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Coarse Woody Debris Dynamics in Two Old-Growth Ecosystems

Comparing a deciduous forest in China and a conifer forest in Oregon

Mark E. Harmon and Chen Hua

Dead trees are associated with many key functions in forest ecosystems. Because they may persist for centuries (McFee and Stone 1966, Triska and Cromack 1980), their influence is as long-lasting as that of living trees. During decomposition, logs and other forms of coarse woody debris (defined as wood pieces more than ten centimeters in diameter and more than one meter in length) reduce erosion and affect soil development, store nutrients and water, provide a source of energy and nutrient flow, serve as seedbeds, and provide habitat for decomposers and heterotrophs (Franklin et al. 1981, Harmon et al. 1986). In addition, coarse woody debris has the potential to store a large amount of carbon in the forest ecosystem. The role of coarse woody debris in storing carbon is often overlooked, with only living plants (Whittaker and Likens 1973, Woodwell et. al. 1978) or soil carbon (Post et. al. 1982, Schlesinger 1977) being considered. Relatively little is known about the formation and rate of decay of coarse woody debris or the factors controlling these processes, despite the relevance of this information to the global carbon cycle.

Forest management (e.g., removal of wood for fuel) significantly affects the amount of woody debris. Furthermore, woody debris is one of the slowest components of the ecosystem to recover after disturbance (Spies et al. 1988). Therefore, short intervals between timber harvests can reduce ecosystem carbon storage in coarse woody debris even when the living portion of the ecosystem has recovered (Harmon et al. 1990). Conversely, allowing debris to accumulate would result in more carbon being stored in the ecosystem than has been predicted by current projections, which assume that a steady state is reached in less than 100 years (Lugo and Brown 1986).

Coarse woody debris has potential to store much carbon

In this article, we compare the dynamics of coarse woody debris in a deciduous old-growth forest system, Changbai Mountain Biosphere Reserve in China, and a coniferous old-growth forest system, H. J. Andrews Experimental Forest in Oregon (Table 1). The forest vegetation at Changbai has been studied extensively since 1979, when the Academia Sinica established the Changbai Mountain Research Station of Forest Ecosystems. The Andrews reserve was established in 1948 by the US Forest Service and has been the site of extensive research on timber and watershed management (McKee et al. 1987).

Most ecological research has occurred in mature second-growth forests (Spies et al. 1988), where coarse woody debris is usually less important than in old-growth forests. Comparison with other sites indicates that the Andrews and Changbai represent the upper and lower limits of the importance of coarse woody debris in temperate forests (Chen Hua 1989, Harmon et al. 1986). Our objective is to compare in these two ecosystems the amount of coarse woody debris; the processes that affect coarse woody debris, such as tree mortality and decay rates; and the role of coarse woody debris in nutrient cycling. To assess importance in the global carbon budget, we use these two old-growth ecosystems to estimate the upper and lower limits of coarse woody debris mass for undisturbed temperate forests.

Tree mortality

We had expected that tree mortality rates for Changbai would be higher than for Andrews because deciduous species generally have shorter lifespans. However, the percentage of trees (greater than five centimeters in diameter at breast height) dying annually was similar between the two sites: 0.3–0.7%/yr for Changbai (Chen 1989) and 0.5–0.7%/yr for Andrews (Franklin et al. 1987). In contrast, old-growth deciduous forests in the eastern United States have been reported to have a higher mortality rate, 1.19–1.26%/yr (Abrell and Jackson 1977, Parker et al. 1985). Tropical

Mark E. Harmon is an assistant professor in the Department of Forest Science, Oregon State University, Corvallis, OR 97331, and Chen Hua is a research assistant at the Institute of Applied Ecology, Academia Sinica, Shengyang, Peoples' Republic of China.

forests also have higher rates of tree mortality; Lieberman et al. (1985) found rates of 1.02–2.03%/yr of trees dying in primary moist tropical forests.

Comparison of tree biomass lost via mortality for the two sites confirms the premise that deciduous forests produce less coarse woody debris than do coniferous forests (Harmon et al. 1986). At Changbai, annual mortality removed from 0.15–0.66 $Mg \cdot ha^{-1} \cdot yr^{-1}$ in forests dominated by deciduous trees to 1.23 $Mg \cdot ha^{-1} \cdot yr^{-1}$ in forests dominated by Korean pine, compared with an average of 2.38 $Mg \cdot ha^{-1} \cdot yr^{-1}$ for Andrews. In other areas of the Pacific Northwest, even higher rates, ranging from 4.54 to 7.0 $Mg \cdot ha^{-1} \cdot yr^{-1}$, have been observed (Grier and Logan 1977, Harcombe et al. 1990, Sollins 1982). As a first approximation, coarse woody debris production appears to be positively correlated with living biomass (Harmon et al. 1986) and should, therefore, increase with forest age and/or productivity.

It is tempting to assume that most trees are killed during major disturbances, but data from Changbai and the Andrews indicate otherwise. Typhoons, such as the one that destroyed 10,000 ha of forest in 1986, cause extensive disturbance at Changbai. Given a return interval of 50–100 years, typhoon-related mortality is roughly equal to the mass dying in an undisturbed forest of equivalent size. At Andrews, the most common catastrophic disturbance is fire, with a return interval of 500 years. A single fire can add as much as 1000 Mg/ha of coarse woody debris (Agee and Huff 1987), although the average is probably closer to 500 Mg/ha (Spies et al. 1988). In undisturbed forests, normal mortality would have added 1200–2200 Mg/ha in 500 years.

Table 1. General site features of Changbai Mountain Biosphere Reserve and H. J. Andrews Experimental Forest.

Parameter	Changbai	Andrews
Location		
Latitude (degrees)	41 N	44 N
Longitude (degrees)	127 E	122 W
Elevation (m)	500–1100	300–1550
Climate		
Mean annual temperature (°C)	3.9*	8.5†
Mean annual precipitation (mm)	782*	2300†
Actual evapotranspiration (mm)	673*	530†
Soil		
Type	Brown forest‡	Typic dystrochrepts§
Parent material	Volcanic‡	Volcanic§
pH	5.3–6.5‡	5.2–5.8§
C:N	15–25‡	14–23§
Trees		
Dominant species	*Acer mono*‖	*Pseudotsuga menziesii*¶
	Betula costata	*Thuja plicata*
	Pinus koraiensis	*Tsuga heterophylla*
	Tilia amurensis	
Above-ground biomass (Mg/ha)	206–383#	492–976**
Age (years)	>160	450

*Chi ZhenWen et al. (1981).
†McKee and Bierlmaier (1987).
‡Chen BoRong et al. (1981).
§Brown and Parsons (1973).
‖Wan Zhang et al. (1980).
¶Dyrness et al. (1976), Waring and Franklin (1979).
#Xu ZhengBan et al. (1985).
**Grier and Logan (1977).

Decay-rate constants

We used the single exponential model (Olson 1963) to compare the least and most decay-resistant dominant species at each site: *Tilia amurensis* and *Pinus koraiensis* at Changbai and *Tsuga heterophylla* and *Pseudotsuga menziesii* at the Andrews. As a first step, we calculated the respiration and leaching losses from changes in log density (Lambert et al. 1980). At Changbai, where logs decay rapidly, rates were 0.027/yr for *Tilia* and 0.016/yr for *Pinus* (Chen 1989; Figure 1). At Andrews, the decay rate for *Tsuga* was 0.016–0.018/yr and, for *Pseudotsuga*, 0.005–0.010/yr (Graham 1982, Means et al. 1986, Sollins et al. 1987).

The exact cause of differences in decay rate is difficult to assess because rates can be affected by temperature, moisture, substrate quality, and size (Harmon et al. 1986). *Pseudotsuga* probably decays more slowly than other species because its heartwood contains fungi-toxic compounds (Scheffer and Cowling 1966). *Pinus* and *Tsuga* logs of comparable size had similar decay rates at the two sites, although *Pinus* elsewhere is generally more resistant to decay (Scheffer and Cowling 1966). Mean temperature at Changbai (3.9° C) is considerably less than at Andrews (8.9° C), which should slow mineralization rates. The higher turnover of coarse woody debris at Changbai may be due to Changbai receiving one-third the precipitation of Andrews. In examining decomposition of *Abies* and *Tsuga* in the western United States, Harmon et al. (1987) found an inverse relationship between decay rate and annual precipitation, perhaps because the fungi responsible for decomposition are obligate aerobes and excess moisture reduces aeration (Griffin 1977).

Fragmentation is another significant factor in the loss of coarse woody debris, yet its importance in the transfer of organic matter and nutrients remains unexplored. Large pools of wood fragments reside in coniferous forest floors (McFee and Stone 1966, Sollins et al. 1987). For example, Little and Ohmann (1988) found that decayed wood comprised 5–70% of the forest floor in *Pseudotsuga-Tsuga* forests.

Although wood fragments are not lost from the ecosystem, they are lost from the coarse woody debris pool as traditionally measured, making the analysis of decomposition of coarse woody debris complex. The decay rates discussed above overestimate the lifespan of coarse woody debris,

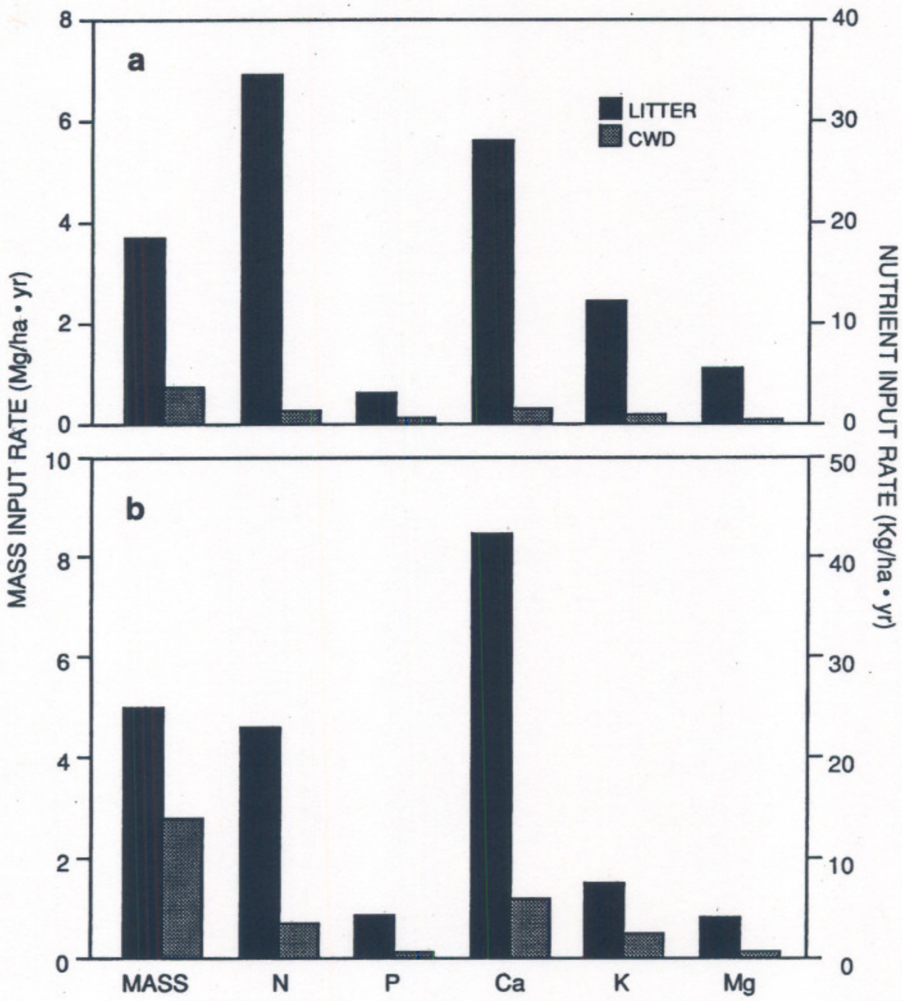

Figure 1. Return of organic matter ($Mg \cdot ha^{-1} \cdot yr^{-1}$) and selected nutrients ($Kg \cdot ha^{-1} \cdot yr^{-1}$) to the forest floor by litter and coarse woody debris (CWD) at (**a**) Changbai and (**b**) Andrews.

unless wood fragments decompose at a similar rate.

Assuming that the mass of coarse woody debris is in a steady state, the input rate can be used to estimate a decay rate that includes fragmentation (Lambert et al. 1980, Sollins 1982). The ratio of input to standing crop indicates a total decomposition rate of 0.039/yr for *Tilia* and 0.023/yr for *Pinus* at Changbai. The difference between rates calculated by density changes and by input to standing crop ratios gives an estimate of the contribution of fragmentation to the overall mass loss (Lambert et al. 1980). This calculation indicates that 30% of the mass of coarse woody debris from these species is lost via fragmentation.

The ratio of input to standing crop for all species at Andrews indicates a total decomposition rate of 0.011–0.016/yr. This ratio was 0.03/yr in a Washington old-growth *Pseudotsuga-Tsuga* forest (Sollins 1982). Because these total rates are approximately twice those calculated from density changes, it would appear that half the losses from coarse woody debris in Pacific Northwest forests is from fragmentation. Direct estimates of fragmentation in *Pseudotsuga* and *Tsuga* logs indicate as much as 57% of coarse woody debris mass is lost via fragmentation (Graham 1982).

Mass of coarse woody debris

As might be expected from the lower input and faster decay rates, there is considerably less coarse woody debris at Changbai than at Andrews (Table 2). There are three times the number of logs at Andrews compared with Changbai, but projected cover and mass are more than 12 times greater because the logs at Andrews are larger. Other old-growth coniferous forests store considerably more coarse woody debris than is found at Andrews. In the cool, wet Olympic National Park, *Pseudotsuga-Tsuga* forests have 537 Mg/ha coarse woody debris (Agee and Huff 1987). In *Sequoiadendron* and *Sequoia* forests in California, coarse woody debris mass is more than 200 Mg/ha (Bingham and Sawyer 1988, Harmon et al. 1987). In contrast, *Pinus* forests have only 29–42 Mg/ha of coarse woody debris (Fahey 1983, Harmon et al. 1987).

At Changbai, the mass of coarse woody debris is relatively low compared with that of other old-growth deciduous forests. In a *Fagus-Betula* forest in New England, coarse woody debris mass ranged from 30–49 Mg/ha (Gore and Patterson 1986, Tritton 1980), and was more than 29 Mg/ha in a *Fagus-Betula* forest in Tennessee (Harmon et al. 1986). Warmer deciduous forests dominated by *Quercus* or *Acer* generally contain less coarse woody debris than do *Fagus-Betula* forests, although amounts of 20–25 Mg/ha have commonly been observed (Harmon et al. 1986, Muller and Yan 1990, Onega and Eickmeir 1990).

Coarse woody debris and nutrient cycles

Nutrient cycles within dead wood are still poorly understood, but a primary role of woody debris may be to stabilize nutrients after major natural disturbances. During periods of normal mortality, coarse woody debris adds fewer nutrients to the forest floor than does fine litter at both Changbai and Andrews (Figure 1), primarily due to its lower nutrient content. During periods of catastrophic mortality, this lower nutrient content is offset by the large mass of coarse woody debris input.

An important feature of woody debris is that nutrients are released at slower rates than from fine litter (Chen 1989, Foster and Lang 1982, Grier 1978, Lambert et al. 1980, Sollins et al. 1987). This slow release allows nutrients to be retained within the ecosystem until tree production

Table 2. Mass and nutrient storage in coarse woody debris.

Parameter	Changbai*	Andrews†
Number of pieces per hectare	90–118	346
Projected area (%)	1.3–2.0	15.2–25.4†
Total mass (Mg/ha)	7.9–16.2	143‡–215§
Aboveground detritus (%)	39–56	74‡–81§
Dead:live tree mass	0.04–0.07	0.20–0.30
Nutrient storage (kg/ha)		
Nitrogen	27–33	199‡–298
Phosphorus	3.7–6.3	9.1‡–13.6
Calcium	33–38	218‡–326
Potassium	2.7–3.9	30.7‡–46
Sodium	1.4–2.8	4.9‡–7.4

*Chen (1989).
†Harmon et al. (1986).
‡Sollins et al. (1987).
§Grier and Logan (1977).

recovers (Figure 2). Timber harvest and salvage after disturbance reduces this pool of stable nutrients, but it is not clear how this affects the long-term productivity and stability of ecosystems.

Few studies have examined processes, other than nitrogen fixation, that are responsible for net changes in nutrient content of coarse woody debris (Sollins et al. 1987). It is tempting to assume that the processes are the same as in fine litter, but recent research being conducted at Andrews indicates some differences. For example, during the early stages of log decomposition, fungal sporocarps transfer nutrients to the forest floor.[1] Thus, in fine litter, fungi immobilize nitrogen, but in coarse woody debris they actively transfer it to the soil.

Another important consideration in understanding nutrient release from coarse woody debris is that tree boles are composed of several distinct substrates. While wood may be slowly releasing nutrients, other parts such as the inner bark (phloem) decompose and release nutrients at rates similar to those of leaf litter. Hence an overall pattern of release from dead trees may be a rapid loss of 10–20% of the nutrients followed by an extended slower release of nutrients.

Finally, the role of fragmentation in transferring nutrients to fine litter in the later stages of woody debris decomposition is not revealed by patterns of net accumulation. The omission of transfers via fragmentation from previous calculations suggests that coarse woody debris may release nutrients faster than is generally supposed (Sollins 1982).

Global carbon stores in coarse woody debris

Past efforts at estimating global detrital storage (including litter, coarse woody debris, and soil organic matter) have assumed that only a small fraction of carbon is stored in coarse woody debris (Post et al. 1982, Schlesinger 1977). This assumption, at least for old-growth forests, is a mistake. Given the lack of data on the mass of coarse woody debris in various biomes, global carbon storage in woody debris cannot yet be directly estimated.

An alternative approach is to calculate a conversion factor from some better-understood ecosystem component, such as above-ground detritus, total detritus, or tree biomass. Data from Changbai and Andrews give an idea of the range of these conversion factors and the mass of coarse woody debris in temperate forests (Figure 3). Although the amount of woody debris in forests varies with forest age and type of management (i.e., slash-and-burn agriculture versus intensive forestry), it is impossible to take these factors into account without detailed land-use data. Our estimates of coarse woody debris mass are, therefore, for undisturbed forests and represent a potential maximum.

Coarse woody debris forms from 39% to 56% of total aboveground detritus (i.e., litter, fine wood, and coarse woody debris) in Changbai and from 74% to 81% at Andrews. These percentages appear fairly typical of what is known from the limited number of old-growth stands that have been examined (Agee and Huff 1987, Grier 1978, Lang and Forman 1978, Tritton 1980). Based on the areal extent of temperate deciduous and coniferous forests in Whittaker and Likens (1973) and the mean forest-floor mass presented by Vogt et al. (1986), we estimate that temperate forests contain 16×10^{15} g carbon as litter. From the range of proportions of coarse woody debris to total aboveground detritus observed for Changbai and Andrews, this gives an estimate of $10–68 \times 10^{15}$ g carbon as coarse woody debris.

Assessing coarse woody debris as a fraction of total detritus (i.e., litter, coarse woody debris, and soil organic matter) is difficult given the small number of old-growth forests with

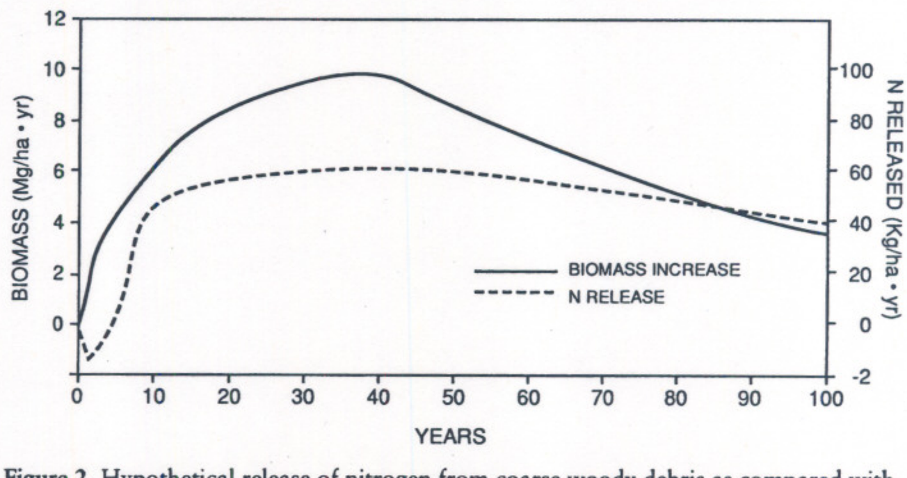

Figure 2. Hypothetical release of nitrogen from coarse woody debris as compared with rates of biomass accumulation for a *Pseudotsuga-Tsuga* forest catastrophically disturbed by wind. Nitrogen content of coarse woody debris is based on Sollins et al. (1987). The pattern of forest regrowth is based on Turner and Long (1975).

[1]M. E. Harmon, unpublished data.

total detrital inventories. Changbai, with 5.8% of total detritus in coarse woody debris, appears to represent the low end of the scale. *Quercus* forests are similar, with 9% of the total detritus in coarse woody debris (Lang and Forman 1978). However, other deciduous forests such as *Fagus-Betula* of New England have 29% of the total detritus in coarse woody debris (Tritton 1980). More than half of the total detritus (54%) at Andrews is in coarse woody debris, a larger percentage than occurs in other conifer forests (Fahey 1983, Grier 1978). Post et al. (1982) estimated the storage of litter and soil organic matter for temperate forests at 104×10^{15} g carbon. If coarse woody debris comprises 5.8% of the total detritus, as at Changbai, then coarse woody debris mass is 6.4×10^{15} g carbon. If, however, the fraction of total detritus is closer to that for Andrews, then the mass in coarse woody debris is 122×10^{15} g carbon. This latter estimate seems extremely high, indicating that coarse woody debris to total detrital ratios may be an unreliable conversion factor. If ratios for other Pacific Northwest forests are used, we calculate a maximal coarse woody debris storage of 28–58 $\times 10^{15}$ g carbon (Grier 1978, Grier et al. 1981).

Given the lack of information on total detrital storage in ecosystems, the ratio of coarse woody debris to live tree mass may give a better estimate of coarse woody debris mass. This ratio is 0.04–0.07 for Changbai and 0.2–0.3 for Andrews. In a *Fagus-Betula* forest the ratio is 0.20 (Tritton 1980) and 0.23 in *Tsuga-Picea* forests (Grier 1978). This range of coarse woody debris to live tree ratios also appears to be typical of tropical forests. Ratios of 0.04 in a moist (Edward and Grubb 1977) and 0.25 in a dry tropical forest (Whigham et al. in press) have been observed.

Assuming that 80% of the live-plant biomass values for temperate forests presented by Whittaker and Likens (1973) is above-ground wood, $5\text{–}40 \times 10^{15}$ g carbon could be stored as coarse woody debris. Because the ratio of live to dead wood appears to be more constant than the fraction of detritus that is coarse woody debris, these estimates are probably more reliable. Assuming a similar range holds for other forested ecosystems, the underestimate of global detritus is in the range of from $25\text{–}180 \times 10^{15}$ g carbon, or 2–10%.

Our final estimate of carbon stores in coarse woody debris is based on the ratio of coarse woody debris production and living tree biomass. The steady-state mass, given these levels of production, can be calculated by dividing input by the decay rate (Olson 1963). At Changbai, mortality averaged 0.18% of living mass, whereas at Andrews it amounted to 0.55% of the living mass. This range of living-tree turnover and the biomass values from Whittaker and Likens (1973) indicate that coarse woody debris production could range from 0.25 to 0.76×10 g carbon/yr. If decay rates (including fragmentation) are as high as at Changbai, then a steady-state value of $6\text{–}20 \times 10^{15}$ g carbon would result. On the other hand, if decay rates are as low as at Andrews, then a range of $25\text{–}76 \times 10^{15}$ g carbon would be stored by coarse woody debris.

Recent studies of the global carbon cycle indicate that a terrestrial ecosystem sink of $1.0\text{–}2.6 \times 10^{15}$ g carbon/yr is required to account for observed atmospheric increases (Post et al. 1990). As organic matter in the soil stores a large fraction of terrestrial carbon, a small increase in storage might account for this sink. However, production of refractory humus substances in soils was estimated to sequester no more than 0.4×10^{15} g carbon/yr, an amount considered too low to account for the terrestrial sink (Schlesinger 1990).

A large Douglas fir snag with green western hemlock seedlings in Olympia National Park.

Although, given the data available,

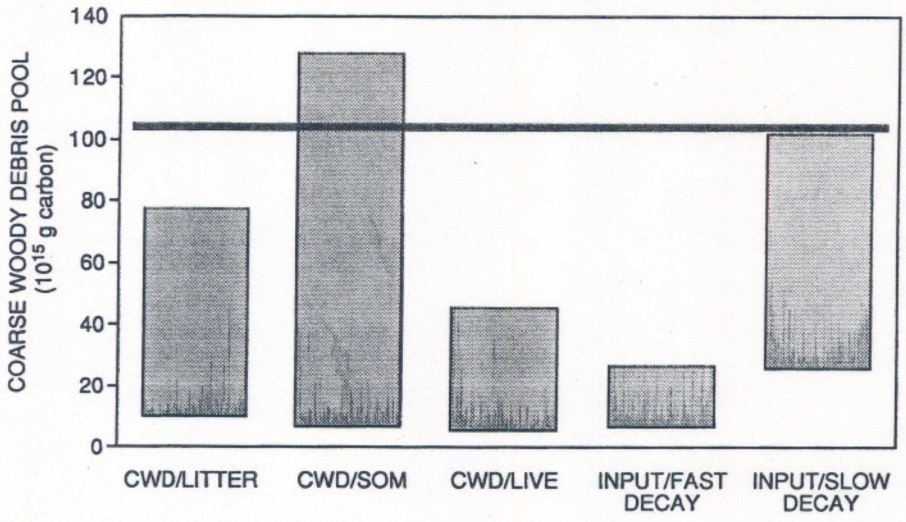

Figure 3. Range of estimates for maximal coarse woody debris carbon stores in temperate forests. In each case, the range of conversion factors for Changbai and Andrews was used to derive estimates. Decay rates of 0.039/yr and 0.01/yr were used to calculate the input/fast decay and input/slow decay. The horizontal line indicates soil organic matter (SOM) stores of temperate forests (Post et al. 1982).

we are unable to estimate the amount of carbon that might be sequestered by coarse woody debris, it is likely to be a large quantity. Our analysis shows that, by excluding coarse woody debris, previous studies have substantially and systematically underestimated detrital carbon. Our estimates are for maximal storage; the actual storage is lower because forest harvest and land clearing remove substantial amounts of coarse woody debris.

When allowed to regrow, however, forests begin to accumulate carbon in both living and dead wood. Successional studies of coarse woody debris stores (Gore and Patterson 1986, Spies et al. 1988, Tritton 1980) and input rates (Harcombe et al. 1990, Tritton 1980) indicate that stores of coarse woody debris reach a steady state decades to centuries after living wood. Thus models of forest recovery that exclude dead wood may not account for a substantial amount of carbon that is being absorbed by recovering forests in the later stages of succession.

Conclusions

A comparison of coarse woody debris dynamics and mass in two old-growth temperate forests in the Pacific Northwest and in China indicates that previous amounts of detrital carbon may have been underestimated by 5–75%. From the data at hand, the contribution of coarse woody debris to global detrital storage cannot be determined with certainty, but given the current pattern of forest regrowth in temperate forests, a large fraction of the currently hypothesized terrestrial sink could be associated with coarse woody debris accumulation. This large range of uncertainty will not be resolved until the dynamics and stores of coarse woody debris are considered in a wider range of biomes.

Acknowledgments

We gratefully thank Xu ZhengBan, Zhao Sidong, Dai HongCai, Wan Zhang, Yan Fazhu, Zhan Sujuan, Zhan Dilan, Gao Zhiqing, Su Jai, Yin Xiaodong, Geng Xiaoyuan, Shao Guaofan, Cheng Borong, and the staff of Changbai Mountain Research Station of Forest Ecosystem, Academia Sinica for their help. We also thank Philip Sollins for sharing information on nutrient stores at Andrews Experimental Forest. The research was supported by grants from the National Science Foundation (BSR8516590, BSR-8514325, BSR-8918643), Man and Biosphere Program, and Pacific Northwest Research Station US Forest Service. This is paper 2620, Forest Research Laboratory, Oregon State University, Corvallis.

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