Amount of CWD in subtropical and tropical forests

CWD mass varies considerably among forest stands in subtropical area of China (Table 5) and the subtropical and

Table 6
CWD amount and quality in world subtropical and tropical evergreen forests

Location	Forest type	Management	Development phase	Snags (Mg/ha)	Logs (Mg/ha)	Stumps (Mg/ha)	Total (Mg/ha)	Reference
Chile	Evergreen broad-leaved forest	Managed	Early–mid-succession	59	30	–	89	Carmona et al. (2002)
Chile	Evergreen broad-leaved forest	Unmanaged	Old-growth	126	47	–	173	Carmona et al. (2002)
Ecuador	Evergreen montane forest	Managed	Early–mid-succession	–	–	–	9.1	Wilcke et al. (2005)
Costa Rica	Tropical rain forest	Unmanaged	Old-growth	–	–	–	46.3	Clark et al. (2002)
Venezuela	Tropical moist forest	Unmanaged	Early–mid-succession	14.8	33.3	–	57.5	Delaney et al. (1998)
Venezuela	Tropical lower montane moist forest	Unmanaged	Early–mid-succession	21.3	42.3	–	63.6	Delaney et al. (1998)
Venezuela	Tropical montane wet forest	Unmanaged	Early–mid-succession	26.3	34.5	–	60.8	Delaney et al. (1998)
Eastern Brazilian Amazon	Evergreen dense moist forest	Unmanaged	Old-growth	–	–	–	52.98	Keller et al. (2004)
Eastern Brazilian Amazon	Evergreen dense moist forest	Reduced impact logging	Early–mid-succession	–	–	–	73.75	Keller et al. (2004)
Eastern Brazilian Amazon	Evergreen dense moist forest	Conventional logging	Early-succession	–	–	–	107.75	Keller et al. (2004)
Australian	Lowland tropical rainforest	Managed	Mid-succession	3.6	5.0	–	8.6	Grove (2001)
Australian	Lowland tropical rainforest	Managed	Early-succession	9.4	7.2	–	16.6	Grove (2001)
Australian	Lowland tropical rainforest	Unmanaged	Late-succession	3.6	9.4		13.0	Grove (2001)
China	Evergreen broad-leaved forest	Unmanaged	Late-succession	3.31	13.9	25.21	42.41	This study
China	Evergreen broad-leaved forest	Unmanaged	Late-succession	8.83	84.45	5.18[a]	98.45	Liu et al. (1995)[b]
China	Evergreen broad-leaved forest	Unmanaged	Early-succession	4.25	0.31	2.79[a]	7.35	Li et al. (1996)[b]
China	Evergreen broad-leaved forest	Unmanaged	Late-succession	8.09	12.55	4.64[a]	25.28	Tang et al. (2003)[b]

[a] Large branches.
[b] Using the criteria of >2.5 cm in diameter.

tropical evergreen forests. The large variations in CWD mass may be due to the differences between forest types and disturbance regimes, as well as to different classification methods. For example, some studies used ≥10 cm at the widest point to define CWD while others used ≥2.5 cm and some studies incorporated stumps as CWD while others did not.

Compared with the CWD amounts in world-wide subtropical and tropical evergreen forests (9.1–173 Mg/ha, Table 6), CWD biomass in our study (42.41 Mg/ha) is greater than those in lowland tropical rainforest in Australian (Grove, 2001), and evergreen montane forests in Ecuador (Wilcke et al., 2005) but lower than other tropical and subtropical forests (Delaney et al., 1998; Grove, 2001; Carmona et al., 2002; Clark et al., 2002; Keller et al., 2004). For instance, Carmona et al. (2002) found that CWD was approximately 173 Mg/ha in an old-growth evergreen broad-leaved forest in Chile and Keller et al. (2004) reported 107.75 Mg/ha CWD for an evergreen dense moist forest in Eastern Brazilian Amazon. Apparently, the large variation of CWD may be is due in part to climatic and phytogeographical shifts.

4.4. Conservation and management implications of CWD in China

Traditional management methods in China include harvesting CWD from the forests. Our results suggest that removal of standing and fallen materials from early- and mid-successional forests leads to a sharp drop in total CWD biomass. Reductions in biomass and volume of CWD in young- and intermediate-successional forests may have negative consequences for populations of endemic, understory bird species, which commonly nest in cavities located in or under logs on the forest floor (personal observation in the LS forest). CWD creates within-stand heterogeneity and provides a favorable environment for many plant species; therefore, removing CWD may have long-term impacts on seedling recruitment and establishment. Consequently, removal of CWD would likely decrease the biodiversity in forested ecosystems. The removal of structural legacies is inconsistent with the scientific understanding of the natural process. One possible alternative management is to retain a combination of trees, snags, and logs within forests.

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