# ORIGINAL ARTICLE

Yang Lipan · Liu Wenyao · Ma Wenzhang

# Woody debris stocks in different secondary and primary forests in the subtropical Ailao Mountains, southwest China

Received: 28 July 2007 / Accepted: 7 October 2007 / Published online: 28 November 2007 @ The Ecological Society of Japan 2007

Abstract Woody debris (WD), including coarse woody debris (CWD) and fine woody debris (FWD), is an essential structural and functional component of many ecosystems, particularly in montane forests. CWD is considered to be the major part in forest WD and it is primarily composed of logs, snags, stumps and large branches, while FWD mainly consists of small twigs. Attributes of dead woody material may change in accordance with trends in stand dynamics. The primary forest (primary montane moist evergreen broad-leaved forest) in Ailao Mountain National Nature Reserve (NNR) preserves the largest tract of natural vegetation in China. The Alnus nepalensis (D. Don) association, Populus bonatii (Levl.) association and secondary Lithocarpus association represent the secondary and chronological types following human disturbance by fires and logging under different intensity. The mass and composition of coarse woody debris (CWD, ≥10 cm in diameter) and fine woody debris (FWD, 2.5-10 cm in diameter) were inventoried in a primary forest and its three secondary counterparts. Estimates of total mass of

Yang Lipan and Ma Wenzhang contributed equally to this work.

Y. Lipan · L. Wenyao · M. Wenzhang Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Kunming 650223, China E-mail: Lipany@xtbg.ac.cn E-mail: dennis@xtbg.ac.cn

Y. Lipan · M. Wenzhang Graduate School of Chinese Academy of Sciences, Beijing 100039, China

L. Wenyao (⊠) School of Environmental Biology, Curtin University of Technology, Perth, WA 6845, Australia E-mail: liuwy@xtbg.ac.cn Tel.: +86-871-5153787 Fax: +86-871-5126788

Y. Lipan

Yunnan University of Traditional Chinese Medicine, Kunming 650200, China woody debris across secondary types to primary forest ranged from 2.4 to 74.9 Mg ha<sup>-1</sup>. The lowest value was found in the *A. nepalensis* association and the highest values were in the primary forest of which logs are the considerable differences. The ratios of CWD to FWD were low in the secondary types (about 1–4) but high in the primary forest (above 15). Our results suggested that for the recovery of woody debris in the secondary forest, it might last longer than the age of the oldest successional stage studied.

**Keywords** Woody debris · Stocks and patterns · Different secondary and primary forest · Ailao Mountains

## Introduction

Stand development, the process of competition, senescence and mortality of trees in the forest canopy generate substantial woody debris that tend to accumulate in advancing stages of forest succession (Harmon et al. 1986). These residues, namely woody debris (WD), including coarse woody debris (CWD) and fine woody debris (FWD), can be an essential structural and functional component of many ecosystems, particularly in montane forests. CWD is considered to be the major part in forest WD and it is primarily composed of logs, snags, stumps and large branches (Harmon and Sexton 1996; Woodall and Nagel 2006; Yan et al. 2006), while FWD is mainly consisted of small twigs and is much less functional compared to CWD. For instance, in temperate forests of the Pacific west coast of North America, fallen logs and snags reach biomass values exceeds 150 Mg  $ha^{-1}$  (Harmon et al. 1986; Spies et al. 1988). The major types of woody residues and their relative contributions to total ecosystem mass vary greatly in the different landscapes, depending on forest types, disturbance regimes, topography, and stand age (Sturtevant et al. 1997; Goodburn and Lorimer 1998; Carmona et al. 2002; Webster and Jenkins 2005). Furthermore, CWD play critical roles in maintaining biodiversity and facilitating biogeochemical processes as they provide habitats for many organisms and store carbon and other nutritional elements for a long time in the forest ecosystems (Means et al. 1992; Griffiths et al. 1993; Crowford et al. 1997).

In the stand scale, it is some believed that CWD biomass is consistency in the temperate forests in a chronosequence of 'U'-shaped that the amounts of CWD may be high in early successional stage, low in mature forests and considerably greater in old-growth forests (Spies et al. 1988; Sturtevant et al. 1997). This is because the first successional stands inherited the large amount of woody residues of the pre-disturbance stands. However, in some secondary successional stands, as most of the large-sized woody residues from the predisturbance were extracted for building materials or fuel wood, the accumulation of the WD was only resulted from the regenerating stands, lacking of large woody pieces (Carmona et al. 2002; Christensen et al. 2005). The WD biomass and its patterns will change accordingly with the development and succession of stands, which in turn will not only reflect the state and directions of the stands succession but also the kind of forest use (Eaton and Lawrence 2006).

Primary montane evergreen broad-leaved forest, dominated by Lithocarpus xylocarpus (Kurz.) Markgr, Lithocarpus hancei (Benth.) Rehder and Castanopsis rufescens (Hook. f. et Th.) Huang et Y. T. Chang, is still well preserved in Ailao Mountain National Nature Reserve (NNR), which is stated of the largest tract of natural vegetation in China (Qiu et al. 1998; Liu et al. 2000). Due to its species composition and the environmental characters such as abundant rainfall, high humidity and high altitude, this forest belongs to the typical mountains types of the subtropical region, central and south Yunnan, and it is better to be called a "temperate rain forest" (Jin 1983). The secondary Alnus nepalensis association, Populus bonatii association are two different stages of succession in a selectively logged but not entirely destroyed forest and the secondary Lithocarpus association represent the advanced natural succession after clear cutting following human disturbance by fires and logging (Wang 1983; Qiu et al. 1998). The well-preserved primary forest and the secondary types made this region an ideal site to examine the accumulation of woody debris from the regenerating stands to primary forest (Liu et al. 2002). Despite their ecological relevance in terms of biomass and ecosystem functions, particularly in high-altitude montane forests, there is a lack of quantitative information on the abundance and biomass of WD from the secondary forests to the primary forest in Ailao Mountains.

The goal of this research is to estimate the attributes of woody detritus among four forest types in the subtropical Ailao Mountains, located in southwest China. The objectives of this study are (1) to determine which woody debris type affect stocks of woody debris from different secondary stands to the primary stand, (2) to determine what percent of total mass of woody debris is in the form of CWD and how it changes during stand development, (3) analysis and discussion the indication of WD components for forest succession. This study will provide useful information on the management and conservational practices of primary forests and shed lights on restoration of secondary forests.

# **Methods and materials**

Study site and vegetation descriptions

The study was carried out in the Ailaoshan Station for Subtropical Forest Ecosystem Studies (ASSFE) at Xujiaba region (24°32'N, 101°01'E), a core area of the Ailao Mountain NNR (Fig. 1). The altitude range is about 2,000–2,650 m. Meteorological observations at the ASSFE during 1982-1992 years show the annual mean precipitation is 1,931 mm, and its seasonal distribution is not even, with 85% falling in the rainy season from May to October. Mean annual evaporation is 1,485.5 mm and the annual mean relative humidity is 86%. Annual mean air temperature is 11.3°C and the coldest month temperature is 5.4°C in January and the hottest month temperature is 16.4°C in July. The frost-free period is about 200 days. The mean active accumulative temperature above 10°C is about 3,420°C, making this area similar to the warm temperate zone. Natural disturbances most commonly affecting forests in the Ailao Mountains are strong winds and the occasional cold spells that may be accompanied by snowfall. The soil under the evergreen broad-leaved forest is typically yellow-brown earth developed over schist, gneiss, and diorite. Soil texture is loam, with acidic pH (4.2-4.9) (Qiu et al. 1998).

Xujiaba consists of six forest communities (You 1983). The *Lithocarpus* association is mapped as being a homogeneous old growth forest, but close observations reveal many secondary patches within this forest type (Young et al. 1992). The three secondary types and the primary forest sampled for woody debris study were as follows:

#### A. nepalensis association

The *A. nepalensis* association was resulted from the repeating cutting, fires, and grazing in the middle of last century. The canopy of *A. nepalensis* association is dominated by a single pioneer tree species—*A. nepalensis*, so it can be described as the first stage of the secondary succession to the evergreen broad-leaved forest in this area (Wang 1983; Qiu et al. 1998).

## P. bonatii association

The *P. bonatii* association also resulted from the repeating cutting, fires, and grazing in the middle of last century. The dominant tree species in the *P. bonatii* 

Fig. 1 Location of the study area



association is a pioneer a *P. bonatii*, and the associated tree species are *L. xylocarpus*, *L. hancei*. They are the main symbols and indication of restoring and successional trend to the evergreen broad-leaved forest, of which the dominance of *P. bonatii* will be replaced by some evergreen broad-leaved trees species. It is believed that this secondary forest would develop into evergreen broad-leaved forest in 30–40 years in the future (Sheng and Xie 1991; Qiu et al. 1998).

# Secondary Lithocarpus association

Many regenerated trees in the secondary *Lithocarpus* association indicated that it was probably cut for timber and/or grazing but not for cultivation. When the reservoir was initially constructed about 100 years ago, some surrounding forested area was cut and this area is now regenerating into a secondary evergreen broad-leaved forest with the most same dominant species with primary forest (Young et al. 1992). According to the stand age and growth rate of major species in *Lithocarpus* association, it can represent the advanced natural succession after cutting (Young et al. 1992; Qiu et al. 1998).

# Primary forest

The primary moist evergreen broad-leaved forest in Xujiaba area has two tree layers and subordinate shrub

layers, as well as abundant epiphytes. The upper canopy of the forest is 18–25 m high and contains a number of tree species including *L. xylocarpus, L. hancei, C. rufescens, Stewartia pteropetiolata* Cheng (You 1983; Liu et al. 2002). Based on the facts such as the presence of large, old trees, and the lack of widespread human disturbance prior to the establishment of the Ailao Mountain NNR, this stand shows the status of being over-mature or old-growth forest, so it is also called oldgrowth forest.

Measurement of mass and composition of woody debris

Based on the pre-study qualitative assessments of vegetation types and woody debris properties, three plots of  $100 \times 100$  m in primary forest, and four plots of  $50 \times 50$  m in each of the secondary forests, were set up for CWD survey. In each plot,  $10 \times 10$  m subplots were established for FWD investigation (48 subplots in total in the primary forest and 16 for each secondary type).

In each plot, all pieces of woody residues with a largeend diameter  $\geq 10$  cm were considered as CWD in the sampling (Harmon and Sexton 1996; Webster and Jenkins 2005). (1) The length, small- and large-end diameter of all pieces of logs, stumps, and large branches were measured and recorded. Species and decay classes were identified in the field. To estimate the volume of woody residues, a cylindrical shape was assumed for each piece. Mass was obtained by multiplying the volume of each piece times the wood density for the respective species and decay classes. (2) Tree species, basal diameter, diameter at breast height (DBH) and decay stages were recorded for all the standing dead trees (snags) with a basal diameter  $\geq 10$  cm on each plot. Mass of the dominant species was estimated using allometric equation,  $W = a(D^2H)$  where W is the mass of a species; a and b are constants; D is the trunk diameter at breast height (cm) and h corresponds to tree height (m) (Liu et al. 2002). To verify the exact mass of snags, each decaying piece was multiplied by the decay class's density ratio. (3) FWD was defined all woody debris fragments with a diameter of 2.5–10 cm and a length greater than 10 cm. Stocks of FWD were measured in 48  $10 \times 10$  m quadrates for primary forest and  $16\ 10 \times 10$  m ones for each secondary forest. All FWD pieces within these quadrates were collected and weighed and 1-4 fragments of FWD at each site were randomly sampled to determine the weight conversion rate from the field state to dried condition. Samples of FWD were dried at 80°C to constant weight.

The modified decay classification system and class definitions used in our study sites are given, which was proposed by Maser et al. (1979) and modified by Pyle and Brown (1999). Carmona et al. (2002) based on field observations and a qualitative description of aspect, consistency of each woody residue. A new modified indirect measurement developed by Rouvinen et al. (2002) was also used in the field. The main contents are as follows: (1) the dead wood dies within 1-2 years, and the cambium is still fresh when investigation; (2) the cambium begins to compose, and the knife blade penetrates a few millimeters into it; (3) the knife blade penetrates 1-1.5 cm into it; (4) the knife blade penetrates 2-3 cm into it; and (5) the knife blade penetrates all the way. If a log, mainly of larger ones, contained more than one stage of decay; it was measured as separate segments by decay stage.

Furthermore, we collected small fragments (n = 9–10) of dominant species of CWD in each decay classes for determination of wood density by dividing the ovendried weight by volume. The fragments were stored in sealed plastic bags and taken to the lab, where we determined their fresh and dry mass, and volume (using water replacement technique within a water jar) and we assumed the same wood density values for the same species at the same decay class among logs, snags, stumps and branches (Table 1).

## Statistical analyses

The mass figures in the three secondary stands are actually standardized with the uniformed unit Mg ha<sup>-1</sup>. Analysis of variance (ANOVA) was used to determine the broad effects of stand types on mass of CWD components and FWD as well as to determine the Density of

 Table 1 Density of CWD by decay classes of the dominant species used to calculate mass in Ailao Mountains

Species	Decay	Density (g cm <sup>-3</sup> )				
	classes	Mean Range		Sample size		
Lithocarpus hancei	1	0.52(0.01)a	0.46-0.55	6		
	2	0.40 (0.02)b	0.33-0.44	5		
	3	0.38 (0.03)b	0.28 - 0.49	7		
	4	0.29 (0.01)c	0.26-0.30	4		
	5	0.18 (0.01)d	0.15-0.21	4		
Lithocarpus	1	0.64 (0.01)a	0.61-0.69	7		
xvlocarpus	2	0.57 (0.03)b	0.45-0.64	7		
	3	0.43 (0.01)c	0.35-0.50	10		
	4	0.34 (0.02)d	0.30-0.42	7		
	5	0.13 (0.02)e	0.10-0.16	4		
Castanopsis rufescens	1	0.52(0.01)a	0.49-0.54	9		
	2	0.47(0.01)b	0.43-0.52	12		
	3	0.42(0.02)c	0.37-0.47	5		
	4	0.33(0.02)d	0.25-0.37	6		
	5	0.19(0.02)e	0.13-0.25	9		
Others	1	0.51(0.04)a	0.38-0.99	16		
	2	0.40(0.02)b	0.22-0.55	19		
	3	0.38(0.02)b	0.23-0.48	19		
	4	0.30(0.02)b	0.28-0.31	2		
	5	0.08(0.02)c	0.07-0.10	2		
Average	-	0.41	0.07–0.99	160		

Values in the parentheses imply the S.E.

In each tree species, values with the same letters in a column are not significantly different (P < 0.05) using LSD test

CWD by decay classes of the dominant species. Significance was set at P < 0.05.

#### Results

Total mass of woody debris

Estimates of total mass of woody debris across three types of secondary forest to primary forest ranged from 2.4 to 74.9 Mg ha<sup>-1</sup> (Table 2). The lowest value of total mass was found in the *A. nepalensis* association and the highest one was in the primary forest. There are significant differences between primary and secondary forests in the mass of logs (P < 0.001), stumps (P < 0.001) and large braches (P = 0.023), while there is no significant variations in the mass of woody debris between *A. nepalensis* association.

Among four stands, logs mass showed more pronounced deviation than other woody debris components. Interestingly, the high mass of snags and FWD found in the secondary *Lithocarpus* association was roughly similar to the largest value estimated for primary forest. In addition, the logs were the dominant component in the CWD mass in the four stands. The primary forest contains a considerable mass of logs, accounting for 87.9% of the CWD stocks. In contrast, snags, stumps and branches contributed less mass. The ratio of CWD to FWD was increased from the secondary successional types (1–4) to the primary forest (above 15) (Table 2).

Table 2 Mass and composition of woody debris in the secondary and primary forests in Ailao Mountains

WD	Secondary forests						Primary forest	
	Ass. Alnus nepalensis		Ass. Populus bonatii		Ass. Lithocarpus			
	Mass (Mg ha <sup>-1</sup> )	Percentage (%)						
CWD								
Logs	0.7 (0.2)b	63.3	5.4(0.4)b	83.0	1.7 (0.3)b	34.1	61.7(14.3)a	87.8
Snags	0.3(0.2)b	23.6	0.7(0.2)b	10.5	2.4 (0.5)a	47.7	3.2(0.3)a	4.5
Stumps	0.2(0.0)b	13.2	_ ` `	_	0.3(0.1)b	5.3	4.0(0.3)a	5.7
Branches	_ ` `	_	0.4 (0.1)b	6.5	0.7(0.1)b	13.0	1.5(0.3)a	2.1
Total	1.1(0.3)	100	6.44(0.4)	100	5.1(0.9)	100	70.3(13.9)	100
FWD	1.3(0.2)b		1.6(0.1)b		4. 8(0.5)a		4.5(0.3)a	
Total WD	2.4 (0.2)b		8.0(0.4)b		9.9(0.89)b		74.9(13.8)a	
CWD:FWD	0.9:1		4.1:1		1.1:1		15.5:1	

Values in parentheses imply the S.E; in each woody debris component, values with same letters in a row are not significantly different (P < 0.05) using LSD test

#### Diameter classes distribution of CWD

There were obvious differences in the diameter classes' distribution of logs and stumps between the secondary types and the primary forest (P < 0.002) (Fig. 2). The proportion of larger-diameter dead trees was higher in the primary forest than in the secondary forests. Larger tree logs and stumps (>40 cm basal diameter) were the leading component in the primary forest and logs and stumps (>100 cm) pieces represented above 50% of total mass. While most of CWD accumulations in secondary forests were composed of pieces with diameter below 40 cm. There was no significant difference in snags and branches diameter (basal diameter) from the secondary forests to primary forest (P = 0.09-0.94).

### Species composition of CWD

The species composition of CWD found in four stands varied from 1 to 18 trees species from the secondary types to the primary forest. The CWD pieces comes form single pioneer tree species (A. nepalensis) in the A. nepalensis association (Fig. 3). Within the secondary P. bonatii association, the CWD components resulted from four species (P. bonatii, L. hancei, L. xylocarpus and Pinus Armandi Franch), of which P. bonatii contributed 85.5% to the total CWD mass, and species L. xylocarpus and L. hancei were typically associated with forest succession according the direction of aspen community succession (Sheng and Xie 1991; Oiu et al. 1998). The CWD components in the L. association are comprised of 15 tree species. Schefflera shweliensis W. W. Smith and Juglans *Regia* L. were common tree species in the composition of CWD in the secondary Lithocarpus association and species such as C. rufescens, L. xylocarpus and L. hancei in total accounted for about 20% of the CWD mass. The number of tree species for CWD composition was the highest in primary forest, up to 18 species, and C. rufescens, L. xylocarpus and L. hancei accounted for 84%



Fig. 2 The mass percentage (%) of different diameter classes of CWD in secondary and primary forests in Ailao Mountains

of the total mass of CWD, of which *C. rufescens* had the greatest value of CWD mass, reaching 53.3 Mg ha<sup>-1</sup>, and the next comes 3.2 Mg ha<sup>-1</sup> for *L. hancei* and 2.6 Mg ha<sup>-1</sup> for *L. xylocarpus*. The rest were *Schima* noronhae Reinw. ex Blume., *Camellia forrestii* (Diels.) Coh, Illicium macranthum A. C. Smith., Symplocos ramosissima Wall. ex G. Don., *S. shweliememsis, Manglietia insignis* (Wall.) Bl, Ilex coralline Franch., Machilus yunnanensis Lecomte., Machilus bombycina King. ex Hook. f., Acer heptalobum Diels., Acanthopanax evodiaefolius Franch., Sorbus rhamnoides Rehd., Eriobotrya bengalensis (Roxb.) Hook. and Meliosma kirkii Hemsl. & E. H. Wilson.

Fig. 3 Species composition of CWD in different secondary and primary forest stands in Ailao Mountains



70%

60%

50%

40%

30%

20%

10%

0%

Secondary Ass.

Alnus nepalensis Populus bonatii

Decay classes distribution of CWD

The distribution of CWD in different decay classes varied among the secondary and primary forests (Fig. 4). Overall, all CWD in lower to intermediate classes of decomposition (decay classes 1-3) were common in the secondary forest while the primary forest contained the full decay classes (from 1 to 5 classes) of woody debris. In the primary forest, the logs and stumps in decay classes 2-3 accounted for 60-90% of the total logs and stumps mass. All the snags belonged to the low to moderate decayed classes within the secondary and primary forests.

## **Discussion and conclusion**

Woody debris mass and composition

The dynamics of CWD can be summarized in two phases: the residual decay of pre-disturbance and disturbance-generated, and the residual accumulation of debris from the regenerating stand (Spies et al. 1988; Carmona et al. 2002). In our study, it was obviously different in the amount and quality of woody debris from the secondary forests to the primary forest in Ailao Mountains. However, the large woody residues of the

Fig. 4 Relative distribution of total mass of CWD among five decay classes in secondary and primary forest in Ailao Mountains

Stand type

Secondary Ass.

Lithocarpus

Secondary Ass.

4

**m**3

2

1

Primary forest

pre-disturbance stand were removed by local people for building materials and fuel wood (Wang 1983; Oiu et al. 1998). Thus, all the contemporary woody debris has been produced from the present generation types. The paucity of larger, decaying logs from the pre-disturbed stands resulted in: (1) less accumulation of woody debris in the secondary forests and (2) FWD held a large proportion of total woody debris mass (about 50% except for aspen stand). Furthermore, the lowest stocks of woody debris in *A. nepalensis* association can be explained in part by the increased decomposition rates of woody detritus in the open stand.

The CWD mass of 70.3 Mg ha<sup>-1</sup> in the primary forest (natural montane evergreen broad-leaved forest) in Ailao Mountains is much higher than that of forests in tropical area (1–30 Mg ha<sup>-1</sup>, Delaney et al. 1998) and other subtropical regions (7.3–25.3 Mg ha<sup>-1</sup>, Li et al. 1996; Tang et al. 2003), but it is somewhat lower than that of the temperate broad-leaved evergreen forest in Chiloe Island, Chile  $(58-381 \text{ Mg ha}^{-1})$  (Carmona et al. 2002). In this study, the high proportion of large-diameter logs in woody debris composition of the primary forest is similar to the old-growth forest ecosystems in other regions (Harmon et al. 1986; Spies et al. 1988; Siitonen et al. 2000). The site productivity, decomposition rates, stand history and disturbance regime will all influence the maximum accumulation of dead wood possible in any old-growth stand (Binham and Sawyer 1988; Siitonen et al. 2000; Webster and Jenkins 2005). The moist evergreen broad-leaved forest in the Xujiaba region belongs to the typical mountainous types of the south subtropical region. The high altitude, low temperature, and high humidity in study area make it difficult for the microorganism to thrive and the dominant CWD species being of the Fagaceae (C. rufescens, L. xylocarpus and L. hancei), whose hardwoods are decayresistant. All these factors contribute to the high accumulation of CWD mass than other forest ecosystem at the same latitude. On the other hand, the high proportion of logs (especially the large-diameter decaying logs) accumulations reflect the slow decomposition rates of dead wood, little or no past anthropogenic disturbance to the natural forest to a great extent (Liu et al. 2002).

#### Species composition of CWD

The species composition of CWD may indicate historical mortality patterns and successional direction of forest stands (Woodall and Nagel 2006). Species composition of CWD is substantially different among the secondary and primary forests in Ailao Mountains. The woody debris species is mainly comprised of single tree species in the A. nepalensis forest, while the CWD composition within the primary forest come from 18 tree species. Woody debris in the secondary forests is mainly of small diameter and high decay rate tree species. P. bonatii is considered the pioneer tree species with a short longevity, based on the analysis of species composition of the secondary P. bonatii association. Mature or old aspen (P. bonatii) is prone to heart-rot that increases its vulnerability to wind throw mortality (Sheng and Xie 1991). In addition, the heart-rot was also popular from young to adult aspen population (estimated of 100% individual attached), which contributed to the following rapid accumulation of aspen wood residues and accelerated the succession and development of other species. The shift of *P. bonatii* communities toward the secondary evergreen broad-leaved forest may be considered forward succession because aspen represents an early successional condition in this area (Sheng and Xie 1991; Oiu et al. 1998).

Species composition was richer in the primary forest than the secondary counterpart types. Above 80% of the CWD mass in primary forest were dominated by decayresistant species of C. rufescens, L. xylocarpus and L. hancei, which being of large diameter and could increase its contribution to CWD accumulation. These CWD components were resulted from the natural senescence and death of old trees. This is the main way of woody debris accumulation in the primary old-growth forests and is very common in other regions (Goodburn and Lorimer 1998; Webster and Jenkins 2005). Furthermore, the primary forest possesses the full decaying classes of woody debris, while the secondary forests have only part decay classes. The high decayed components of CWD are increasing with the forest development and succession, but differences in decay stages are probably due to species differences and the effect of forest types (Eaton and Lawrence 2006). It is necessary to develop site- and species-specific decay classification schemes for the secondary and primary forest in Ailao Mountains.

In conclusion, the stocks of woody debris were significantly different from the three secondary types to the primary forest, of which the logs (especially largerdiameter decaying pieces) are the most considerable changing components from secondary to primary forest. The stocks of woody debris are greater than the same latitude forests and reach the upper limit of subtropical regions which helps to illustrate the nature of 'temperate rain forest'.

Conservation and restoration implication

The amount and quality of CWD, especially large logs, are thought to be the most outstanding structural differences distinguishing secondary forests and old-growth primary forest (Harmon et al. 1986; Siitonen et al. 2000). Our results suggest that the residual accumulation of woody debris from the regenerating stand are low, and the current accumulation of higher stocks of woody debris, particularly larger decaying logs, need a long time in the primary forest. The development of oldgrowth stands starts at the minimum age of 300 years and a longer time required for CWD patterns and characteristics (especially larger-diameter logs distribution) to develop (Wang 1983; Young et al. 1992). Recovering time for CWD structure and composition similar to primary forest may exceed several centuries, so it is very important to preserve the current primary forest and maintain the structural and functional integrity of woody debris.

Acknowledgments This project was funded by the National Natural Science Foundation of China (No. 30470305), the Knowledge

Innovation Program (No. KSXC2-YW-N-066) and the Program of Hundreds of Talent Scientists of the Chinese Academy of Sciences. The Management Authority of the Ailao Mountain Nature Reserve is thanked for granting permission for the research reported. We also wish to thank Mr. Yang Guoping Li Dawen, Li Changjun, Yang Wenzheng, and Luo Chengchang for their assistance in fieldwork.

#### References

- Binham BB, Sawyer JO (1988) Volume and mass of decaying logs in an upland old growth forest. Can J For Res 18:1649–1651
- Carmona MR, Aravena JC, Pérez CA, Armesto JJ (2002) Coarse woody debris biomass in successional and primary temperate forests in Chiloé Island, Chile. For Ecol Manage 164:265–275
- Christensen M, Hahn K, Mountford EP, Odor P, Standovár T, Rozenberger D, Diaci J, Wijdeven S, Meyer P, Winter S, Vrska T (2005) Dead wood in European beech (*Fagus sylvatica*) forest reserves. For Ecol Manage 210:267–282
- Crowford RH, Li CY, Floyd M (1997) Nitrogen fixation in rootcolonized large woody residue of Oregon coastal forests. For Ecol Manage 92:229–234
- Delaney M, Brown S, Lugo AE, Torres-Lezama A, Quintero NB (1998) The quantity and turnover of dead wood in permanent forest plots in six life zones of Venezuela. Biotropica 30(1):2–11
- Eaton JM, Lawrence D (2006) Woody debris stocks and fluxes during succession in a dry tropical forest. For Ecol Manage 232:46–55
- Goodburn JM, Lorimer CG (1998) Cavity trees and coarse woody debris in old-growth and managed northern hardwood forests in Wisconsin and Michigan. Can J For Res 28:427–438
- Griffiths RP, Harmon ME, Caldwell BA, Carpenter SE (1993) Acetylene reduction in conifer logs during early stages of decomposition. Plant Soil 148:53–61
- Harmon ME, Franklin JF, Swanson FJ, Sollins P, Gregory SV, Lattin JD, Anderson NH, Cline SP, Aumen NG, Sedell JR, Lienkaemper GW, Cromack KJr, Cummins KW (1986) Ecology of coarse woody debris in temperate ecosystems. Adv Ecol Res 15:133–302
- Harmon ME, Sexton J (1996) Guidelines for measurements of woody detritus in forest ecosystems. US Long-Term Ecological Research Network Office, University of Washington. Washington Publication, Seattle
- Jin ZZ (1983) On the characteristics and nature of the evergreen broad-leaved forest in Xujiaba region of the Ailao Mountains (in Chinese with English abstract). In: Wu CY (eds) Research of forest ecosystems on Ailao Mountains, Yunnan. Yunnan Science and Technology Press, Kunming, pp 204–214
- Li LH, Xing XR, Huang DM, Liu CD, He JY (1996) Storage and dynamics of coarse woody debris in *Castanopsis eyrei* Forest of Wuyi Mountain, with some considerations for its ecological effects (in Chinese with English abstract). Acta Phytoecol Sinica 20(4):132–134
- Liu W, Fox JED, Xu ZF (2000) Leaf litter decomposition of canopy trees, bamboo and moss in montane moist evergreen broad-leaved forest on Ailao Mountain, Yunnan, south-west China. Ecol Res 15(4):435–447
- Liu WY, Fox JED, Xu ZF (2002) Biomass and nutrient accumulation in montane evergreen broad-leaved forest (*Lithocarpus xylocarpus* type) in Ailao Mountains, SW China. For Ecol Manage 158:223–235

- Maser CR, Anderson RG, Commack K, Williams JT, Martin RE (1979) Dead and down woody material. In: Thomas JW (eds) Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington, vol 553. USDA Agricultural Handbook, Washington, DC, pp 78–95
- Means JE, MacMillan PC, Cromack K (1992) Biomass and nutrient content of Douglas-fir logs and other detrital pools in an old-growth forest, Oregon, USA. Can J For Res 22:1536– 1546
- Pyle C, Brown MM (1999) Heterogeneity of wood decay classes within hardwood logs. For Ecol Manage 114:253–259
- Qiu XZ, Xie SC, Liu WY (1998) Studies on the forest ecosystem in Ailao Mountains, Yunnan (in Chinese with English summary). Yunnan Sciences and Technology Press, Kunming
- Rouvinen S, Kuuluvainen T, Karjalainen L (2002) Coarse woody debris in old *Pinus sylvestris* dominated forests along a geographic and human impact gradient in boreal Fennoscandia. Can J For Res 32:2184–2200
- Sheng CY, Xie SC (1991) Studies on the growth regularity and the successional status of *Populus bonatii* in the Ailao Mountains (in Chinese with English abstract). J Southwest Forestry College 11(1):33–40
- Siitonen J, Martikainen P, Punttila P, Rauh J (2000) Coarse woody debris and stand characteristics in mature managed and oldgrowth boreal mesic forests in southern Finland. For Ecol Manage 128:211–225
- Spies TA, Franklin JF, Thomas TB (1988) Coarse woody debris in Douglas-fir forests of western Oregon and Washington. Ecology 69:1689–1702
- Sturtevant BR, Bissonette JA, Long JN, Roberts DW (1997) Coarse woody debris as a function of age, stand structure, and disturbance in boreal Newfoundland. Ecol Appl 7:702–712
- Tang XL, Zhou GY, Zhou X, Wen DZ, Zhang QM, Yin GC (2003) Coarse woody debris in monsoon evergreen broadleaved forests of Dinghushan Nature Reserve (in Chinese with English abstract). Acta Phytoecol Sinica 27:484–489
- Wang BR (1983) The dynamic analysis of evergreen broad-leaved forest in Xujiaba region of the Ailao Mountains (in Chinese with English abstract). In: Wu CY (eds) Research of forest ecosystems on Ailao Mountains, Yunnan. Yunnan Science and Technology Press, Kunming, pp 151–182
- Webster CR, Jenkins MA (2005) Coarse woody debris dynamics in the southern Appalachians as affected by topographic position and anthropogenic disturbance history. For Ecol Manage 217:319–330
- Woodall CW, Nagel LM (2006) Coarse woody type: a new method for analyzing coarse woody debris and forest change. For Ecol Manage 227:115–121
- Yan ER, Wang XH, Huang JJ (2006) Concept and classification of coarse woody debris in forest ecosystems. Front Biol China 1:76–84
- You CX (1983) Vegetation classification in the Xujiaba region of the AilaoShans (in Chinese with English abstract). In: Wu CY (eds) Research of forest ecosystems on Ailao Mountains, Yunnan. Yunnan Science and Technology Press, Kunming, pp 74–117
- Young SS, Carpenter C, Wang ZJ (1992) A study of the structure and composition of an old growth and secondary broad-leaved forest in the Ailao Mountain of Yunnan, China. Mt Res Dev 12:269–284