Ecological functions of coarse woody debris in forest ecosystem

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Abstract: Coarse woody debris is an important structure and function unit in forest ecosystem. This review analyzed the ecological functions of coarse woody debris in forest ecosystem and introduced several hotspots and existing problems in coarse woody debris research field. It is suggested that quantitative research should be intensified in the ecological demands of coarse woody debris for providing a technical guidelines in management of productivity, biodiversity and other ecological processes.

Keywords: Coarse woody debris; Ecological function; Biodiversity; Decomposition
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Introduction

Coarse woody debris (CWD), primarily in the form of down wood (logs), large branches, pieces of fragmented wood, stumps, and standing dead trees (snags), plays an important role in the structure and function of forest ecosystem. The earliest researches of CWD can be roughly dated to the 1920s. Graham (1925) firstly pointed out that fallen wood was an important ecological unit of forest ecosystem. And following it, increasing concern was expressed for the roles of CWD in forest ecosystem. Particularly in America and Canada, many studies focused on the nutrient dynamics of CWD, and its role in forest successions. The extensive studies on CWD functions were carried out until recent thirty years (Hou *et al.* 2001). Harmon *et al.* (1986) published a comprehensive review of the ecological function of CWD in temperate forest, which marked the establishment of CWD ecology as a scientific subject, as well as a fully attitude change towards CWD in forest. And then, large numbers of systematical research projects came forth.

Due to most research funds having a short-term feature to the long-term ecological processes of CWD, in China, the literatures about CWD did not emerge until recently two decades (Chen *et al.* 1992). Up to now, some studies have been conducted in temperate forests of Changbai Mountains (Chen *et al.* 1992; Dai *et al.* 2000; Dai *et al.* 2002; Deng *et al.* 2002b; Yang *et al.* 2002), while only several researches were concerned with the long-term dynamics and role of CWD in extensive tropical and sub-tropical forest (Liu *et al.* 1995; Li *et al.* 1998; Tang *et al.* 2003) in Northeast China. Furthermore, related researches have not been conducted systematically. Most of the studies have focused on CWD stocks, distribution and dynamics (Gao *et al.* 2003). Few researches were done in understanding the ecological role of CWD and the role of CWD in forestry biochemistry cycle.

Input of coarse woody debris

CWD mostly comes from whole dead trees, and thus tree mortality is closely related to inputting of CWD. The following agents are responsible for most of the tree mortality.

Wind: Stems or branches snapping and uprooting caused by strong winds add CWD to forest floor immediately. Wind-impacts vary with soil depth and moisture content, stand structure, tree age and tree species.

Fire: Fire creates CWD directly or makes trees be more susceptible to wind, disease, and pests disturbance.

Disease and pests: Both can cause tree death directly or weaken tree resistance, and eventually contribute to tree death.

Competition: Suppressed trees under the stress of water and energy are easily be attacked by disease and pests.

Senescence: old age may contribute to the susceptibility of tree to pests, disease and wind.

These factors influencing on tree mortality vary enormously in different stands. The studies (Yang *et al.* 2002) showed that the shallow soil and strong winds were responsible for most volume of down wood in dark coniferous forest of Changbai Mountain. The studies on evergreen broad-leaved forests of Dinghu Mountain indicated that competition was the main drive of CWD input (Tang *et al.* 2003).

The input rate of CWD is closely related to tree species. Rimvydas *et al.* (2004) in an unmanaged north-temperate forest found that the standing dead trees was dominated by pine and alder, and broken trees comprised almost a half of aspen, while most uprooting trees often occurred in spruce, aspen and birch. Harmon *et al.* (1986) reported that the input rates of CWD for coniferous forests in the United States ranged from 0.17–30 $t \cdot hm^{-2} \cdot a^{-1}$, with most values less then 5 $t \cdot hm^{-2} \cdot a^{-1}$. The input rates for deciduous broadleaved forests ranged from 0–14.5 $t \cdot hm^{-2} \cdot a^{-1}$, with most rates less than 2 $t \cdot hm^{-2} \cdot a^{-1}$.

The CWD input rate also varies widely during the life of a forest stand. Generally, the stand begins with a large input of CWD after a catastrophic impact (such as fires, storms, insect outbreaks, and clear cutting) on forest, and then as a young forest, the input rate drops to near zero for many decades. As the trees growing, competition and disease begin to stress some trees, and the input rate increases until a large disturbance by nature or

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human happens again. Accordingly, the amount of CWD was found to be highest in old stands. In stands of an intermediate age, the amount of CWD was lowest, especially for large size CWD. This process roughly appears as U-shape as reported by many researchers (Pies 1988; McCarthy *et al.* 1994; Hou *et al.* 2001). For example, a study in temperate forests of Chile showed that CWD biomass ranged from 18 to 413 t·hm^{-2}. The largest values appeared at recently disturbed and old-growth forests and the lowest values at early- and mid-successional stands. CWD amount in old-growth and primary forest was nearly 10 times higher than that in young-successional forests (Martín *et al.* 2002).

The role in soil ecology

Providing organic matter and nutrient

The forest soil is a key element in evaluating the health of forest. To maintain the productive potential of a forest ecosystem, forest soil needs a continuous source of organic matter and nutrient. CWD can improve the physical and chemical characteristic of soil significantly through protecting and enhancing the forest soil's organic matter and nutrient contents (Harmon *et al.* 1994).

The decaying CWD is a steady supplier of soil organic matter, because well-decayed wood has high lignin and humus in carbon constituents. The nutrient pool of CWD includes the nutrients accumulated in the bole, large branches, roots and stumps during tree growth. When CWD decompose, the nutrients will be returned to soil. Particularly, after large-scale disturbance, such as fires and blow down, the nutrient pool of CWD will be an important source to the regenerating forest during secondary succession (Hyvonen *et al.* 2000).

Most forests have few nodulated plants to fix N directly, especially after many years of fire suppression, therefore, the lack of nitrogen is a common feature in most forest ecosystems, which greatly limits the production of forest ecosystem. CWD in the soil can create acidic soil conditions, which are favorable for soil microbial activity that helps fix nitrogen. In additional, although CWD itself is low in nitrogen, it contributes to the N input by fostering the bacteria and fungi, which could be a significant source of nitrogen in some forest ecosystems. For example, the fungi can remove the nutrients from CWD and form available nutrients pool in the forest soil. Harmon *et al.* (1994) found that during early stages of CWD decomposition, the concentrations of N, K and P for mushrooms growing on decaying logs increased by 38, 115 and 136 times, respectively. When the mushrooms fall off the logs and decayed, they would return nutrients from the fallen wood into the available nutrient pool. Roskoski (1981) summarized the past studies in North America and found that in a range of forest ecosystems, there was a range of non-symbiotic nitrogen fixation of 0.3–2.1 kg·hm^{-2}·a^{-1}.

Additionally, CWD is an important structural component that serves as a habitat for many saprophagous species and thus locally improves the nutritional situation of a forest stand. For example, arthropods and earthworms can digest the lignin in CWD with the help of micro-organisms in their digestive systems and return the nutrients to the forest in their dejecta. CWD usually decays slowly, and some large woody debris may hold more than 1000 years. Thus, CWD can be viewed as a long-term and steady nutrients pool for forest stands.

Water and soil conservation

Many studies have documented the important role of CWD in montane and riparian forest (Deng *et al.* 2002b; Liu *et al.* 2004; Zhao *et al.* 2002). The physical properties of large pieces of wood are important to water and soil conservation in these ecosystems. CWD can contribute to slope stability, prevent erosion and control soil surface runoff. Particularly, on a steep slope, CWD may play an important role in soil stabilization. Larger pieces of CWD lying across the slope can reduce velocity of water flow, and create a substrate for invertebrate and small mammal through collecting materials on their upslope side.

CWD has a high pore volume and thus can improve the moisture-carrying capacity of the soil. It usually serves as moisture reservoirs and provides refuge for tree roots and fungi during dry periods. Accordingly, removing natural CWD from soil horizon could reduce soil moisture retention and increase soil compaction. In the Pacific Northwest, the moisture content of a decaying Douglas-fir wood increased as the decay class increased, and at later decay stage, the moisture content in summer was up to 25 times of the dry weight (Amaranthus *et al.* 1994). The research made by Zhao *et al.* (2002) in a sub-alpine dark coniferous of upper reaches of Yangtze River showed that, CWD can hold about 7.41 mm precipitation under natural condition, and 9.91 mm under saturated condition, which is a great contribution to the hydrological function of whole forest ecosystem.

The role in maintenance of biodiversity

CWD plays an important role in maintenance the biodiversity of forest ecosystem. It can provide habitat for small mammals and microbial decomposers, and refuge for plants and fungi during disturbance and environmental stress. In many temperate forests, the dynamics of CWD input and distribution have been grossly altered across the landscape, due to centuries of clear-cut harvesting activity. This contributed to the decline, in some cases, extinction of a range of insect and fungal species relying on CWD (Martikainen *et al.* 1999).

Small mammals and arthropods

Along with understorey vegetation, CWD is the most important habitat for small animals and arthropods. Rabe *et al.* (1998) found bats always use snags as breeding roosts in a pine forest. An experiment about the demographic responses of shrews to removal of CWD in a pine forest showed that capture rates of shrews were lower at CWD-removed plots than those at control plots (Timothy *et al.* 2004). Retained CWD in forest can help to maintain the biodiversity, because CWD provides food, shelter, protection, cover, and substrate or climate amelioration for many animals. In turn, enough small animal populations help to sustain the ecological processes of forest succession through dispersing seeds and preying on pests.

CWD is also an important substrate for arthropods, such as ants. In a mixed conifer stand in northeastern Oregon, Torgersen & Bull (1995) found that approximately one-third of the fallen wood contained ants. In turn, arthropods associated with CWD can increase the availability of organic particles for decomposer communities, and contribute to nutrient cycling (Setälä *et al.* 1994). CWD is composed principally of cellulose (40%–50%), hemicellulose (20%–35%) and lignin (15%–35%), and a small quantity of tannins, oils and resins (Yee *et al.* 2001). Most animals can't digest the complex organic molecules in it. However, some arthropods, such as termites, have symbiotic protozoa in their gut that can break down cellulose. They are ecologically significant members in helping decomposition of CWD.

Additionally, in aquatic system, the barrier effects of CWD are significant in decreasing velocity of water flow and constructing food-accumulation pools for fish and other aquatic animals (Deng *et al.* 2002a).

Plants and fungi

CWD has a close relationship with the diversity of many plants and fungi in forest. It acts as a moisture-retaining substrate, and provides refuge for seedlings and mycorrhizal fungi, particularly in more arid forests or at time of dry season.

Healthy forests typically have highly diverse fungi (Amaranthus *et al.* 1994). This diversity is susceptible to human-caused disturbance, especially to the CWD clearing strategy. In Finnish and Swedish forests, natural fungi were found to be missing where there are activities of clear-cutting and CWD removal (Amaranthus *et al.* 1994). In some wet ecosystems, mostly tree seedlings sprout on large pieces of woody debris (Harmon *et al.* 1986). The decaying wood provides a platform for successful seeds sprouting and growth. In some riparian spruce forest, seeds sprouting only occurred on CWD, because other sites in this forest are too wet to allow seed germination. Graham & Cromack (1982) reported that 94%–98% of the tree seedlings germinated on CWD in rain forests of Olympic National Park, but only 6%–11% on the forest floor. Gray & Spies (1997) found that most western hemlock seedlings grew on decayed wood, rather than on forest floor or mineral soil. Schreiner *et al.* (1996) found that with the intensive browsing pressure, CWD were the only places where some shrub species could flower and set seed in a spruce–western hemlock forests in Olympic National Park.

The role in long-term carbon budget and storage

Biometric measurements, including measurements of tree growth, litter fall and soil respiration, are always be used to estimate net ecosystem carbon exchange of forest (NEE). However, microbial respiration from CWD is rarely included in the biometric measurements, resulting in overestimates of NEE. CWD is the only C pool that consistently shows net emissions, and it accounts for approximately 10% of total carbon stock in global forests (Turner *et al.* 1995). In a Douglas-fir and western hemlock forest ecosystems, Harmon *et al.* (1990) found that the CWD stored nearly 30% of the total carbon in the forest. In an old-growth Amazonian forest, CWD accounted for 25% of the aboveground C stock, and CO_2 respiration from it was approximately 630 $g\cdot m^{-2}\cdot a^{-1}$, which exceeded the average flux of fine litterfall (570 $g\cdot m^{-2}\cdot yr^{-1}$), (Rice *et al.* 2004). A study in a Russian boreal forest after wind disturbance showed that C efflux from CWD accounted for more than 40% of C respiration of total ecosystem (Knohl *et al.* 2002). Long-term carbon storage of forest was affected by the removal of CWD, because when CWD was removed, the carbon was often released more quickly than that in the decay cycle. Carbon is slowly released by CWD as it decays in the forest. Some large, decay-resistant pieces may hold more than one thousand years.

CWD decomposition

The decomposition of CWD is an extremely complex process, varying among different tree species and environmental conditions. Generally, it includes three physical-chemical processes. **Fragmentation**—fragmentation is the breaking up of CWD into smaller pieces, which occurs as insects chew the wood, as predators search for insects in decayed wood, and as wind, rain or other physical disturbances. This process can increase the surface-to-volume ratio of woody debris, thus increase the contact of the wood with the ground, and then increase the activity of microbes, invertebrates and vertebrates at the soil-wood interface. **Leaching**—leaching is the process that soluble materials in CWD penetrate into soil with rain agent. It is less important in early decay stages as most of the material in these stages is not soluble. As fragmentation begins, decomposers change the organic polymers into soluble material. **Respiration**—respiration loss of organic matter is the main process behind the complex phenomenon of CWD decomposition. During this process, microbes transform organically carbon, which accounts for approximately 50% of the organic material, into CO_2 through respiration. Respiration from surface litter results in CO_2 emissions to the atmosphere, whereas the former two processes result in organic matter inputs to soil or streams.

Besides above mentioned, there are still some other processes contributed to the decomposition of CWD, such as biological transformations. Biological transformations are the metabolic transformation of woody material. This process begins while the trees are still living. In an ongoing long-term experiment in Oregon, Harmon *et al.* (1994) found that mushrooms growing on down wood remove the nutrients from CWD into the forest soil, this process accelerated the decomposition of CWD significantly. Mattson *et al.* (1987) also found that density loss rates for fungi covered logs were nearly 40% higher than those with no cover.

Currently, it is known that decomposition rates of CWD are highly variable for different environmental conditions and different parts of a dead wood (e.g., bark, sapwood, heartwood). Temperature is generally viewed as the most important environmental factor controlling decomposition rates. In a study in Sweden, birch CWD decomposed two to four-folds faster in southern Sweden than in northern Sweden, because that the former is much warmer than the latter (Kruys *et al.* 1999). Keenan *et al.* (1993) found that the cool temperatures on northern Vancouver Island cause slow decomposition rates, which contribute to the high level of CWD in those forests. The significantly high level of CWD in broad-leaved forest of Ailao Mountain in China was also ascribed to the low temperatures (Liu *et al.* 1995). The analysis of a global data on decomposition rates of CWD showed that the mean annual temperature was a main driver of decomposition, accounting for 34% of the variation in decomposition rates (Mackensen *et al.* 2003). Knohl *et al.* (2002) also found a strong correlation between yearly average temperature and decomposition rate on a global scale. Besides, humidity is also viewed as an important environmental factor controlling decomposition rates. The study in a black spruce forest in Canada showed that moisture was a significant predictor of CWD decomposition when moisture was below 43%, but when above this level, it was not significant (Bond-Lamberty *et al.* 2003).

Each part of a fallen tree has its own decomposition rate. A study on a radiata pine forest in New Zealand showed that the decomposition rate was the fastest for wood, followed by bark, and the slowest for branch material (Girisha *et al.* 2004). The further analyses showed that the faster rate of decomposition of wood was mainly due to greater carbohydrate concentration, while greater concentrations of polyphenol and lignin were responsible for the slower decomposition rate of bark. The slow rate of decomposition of branches was due to unfavorable micro-climate (most of the side branches were not in contact with soil even after several years of decomposition), as well as greater lignin and polyphenol concentrations. The studies on the decomposition rate of roots are scarce, especially on large roots (Scheu *et al.* 1994). Limited researches seem to indicate that the roots decomposition rate is much lower than that of above-ground material. Scheu and Schauermann (1994) compared C loss in branches and roots of *Fagus sylvatica* with similar small-diameter sample, and found that the decomposition rate constants for root material were only about 60% of branch material.

Additionally, CWD size and positions are also responsible for the variation in decomposition rate. For example, decomposition rates of logs on the soil surface tended to be higher than those for elevated logs. The contact of CWD with soil may improve the availability of water and nutrients for wood-colonizing fungi. Erickson *et al* (1985) found that decomposition rate of CWD with soil contact was twice as fast as that of elevated logs. Edmonds *et al.* (1986) reported that the decomposition rates for logs buried in soil were faster than that of logs on the soil surface. In terms of CWD diameter, it is generally acceptable that decomposition rate decreases with increasing CWD size until the piece diameter is over 20 cm and then remains approximately constant. The change pattern remains the same for majority of the tree species (Edmonds *et al.*1986).

It can take more than 1000 years for the complete decay of large wood debris in some boreal forest ecosystems. Thus, changes in material density or mass loss in unit time were used to quantify the decomposition rates of CWD. Jens *et al.* (2003) found that the times spent for loss of 95% material ($t_{0.95}$) density of *Pinus radiata*, *Eucalyptus regnans*, and *Eucalyptus maculata* were 24, 43, 62 years, respectively. Furthermore, decomposition models are always used to describe the processes of decomposition. Two mathematical models have been widely used. One is the single-exponential model, which is the most common model used to describe decomposition patterns. It is based on the assumption that the decomposition rate is proportional to the amount of matter remaining. Another is the multiple-exponential model, which is considered that CWD is not a homogeneous substrate, but consists of various components. If some components are susceptible to decay, while others are resistant, actual decomposition curves can differ significantly from the single-exponential model.

Discussion

Currently, it is wide realization that preserving biodiversity and maintaining the health of forest ecosystem should include the maintenance of CWD. In Europe and North America, many active practices were taken to maintain CWD (Schiegg 2001). However, we are yet unable to provide quantitative guidelines for what type and how many CWD are needed to maintain specific levels of productivity and other ecosystem processes. For example, to maintain peak mycorrhizae amounts in the dry forests of western Montana, Harvey *et al.* (1981) has initially recommended that, about 22-34 $t \cdot hm^{-2}$ of down wood should be retained in soil horizon to provide a moisture-retaining substrate and a steady supply of organic matter. However, such large volume of woody material also imparts a big fire hazard. Additionally, it is difficult to quantify the ecological demands of CWD for other complex ecological processes in various forest ecosystems. Thus how to maintain optimum levels of CWD throughout a forest rotation remains an issue of concern. Complementary studies are urgently needed to provide information for adaptive management of CWD in forest ecosystem.

In recently years, the computer models, such as DecAID model (Mellen *et al.* 2002), are commonly used to project the dynamics and functions of CWD for managed and nature forest ecosystems. But the models are always constrained by the lack of spatial information of CWD when scaling up them to larger spatial scales. Many researches suggest that complex factors affect the distribution of CWD inputs across the landscape, while CWD biomass and inputs are poorly documented in many forests, and the causes for their variation at landscape-scales have not been studied (David *et al.* 2002). Thus, though the volumes of CWD pool are likely to change with global climate change, practically to the global warming, the overall direction of change is still uncertain. Given its importance in forest ecosystems, a better understanding of CWD spatial distribution is necessary if CWD dynamics and function are to be fully understood on regional or global scale.

Temperature and moisture content are two dominant and interacting factors in CWD decomposition. However, the models of temperature, moisture content and other environmental factors acting on CWD decomposition are not well established. Marra & Edmonds (1996) concluded from studies at a clear-cut site in the Pacific Northwest that temperature was more important factor than moisture. Conversely, Chambers *et al.* (2001) concluded that moisture content was the most important factor for CWD decomposition. For well understanding the ecological role of CWD, more studies, especially laboratory incubation factorial experiments are still needed, to quantify the effect of temperature and moisture content, decay status, tree species, and wood size on CWD decomposition.

Though many studies have been done on the decay processes and nutrient cycle of CWD, there are still some unclear issues to be explored. For example, Raija & Cindy (2004) suggested that CWD was initially a sink for N and P, and then became a source in late decay stage. In contrast to it, the study in a radiata pine forest showed that although the concentrations of most nutrients increased with time, net release of CWD nutrients (N, P, K, Ca and Mg) occurred during all stage of decomposition (Girisha *et al.* 2004).

To quantify the turnover of CWD and its contribution to the C cycle at the regional and global scale, the understanding of CWD respiration is critical. However, there are relatively few studies on this subject because of the challenges in making accurate measurements. In the past, the information was generally got through sampling and re-sampling research plots. For example, based on mass loss rates of CWD pool in a mid-latitude hardwood forests, Barford *et al.* (2001) estimated that CWD respiration, from logs, snags and dead woody roots, was (30±30) $g \cdot m^{-2} \cdot a^{-1}$. This method didn't differentiate between the flows of carbon to the atmosphere and to the forest soil during CWD decomposition, thus CO_2 efflux always was overestimated by the method when the mass losses caused by leaching and fragment processes are also added to respiration effects. Soda lime traps method has also been used for *in situ* measurements of CWD respiration (Progar *et al.* 2000). However, recent researches found that this method usually overestimates CWD CO_2 efflux due to the 'pump' effects (Chambers *et al.* 2001). Currently, infrared gas analyzer is the preferred method to measure CWD respiration, in virtue of its precise and rapid concentration measurements (Wang *et al.* 2002).. However, this method is not unimpeachable too. It generally involves destructive sampling, as well as removes the CWD sample from its original microclimate. Moreover, sampling from a CWD can change the ratio of the surface area to sample volume, which has an unknown effect on respiration rates. Available data in recently published literature suggested that Chinese forests contained large amounts of carbon stored in CWD, especially in the evergreen broad-leaved forests of Southeast China (Hou *et al.* 2001). Potential climate change would increase decomposition rates, release more carbon stored in CWD, and then affect the forest carbon dynamics. In the past few years, several projects have been initiated to study the carbon budgets of Chinese forests. However, information is limited for the dynamics of CWD, particularly for CWD respiration efflux. For example, the broad-leaved Korean pine forests of Changbai Mountain are acting as a net carbon sink of about 1.8 $t \cdot hm^{-2} \cdot a^{-1}$ (Guan *et al.* 2004). However, only the biomass of fallen trees is more than 16.2 $t \cdot hm^{-2}$ (Dai *et al.* 2002), the potential incensement of respiration efflux from CWD may largely offset the proposed carbon sink. Thus, independent measurements of carbon efflux from CWD, as well as from other individual carbon pools, are important to help evaluate eddy covariance results, and to better understand the factors that control C budget processes. Unfortunately, as yet, few studies have been done on this.

Nowadays, the increasing interest in CWD roles and decomposition provides an excellent opportunity to integrate many related research objectives into a comprehensive, long-term, multi-scale research program. Based on the information presented in the above sections, we recommend that a program should focus on the following areas of research:

1) the basic information of CWD stocks, and distribution in different forest types, and at different seral stages;

2) the diversity, abundance, and distribution of animals, plants and microbes in CWD, and the impacts of CWD biomass changes on their dynamics;

3) the roles of CWD in both early seedling establishment and long-term forest health;

4) the effects of CWD on forest soil physical and chemical properties, as well as the effects of water and soil conservation;

5) the roles of CWD in forestry biochemistry cycle, particularly in the nutrients cycle and carbon cycle;

6) the decomposition rates of various CWD components in different decay stages, and the effects of key environmental conditions on these decomposition rates.

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