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The Ecological Role of Coarse Woody Debris

An Overview of the Ecological Importance of CWD in BC Forests

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BRITISH COLUMBIA

Ministry of Forests Research Program

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Victoria Stevens

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Compiled by
Victoria Stevens
for
B.C. Ministry of Forests
Research Branch
31 Bastion Square
Victoria, B.C.   V8W 3E7

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B.C. Ministry of Forests
Forestry Division Services Branch
Production Resources
595 Pandora Avenue, 1st Floor
Victoria, B.C.   V8W 3E7

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CONTENTS

1 INTRODUCTION

The approach taken by the Forest Practices Code *Biodiversity Guidebook* is that given our incomplete knowledge of the quantity and identification of species in the ecosystems of B.C., biodiversity is more likely to be sustained if managed forests are made to resemble those forests created by the activities of natural disturbance agents such as fire, wind, insects, and disease. There is wide realization that the preservation of species and the ecological functions that link them must take place both inside and outside of reserves and that it is more efficient than a species-by-species conservation effort (see Walker 1994). This paper describes what is known about the contribution to ecosystems of large pieces of dead down wood. Much of this information was compiled by Harmon et al. (1986).

The living parts of a natural forest can be viewed as having two important phases—the building phase during which available elements are assembled into structures we know as plants and animals, and the deconstruction phase during which these structures are disassembled into pieces available for rebuilding. We call these the living and decaying parts of the whole life-and-death cycle; however, both the living and decaying processes involve living organisms. One of the roles of the growing organisms is to build structure, while one of the roles of the decay organisms is to break down structure. Both phases are essential to the ecological processes that have evolved in forests. These processes include the life cycles of vertebrates and invertebrates (wildlife), fungi and bacteria, and the strategies used by plant structures to accumulate nutrients. All living organisms in forests have finite life spans after which they become part of the decaying portion of the ecosystem. Soft-bodied organisms and small plant structures generally decay rapidly and provide a quick turnover of nutrients, an addition to the forest floor, and/or a meal for forest wildlife. Large woody material contains very significant stores of carbon and energy and is the foundation of an important forest food web. This large material usually decays more slowly and therefore provides a more steady input of energy and nutrients and longer-lasting structures. For example, approximately half of the time that a mature Douglas-fir tree is in an ecosystem, it is dead wood. This paper describes the ecological role of the larger, down pieces of wood in both the living and decaying processes in the forest. These pieces are referred to as coarse woody debris (CWD).

2 DEFINITION

Coarse woody debris is defined in the literature in many ways. As this review provides background information for decision-making under the Forest Practices Code of British Columbia, the definition from the *Biodiversity Guidebook* (p. 74) will be used as the starting point for a working definition. Coarse woody debris is:

> Sound and rotting logs and stumps that provide habitat for plants, animals and insects and a source of nutrients for soil development. Material generally greater than 8–10 cm in diameter.

The New Vegetation Inventory (NVI) defines CWD as "[T]he larger dead and mostly down woody material which is in various stages of decomposition." In a more detailed description following this definition, the NVI includes pieces > 7.5 cm and overturned stumps < 1.3 m with attached roots, or > 1.3 m without roots. It excludes self-supporting, dead and upright, rooted stumps. The major difference in the two definitions is that the *Biodiversity Guidebook* includes rooted stumps whereas the NVI excludes them. Assuming they are not living, stumps fulfill most of the functions described below and will therefore be included. The NVI sets a lower size limit for CWD that will be adopted in the working definition for consistency.

Neither of these definitions considers the below-ground component that can account for up to 20% of the rotting wood on a site. Because of the importance of this component, particularly to soil structure, nutrient cycling and habitat for soil organisms, an addition to the working definition is suggested (although it is recognized that this component will not be sampled as frequently as the above-ground component). Additions are in italics:

> Sound and rotting logs and stumps, *and coarse roots in all stages of decay*, that provide habitat for plants, animals and insects and a source of nutrients for soil *structure and* development. Material generally greater than 7.5 cm in diameter.

3 ECOLOGICAL ROLES

The importance of coarse woody debris in forests, including those of British Columbia, has been partially documented, although much remains to be discovered. What is known of these roles is divided into four, inter-related categories:

- the role in productivity of forest trees;
- the role in providing habitat and structure to maintain biological diversity;
- the role in geomorphology of streams and slopes; and
- the role in long-term carbon storage.

The importance of each of these roles to an ecosystem varies throughout the province by natural disturbance type, biogeoclimatic zone and moisture regime. The following discussion is general and outlines the important roles that could be played by CWD.

3.1 The Role in Forest Productivity

To a greater or lesser degree, depending on the moisture and temperature regimes of an ecosystem, CWD may

- add a significant amount of organic matter to the soil;
- provide habitat for decomposer organisms;
- retain moisture through dry periods, providing a refuge for ectomycorrhizal roots and their associated soil organisms;
- provide a site for asymbiotic or associative nitrogen-fixing bacteria;
- represent a capital pool of nutrients for the ecosystem;
- provide a site for the regeneration of conifers; and
- contribute to soil acidification and podzolization.

3.1.1 Accumulation of organic matter All size classes of decaying pieces of wood contribute to the long-term accumulation of organic matter because the lignin and humus of well-decayed wood are high in carbon constituents (Maser et al. 1988). In the dry, inland forests of the Pacific Northwest of the U.S. (comparable to parts of the IDF, ICH, ESSF, PP, SBS, BWBS and MS), woody material is the most important organic material added to forest soils during a stand rotation (Harvey, et al. 1981). It improves the moisture-carrying capacity and structure of the soil. To protect the productive potential of a forest soil, a continuous supply of organic materials must be maintained.

> Without an adequate soil base, the potential for a good tree crop simply does not exist (Harvey et al. 1981).

3.1.2 Ectomycorrhizal root tip associations Ectomycorrhizal activity has been found to be essential to the healthy growth of conifers. This activity is a moisture-dependent phenomenon (Harvey et al. 1983). Both diameter and state of decay affect the ability of down wood to hold moisture. In the Pacific Northwest, the moisture content of a decaying Douglas-fir tree bole increased as the decay class increased until at about decay class IV the moisture content in summer was 250% of the dry weight (Maser et al. 1988). All size classes of decaying wood act as a moisture store and provide refugia for tree roots and ectomycorrhizal fungi during dry periods; however, the larger pieces can hold more water and are therefore more effective at holding moisture and acting as refugia through long, dry spells. When moisture returns to the site, it is a much faster process to reinvade the organic layer of soil with ectomycorrhizal root tips when refugia are scattered throughout the forest floor. Wood is only a moderate source of nutrients, but usually occurs in sufficient volumes to be a significant source of moisture (Harvey et al. 1986).

3.1.3 Nitrogen fixation Dry forests on the east side of Vancouver Island and in the interior tend to be nitrogen limited from a forest manager's point of view (Trofymow, pers. comm.; Harvey et al. 1987). There are four natural sources of nitrogen:

1. precipitation that collects nitrogen from electrical discharge (lightning), dust, pollen and air pollutants;
2. symbiotic nitrogen fixation by actinomycetes that are associated with root nodules on species such as red alder, *Shepherdia canadensis*, and *Ceanothus*;
3. nonsymbiotic (or symbiotic) nitrogen fixation by free-living, nitrogen-fixing bacteria that occur in soil and plant residues, and
4. associative nitrogen fixation.

Symbiotic N fixation is the most efficient, putting many times more N into the system than any other means (Kimmins pers. comm.; Harvey et al. 1987), but in some interior forests there are few known nodulated species, especially after many years of fire suppression. These ecosystems rely primarily on nonsymbiotic sources of nitrogen. On the coast, the primary nodulated species (red alder) can only grow in early stages of succession, and thereafter the ecosystem may benefit from nonsymbiotic N in decaying wood. Although itself low in nitrogen, by hosting the bacteria responsible for nonsymbiotic nitrogen fixation, CWD is a significant contributor of nitrogen in some ecosystems. Harmon et al. (1986) summarized the available studies and found that in a range of forest ecosystems with a CWD biomass ranging from

50–113 Mg (mega-grams = 10^6) CWD/ha, there was a range of asymbiotic nitrogen fixation of 0.3–1.4 kg/ha/year.

An important component of interior forests are the lichens such as the arboreal *Lobaria* spp. and the terrestrial *Peltigera* spp. These lichens are an association between a fungus and a nitrogen fixing blue-green algae. Although the blue-green algae can survive and fix nitrogen independently, a symbiosis is established whereby the fungi provide a more stable habitat and benefit from the nitrogen fixed by the algae.

3.14 Nutrient pool CWD can also contribute to nutrient storage. This includes the nutrients accumulated in the woody bole, large branches, roots and stumps during tree growth and the nutrients added from litterfall and throughfall (rain falling through the forest canopy) being intercepted by a down log rather than falling on the forest floor. If the nutrients are added faster than they are leached out by rain, the result is positive nutrient storage. As the wood decays, the nutrients are added to the available pool. Mechanisms for removing the nutrients from CWD and adding them to the available pool vary. Harmon et al. (1994) found that during early stages of decomposition, fungal sporocarps (mushrooms) growing on decaying logs increased the concentrations of nitrogen, potassium and phosphorous 38, 115 and 136 times, respectively, over the concentrations found in the logs. When these mushrooms fall off the logs and decay, they are returning nutrients from the downed wood into the available nutrient pool. Arthropods and earthworms digest the complex, organic molecules in down wood with the help of micro-organisms in their digestive systems and return the nutrients to the forest in their frass. Thus, CWD can be a reliable and steady source of nutrients over more than 100 years. When coarse woody debris is added to the ecosystem at regular intervals and is well distributed, it represents a long-term source of nutrients.

3.1.5 Regeneration In some wet ecosystems, the tree seedlings with the best chance of success are those that germinate on large pieces of woody debris (Harmon et al. 1986). The understorey is so thick in these ecosystems that no light is available to seedlings on the forest floor. The decaying woody boles provide a platform for successful germination and growth.

In some wet, riparian forests in the montane spruce zone, researchers found that germination only occurred on the hummocks of very decayed wood (Gyug 1996). Other sites in these forests are too wet to allow germination.

The root mats of fallen trees and the spaces within a matrix of fallen trees can provide refugia from ungulates for some favoured shrub species. Schreiner et al. (1996) found that on the valley bottoms of the Sitka spruce–western hemlock forests in Olympic National Park, these refugia were the only places where some shrub species could flower and set seed. Outside of the refugia, the browsing pressure was too high.

3.1.6 Soil biology Forests grow in soil. The health of the soil is reflected in the health of the forest. Soil health is a result of the myriad of biological organisms and interactions that are a part of the forest ecosystem we call soil. This involves soil arthropods, fungi, bacteria, animal waste and among other things, decaying wood. There are many more species and interactions than we currently know, but the strategy for assembling available nutrients into parts of a forest ecosystem is present in all natural forests. These pieces and processes may differ between ecosystems, depending on both biotic and abiotic components available. Removing large portions of decaying wood may alter the components of a forest that are part of the place-specific, evolutionary history that has resulted in processes and interactions essential for maintaining that forest.

In forests, both the nutrients and the means of acquiring them are highly dependent on the presence of organic soil components.

> Protection or enhancement of the forest soil's organic mantle, via manipulation of woody residues and other organic soil components, provides a major tool for impacting growth in forest ecosystems. In many ways, manipulation of the organic constituents of soils is the only practical tool available for mitigating effects of harvesting systems that remove most of the standing crop or that cause extensive soil disturbance (Harvey et al. 1987, p. 10).

3.2 The Role in Providing Habitat (Maintenance of Biodiversity)

There is no doubt that coarse woody debris plays an important part in creating habitat for many species of plants and animals in B.C. What is known of the ecological value of CWD to wildlife and plants has been summarized in many places (Caza 1993; Harmon et al. 1986; Lofroth 1995; Maser et al. 1988). Lofroth (1995) has put together tables of wildlife associated with CWD in B.C. These and others are provided in Appendix 1. Of these species, 11 are known to be at risk in the province. In terrestrial systems, down wood provides:

- sites for nests, dens and burrows;
- habitat for microbial decomposers (e.g., bacteria, fungi and actinomycetes);
- a primary energy source for a complex food web;
- hiding cover for predators and protective cover for their prey;
- moist microsites (e.g., for amphibians, insects, worms, plants, ectomycorrhizal fungi and tree roots);
- travel-ways across streams, across the forest floor, beneath and through the snow; and
- refugia during disturbance and environmental stress (e.g., low moisture and temperature extremes).

In aquatic systems:

- structure to slow stream flow and create pools;
- places for food to accumulate; and
- cover from temperature extremes and predators.

There is a lot of literature on the subject of CWD as habitat (see Caza 1993; Lofroth 1995). The following are a few examples of CWD use by a some species types.

3.2.1 Small mammals Coarse woody debris provides a structural link with the previous stand in some natural disturbance types, and as such provides continuity of habitat for some species (Hansen et al. 1991). Carey and Johnson (1995) reported that along with understorey vegetation, CWD is the most important habitat factor for small mammals. Several studies in B.C. have linked small mammals to CWD for nesting, cover and travel-ways (Craig 1995; Carter 1993). Healthy small mammal populations help to sustain the ecological processes in which they are an integral part (e.g., the dispersal of seeds and mycorrhizal fungi spores, the maintenance of healthy predator populations, and the control of potentially harmful invertebrate populations).

3.2.2 Arthropods Arthropods are one of the most diverse groups of animals and one of the least understood. Many forms associated with old forests are flightless (Lattin and Moldenke 1990). Flightlessness is one result of habitat stability. For these species, the need to recolonize new habitats because of frequent disturbance has been eliminated. The practice of clearcut logging is a disturbance that is not part of the evolutionary history of these insects. In the western Cascades of Oregon, where 90% of the total soil arthropods were destroyed by clearcutting and burning, many species were able to survive within and under decaying logs (coarse woody debris) (Moldenke and Lattin 1990).

Downed logs are also an important colonizing substrate for ants. These ants are ecologically significant members of the forest community, acting as agents of wood decay, as a prey species for pileated woodpeckers, and as predators of spruce budworm. In a recent study by Torgersen and Bull (1995), approximately one-third of the down wood log sections contained budworm-foraging ants. This translated to 92 colonies of budworm-foraging ants per hectare in a mixed conifer stand in northeastern Oregon.

Soil microarthropods, although largely unidentified, are the most important arthropods in terms of their impact on nutrient cycling. Groups of them associated with CWD have been shown to increase the availability and suitability of organic particles for decomposer communities (Norton 1990 in Nadel 1995), and contribute to nutrient cycling and soil formation (Behan-Pelletier 1993 in Nadel 1995; Setälä and Marshall 1994).

The variability in coarse woody debris contributes to the diversity of decay organisms in the province. The diversity in B.C. that results from its size, proximity to the Pacific Ocean and topography creates forests with widely different characteristics, including CWD characteristics. In addition to the more obvious differences related to size and species, each piece is in a different stage in the decay cycle. It can take > 1000 years for the complete decay of large individuals of some tree species in some ecosystems (Daniels et al., in prep.). The stages of decay create varied habitats over time that are used by a variety of organisms. Arthropod invaders inoculate their tunnels with fungi, bacteria, phoretic mites, nematodes and protozoans (Parsons et al. 1991). Later, beetles that feed on sapwood and heartwood tunnel deeper into the log-opening access for other arthropods and micro-organisms. These processes involve hundreds or possibly thousands of species and are a critical link in the carbon and nutrient cycles in the forest.

3.2.3 Nonvascular plants and fungi Many species of nonvascular plants and fungi are associated with CWD. The diversity of these species is related to the diversity of substrates, including a variety of decay stages, and has been linked to forest health (Amaranthus et al. 1994; Crites and Dale 1995). Variability in piece size contributes to this diversity. Some bryophytes and fungi are restricted to very large pieces (Soderstrom 1988, 1989; D. Luoma, pers. comm.). In B.C., diversity is also linked to recent glacial history. Fungi are still colonizing the province because of the recent recession of continental glaciers (D. Luoma, pers. comm.).

In Finnish and Swedish forests naturally occurring fungi have been shown to be missing where there is a history of clean logging and a lack of CWD. Forest decline in other parts of Europe has shown a relationship to decreased ectomycorrhizal fungal diversity (Arnolds, 1991 in Amaranthus et al. 1994). Although it is not clear whether the forest decline is a direct result of decreased fungal diversity or if the two are correlated for some other reason, healthy forests typically have a highly diverse ectomycorrhizal flora (Amaranthus et al. 1994). Soil fungi have a diversity of habitats and physiological characteristics, which makes each unique in its requirements and contributions to the ecosystem. This diversity may prove important to the response of forests to rapid, human-caused changes.

> [T]his diversity equips both tree and forests to functionally adapt to changes in season, habitats, assaults by pollution, or climate change, and may be linked to the ability of Douglas-fir to grow well over decades and centuries. (Amaranthus et al. 1994, pp. 2158–59)

At the landscape level, difficulties associated with the maintenance of some nonvascular species that inhabit CWD are similar to those of other species. Spore dispersal is often limited in area, and particularly with lichens, the probability of colonization is greatly reduced when habitat patches are too widely dispersed (M. Harmon, pers. comm.).

3.2.4 Summary The maintenance of the natural diversity of species across B.C., and the ecological processes of which they are a part, will require a realization on the part of forest managers that CWD provides food, shelter, protection, cover, and substrate or climate amelioration for many species. Protected areas alone will not prevent species from becoming at risk or extinct in the next 50 years (Sinclair et al. 1995). Areas of habitat renewal are also critical. Habitat renewal is faster if old forest legacies are left on a site. One of these legacies is coarse woody debris.

3.3 The Role in Geomorphology

The physical properties of large pieces of wood are important to soil and stream geomorphology. Upland sources of coarse woody debris contribute to:

- slope stability;
- soil surface stability, prevention of erosion and control of storm surface runoff; and
- large woody debris loads in streams.

Particularly where there is a significant slope, CWD may play a role in soil stabilization, controlling the flow of water, soil and litter across the forest floor. Material in any decay class, lying across the slope, will reduce soil movement downslope. Larger pieces collect more material on their upslope side, creating a substrate for invertebrate and small-mammal burrowing (Maser et al. 1988) and higher decomposition rates for the debris.

More studies have documented the important role of CWD in the geomorphology of stream ecosystems than in terrestrial ecosystems (see Gregory and Ashkenas 1990). Most large woody debris in streams in NDT1 comes from upland sources, and about 50% in NDT2. Other NDTs have a significant input from forests outside riparian areas (S. Chatwin, pers. comm.). Therefore, CWD outside of riparian areas cannot be overlooked as a contributor to stream ecosystems.

3.4 The Role in Long-term Carbon Storage

Next to fossil-fuel burning, the most critical factor in the increase of CO_2 in the atmosphere is the reduction in carbon storage in our forests (Harmon et al. 1990). The conversion of old-growth forest to young forest increases the CO_2 released, despite the greater uptake of carbon in the young forest, because of the reduced storage capacity of the young forest. In Douglas-fir and western hemlock ecosystems, the detrital components (coarse woody debris + soil organic matter) of the forest store 25–30% of the total carbon in the forest (Harmon et al. 1990). Carbon storage is most important in ecosystems with infrequent catastrophic disturbance regimes (e.g., the coastal and interior wet forests in NDT1or NDT2) or in boreal and sub-boreal (NDT3) forests where soil organic matter increases with latitude. Frequent fires and lower productivity in dry forests keep the carbon storage capacity of these ecosystems naturally low.

Long-term carbon storage is affected by the removal of material from the forest only if, after removal, the carbon is released more quickly than in the decay cycle. Carbon is slowly released by CWD as it decays in the forest. For large, decay-resistant pieces this can take several hundred to more than a thousand years. Wood that is removed from the forest is made into pulp or lumber. Pulp is often a short-term use and therefore cannot be considered carbon storage. If the pulp-derived products go to landfills, they can be stored for a very long time. Recycling paper products can also extend the storage time of pulp-derived products. Under current practices, lumber-grade wood removed from a forest is depleted of carbon in 50 to 100 years (Figure 1).

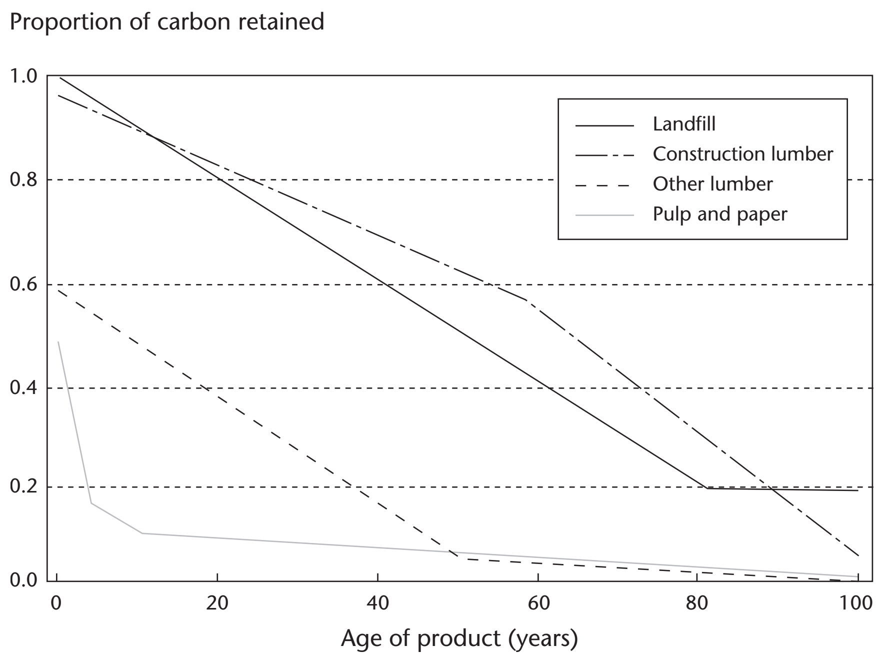

FIGURE 1 *Carbon retention curves for three forest-product categories and for forest products discarded in landfills (from Kurz et al. 1992, p. 33).*

In order to reflect the overall biodiversity management strategy for B.C., natural cycles of CWD input and decay found in the province should be used as a basis for management prescriptions. These will vary within and among natural disturbance types (NDTs), with a general pattern common to each NDT.

This section of the paper will describe the fundamental input and decay processes involved in coarse woody debris dynamics. To assist in understanding these processes, a brief outline of the physical and chemical properties of wood and how they change through decomposition is included. The variations in the overall pattern of input and decay between natural disturbance types identified in British Columbia is described. This leads to the obvious role played by wildlife tree management in the management of CWD. Finally, there is a look at what is required to model the whole process of CWD inputs and decay.

4.1 Physical and Chemical Properties and Processes of Wood

- Wood is composed principally of organic polymers; primarily cellulose (40–50%), hemicellulose (20–35%) and lignin (15–35%); secondary components include tannins, oils and resins.
- Wood has a relatively low mineral nutrient content compared to that in leaf (needle) litter except for Ca.
- Most animals can't break down the complex organic molecules in plant litter. Some animals, such as termites, have symbiotic protozoa in their gut that can break down cellulose.
- Fungi are the primary decomposers of wood as they can produce cellulase and lignase (the foregoing modified from S. Taylor, pers. comm.).

4.2 Input of CWD

CWD comes from large branches, tree tops and whole trees that fall to the forest floor. The following agents are responsible either alone or in concert.

- Wind—both strong winds and more chronic small scale disturbances cause tree damage (broken branches and tops) and stem breakage. This varies with soil depth and moisture content, geographic location, stand structure, tree age, location in a stand, aspect, and tree species. Often wind is the final agent causing a wildlife tree to fall to the ground and become CWD. The original damage to the tree could have been any of the agents below or a combination of them.
- Fire—fire creates CWD directly or by making trees more susceptible to wind, disease, or insect damage.
- Insects—insects can cause tree death directly or weaken a tree, thereby contributing to its death and eventual fall to the forest floor.
- Disease—tree diseases are usually caused by fungi, but parasitic vascular plants and abiotic agents (e.g., acid rain) are also contributors to tree death.
- Suppression and competition—during the course of stand development, stand density is reduced by competition, or self-thinning. Suppressed trees that exhibit slow growth are stressed and susceptible to attack by insects and disease. These trees are typically of small diameter and remain standing until blown down by wind.

- Slope failure—trees may fall due to landslides or erosion of surrounding soil by streams. This is often the cause of input of large organic debris into streams.
- Senescence—old age may contribute to the susceptibility of a tree to insects, disease and/or wind (the foregoing modified from Harmon et al. 1986).

These influences on CWD input vary enormously in time and space, but when viewed broadly, such as within NDTs, patterns are discernible.

4.3 Decay and Material Transfer Processes of CWD

The dynamics of the mass of CWD on a site are affected by decay processes and material transfer processes.

- Fragmentation—fragmentation is the breaking up of CWD into smaller particles. This occurs as insects chew the wood, as vertebrates forage for insects in decaying wood, when partially or fully decayed snags fall, and when decayed wood is disturbed by falling trees, wind, rain or other physical disturbances. Little and Ohmann (1988) found that the forest floor in Douglas-fir/western hemlock forests were 5–70% decayed wood; Keenan et al. (1993) reported that in the forests of northern Vancouver Island, 60% of the forest floor mass was decaying wood (including fragmented and coarse woody debris). Leaching, collapse and settling, and seasoning are all aspects of fragmentation.
- Leaching—leaching (water percolating through the log) dissolves soluble materials. It is less important in early decay classes as most of the material in these classes is not soluble. As the decay process proceeds, decomposers change the polymers into soluble material and leaching becomes more important. In addition, in later decay classes, as fragmentation begins, the importance of leaching increases as the surface-to-volume ratio increases.
- Collapse and settling—as the tree decays, the internal structure becomes weak and settling occurs. This usually increases the contact of the log with the ground, which can increase the activity of microbes, invertebrates and vertebrates at the soil-log interface where there is likely to be increased moisture retention and access for the above organisms.
- Seasoning—seasoning refers to a series of changes, including a decrease in moisture, shrinkage and the formation of cracks that increase access to microbes. Initially, it can harden the outside of a log and reduce its susceptibility to fragmentation and interior moisture losses.
- Transport—transport occurs when material is transported out of an ecosystem by falling down a hill or being carried away in a stream. This varies in importance to an ecosystem, depending on the steepness of the slope and the proximity to a stream.
- Respiration—respiration by organisms in down wood reduces CWD mass by converting the carbon in the dead wood to CO_2.
- Biological transformations—biological transformations are the metabolic transformation of woody material (e.g., to invertebrates or fungi). This process begins while the trees are still standing. In an ongoing, 200-year experiment in Oregon, Harmon et al. (1994) found

that mushrooms growing on down wood after one year on the ground were many times higher in nutrient content than the original concentration in the log. This bioconcentration removes the nutrients from the logs and adds it to the available nutrients in the ecosystem (the foregoing modified from Harmon et al. 1986).

4.3.1 Relationship of size to decay rate Decay rate is faster for fine materials. It decreases with increasing size until the piece is about 20 cm in diameter and then remains approximately constant (M. Harmon, pers. comm.). This varies between species, but the pattern remains the same.

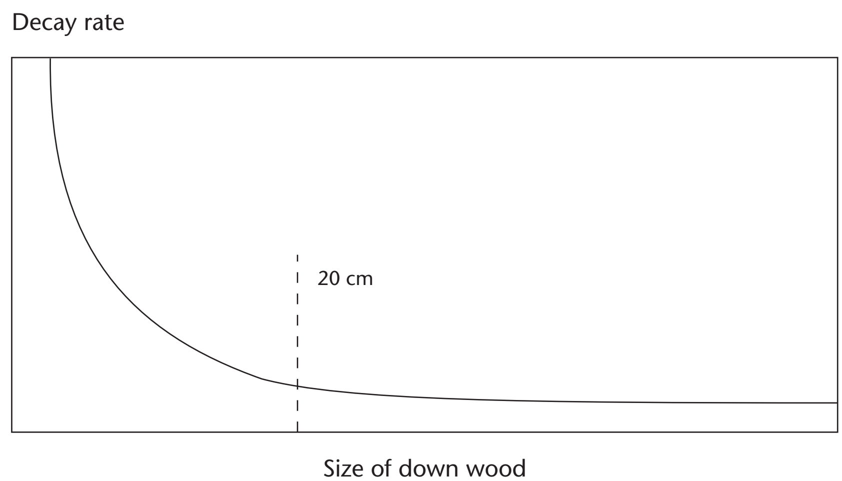

FIGURE 2 *Relationship of decay rate to CWD piece size.*

The rates at which these processes occur are also variable between ecosystems, depending on temperature, moisture, stand history, tree species, and soil organic matter mass and depth.

4.4 Comparison of CWD Input and Decay Patterns in Natural Disturbance Types

4.4.1 NDT1—ecosystems with rare, stand-initiating events (250- to 350-year mean fire return interval) These ecosystems have the most infrequent stand-level disturbance events. In some areas the frequency is so low that the forest can be completely replaced by single, multi-tree gaps before a stand level disturbance occurs (350–950 years) (Lertzman et al. 1996). These forests are characterized by large volumes of CWD of large size with the highest input rates in North America (Caza 1993). Some large pieces can be part of the ecosystem for > 1200 years (Daniels et al. in prep).

As a general rule, Figure 3 describes the pattern of CWD volume in a forest stand. Most measurable canopy or tree attributes of a stand (tree height, canopy cover), begin with low values after a stand-initiating disturbance, but CWD begins at its highest value after such an event. Over the next several decades the CWD decays while the trees grow, but there is little input of CWD (Harmon 1993). Finally, the forest gradually reaches a steady state (decay rate = input rate), where it remains until the next major disturbance.

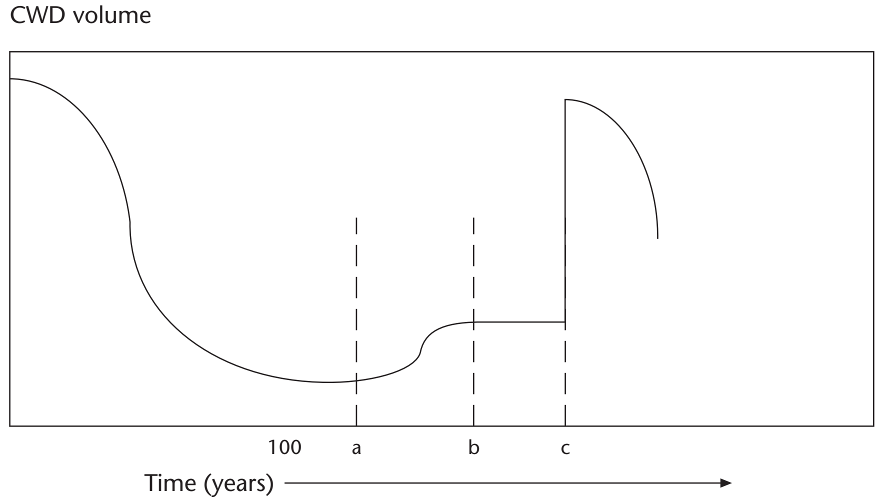

FIGURE 3 *The general pattern of coarse woody debris volume through the life of a stand in NDT1. This diagram uses a broader definition of CWD to include standing dead as well as dead and down. Volume is used in this and following diagrams as a surrogate for mass. The actual volume may remain constant for some time as mass decreases because of the structural characteristics of a log.*
a—the point after a major disturbance at which input begins to exceed decay.
b—the point after a major disturbance at which input and decay are equal and stasis is reached.
c—the point at which the next stand-replacing disturbance occurs.

Gaps are created when trees die or fall. This results in input of CWD to the system immediately or after some unspecified delay. In a study on the west coast of Vancouver Island (CWHvm1) canopy gaps were created by three mechanisms—stem-snapping (42.6%), standing dead tree (33%) and uprooting (24.6%) (Lertzman et al. 1996). Stem-snapping and uprooting add CWD to the system immediately (67% of the tree mortality). The remaining 33% of the trees go through a wildlife tree (snag) stage before falling, in some state of decay, to the forest floor.

Input rates vary widely during the life of a stand. Generally, the stand begins with a large input of CWD and then the input rate drops to near zero for many decades. As the trees grow and suppression and competition begin to cause some tree mortality, the input rate increases. The larger diameter trees of older stands add more to the volume upon falling than the smaller trees of younger stands. Input rates have been reported from 2.4–7 m^3/ha/year in similar, old-growth ecosystems in Oregon and Washington (*Pseudotsuga menziesii* and *Pseudotsuga menziesii—Tsuga heterophylla*). Unfortunately, the sampling periods, which ranged from 2 to 36 years, are not long enough to give a true picture of total input over a stand's history. However, it is a snapshot of the input during the period of time during which it is assumed that the total CWD (input + decay) is in stasis.

Most of the research on decay rates has been conducted in the ecosystems on the west side of the Cascade Mountains of Oregon and Washington that are roughly equivalent to NDTs 1 and 2. A 200-year experiment has been set up in western Oregon to examine many aspects of decomposition (Harmon 1992). From this and other experiments it is known that decay rates are variable for different decay processes (e.g., fragmentation, transformation, respiration), for different parts of a log (e.g., bark, sapwood, heartwood), for different site conditions (e.g., temperature and moisture), and for different species. Temperature can have an effect on decay rates. In a study in Sweden, birch logs decomposed two to four times faster in southern Sweden than in northern Sweden where it is colder (Tamminen 1979 in Samuelsson et al. 1994). Keenan et al. (1993) hypothesize that the cool temperatures on northern Vancouver Island cause slow decay rates, which contribute to the high level of woody debris in those forests.

4.4.2 NDT2—ecosystems with infrequent, stand-initiating events (200-year mean fire return interval) These ecosystems have stand-initiating disturbances with enough frequency to eliminate the long period of stasis beginning at b. Somewhere between a and b, a disturbance causes a large influx of CWD into the system (Figure 4).

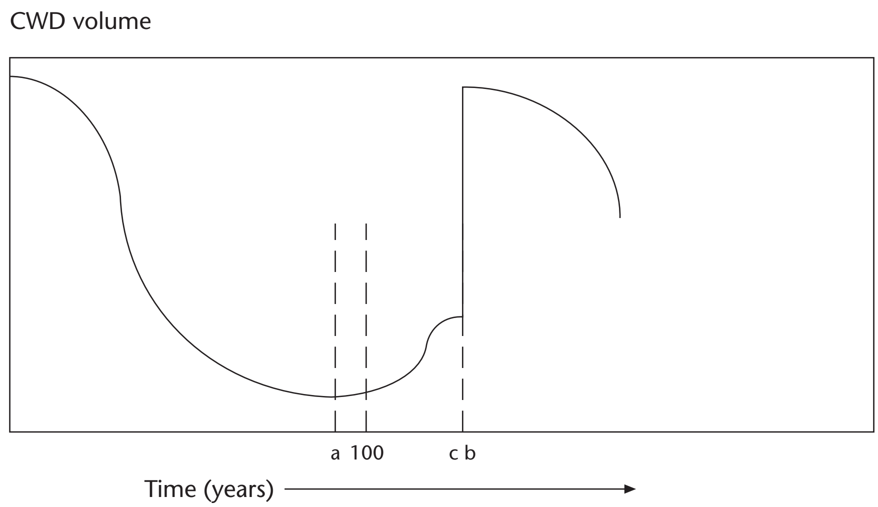

FIGURE 4 *Changes in CWD volume throughout the life of a stand in NDT2.*
a—the point after a major disturbance at which input begins to exceed decay.
b—the point after a major disturbance at which input and decay are equal and stasis is reached.
c—the point at which the next stand-replacing disturbance occurs (the fire or wind frequency).

4.4.3 NDT3—ecosystems with frequent, stand-initiating events (100- to 125-year mean disturbance return interval) These ecosystems, like those of NDT2, rarely, if ever, reach a stasis of input rates and decay rates. They are characterized by densely regenerating stands that provide CWD during the life of the stand by death of seral species and suppression (Figure 5).

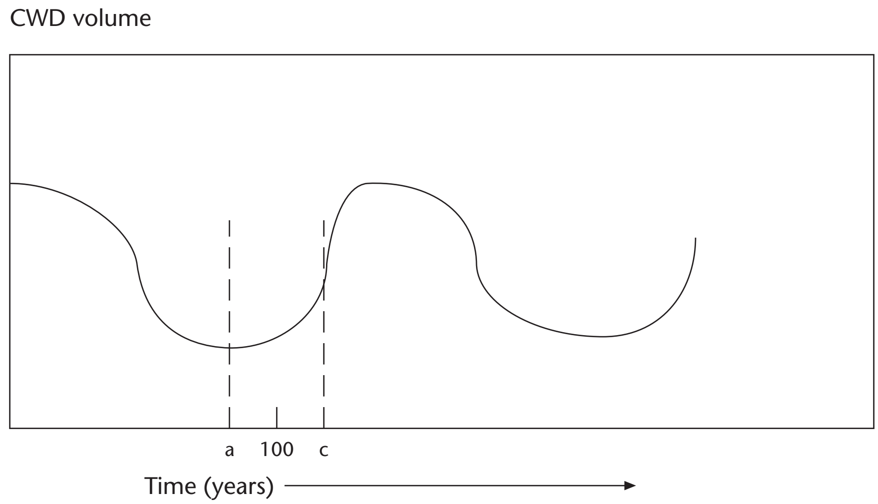

FIGURE 5 *Changes in CWD volume throughout the life of a stand in NDT3.*
a—the point after a major disturbance at which input begins to exceed decay.
c—the point at which the next stand-replacing disturbance occurs (fire, wind or insects).

4.4.4 NDT4—ecosystems with frequent, stand-maintaining fires (surface fire return interval 4–50 years) In the absence of human fire-suppression activities, the CWD in this NDT is kept low by frequent fires that may leave the canopy intact (Figure 6). The low intensity of these surface fires would leave CWD in the early decay stages. Later stages (4 and 5) would burn readily.

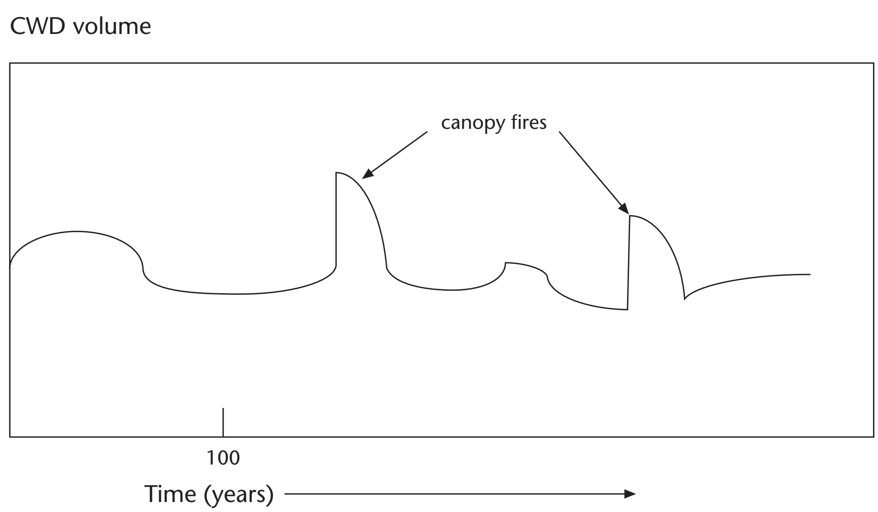

FIGURE 6 *Changes in CWD volume throughout the life of a stand in NDT4.*

4.5 Link Between Wildlife Tree Management and CWD Management

Management recommendations for CWD need to go beyond simply considering the volume of CWD. During the life of a stand, there is CWD input so that a constant mix of decay classes is always present in a stand, and the CWD volume rarely, if ever, drops to zero. Input is often caused by a previously damaged tree (a wildlife tree) falling in the wind. Integrating the wildlife tree recommendations with the CWD recommendations creates a more dynamic system with CWD input during the course of a forest stand's history. The patterns illustrated above can help to provide the guidance to create management recommendations for green tree retention, wildlife tree retention, and CWD retention to build the appropriate model for each NDT.

4.6 Modelling and Management: Information Needs

Models are useful tools for understanding and projecting CWD dynamics. We can use models to increase our understanding of CWD and to identify information needs. However, an identified lack of information does not prevent us from using the models as a foundation for reasonable (i.e., best available) management recommendations.

Basic information for understanding CWD dynamics is needed for most ecosystem types in British Columbia. It is important to collect this information to clarify what is happening in the ecosystem during the decay cycle. Basic information such as the following is needed:

1. *Input rates of coarse woody debris.* This information includes items such as does a species most often die standing, what is the state of decay when the tree falls, and does the tree fall as a whole log or in pieces? Some of this information is currently being collected from the growth and yield, permanent sample-plot programs of the Resource Inventory Branch and Research Branch. Additionally, the amount of available CWD input (i.e., live trees that die) under different silvicultural regimes may be determined by the mortality projections from existing growth and yield models.
2. *Rates of fragmentation and decay.* Coarse information is needed for most ecosystems on how long CWD remains in various stages of decay (e.g., the time taken to go from a solid tree to a pile of crumbs, or the difference in decay rate between small and larger pieces). Until detailed information is available from long-term studies or intensive, short-term studies, initial models and management recommendations, an array of decay rates can be used to determine the sensitivity of coarse woody debris to different management scenarios.
3. *The role of CWD.* In order to determine the objective of our models it will be important to know the characteristics that we wish to model. These characteristics should be driven by the roles (e.g., seedling regeneration, mycorrhizae refugia, wildlife habitat) that CWD plays. Research is needed to determine the processes and variability in CWD dynamics in different ecosystems.

Beyond the coarse level of information needed to understand and model CWD, there is a need to understand finer-level processes. Knowledge of these processes will assist in modelling of both the fine- and coarse-level processes. However, often it is just the understanding (rather than actual modelling) of the finer processes that lead to improved decisions derived from coarser models. Finer-level information would include:

1. *The decay rate of different wood components.* Not all wood components decay at the same rate. Knowledge of the differences between bark, sapwood and heartwood decay rate is important in understanding

the overall decay and the characteristics associated with the stages of decay.
2. *Different moisture and temperature regimes.* Understanding the direct influence of moisture and temperature (versus a biogeoclimatic subzone approach) will enable model projections to be extrapolated to specific sites and into the future if there are changes associated with a site due to specific management or climatic changes.
3. *Decay organisms.* Ultimately the decay processes are dependent on the organisms that fragment and decay the CWD. Knowledge of the biology of these organisms and how they break down CWD will assist in understanding the variation found within CWD dynamics.

5 INVENTORY

The B.C. Ministry of Forests' New Vegetation Inventory includes an inventory of CWD because of the recognition of its importance in the ecosystems of B.C. The important attributes needed to describe natural levels of CWD and to make prescriptions for future levels that will fulfill the ecological roles described below are:
1. Piece size (length and diameter): this can be used to calculate volume and provides more control in the prescription of CWD within a site.
2. Decay class and type: decay classes will follow Resource Inventory Committee (RIC) standards; decay type refers to the difference between heartrot (from the inside out) and sapwood rot (from the outside in) (see Appendix 3 for decay-class definitions).
3. Species: tree species is not always known at later decay stages.
4. Position: above ground, on the ground or underground.

Historical sources of CWD data are inconsistent, but can be extensive. The B.C. Ministry of Forests has been collecting information from growth and yield plots for many years. These data can be used to compare the volume of dead potential (decay classes 1 and 2) between different ecosystem types and to compare the dead potential volume to the live volume. Standard cruise data may also contain dead potential and dead useless (decay classes 3 and 4) volume by species.

6 CONCLUSIONS

Trees that are removed from the forest cannot fulfill their role in the decay cycle. However, between the extreme cases of clearcutting followed by burning, and no removal, there is an infinite array of scenarios that leave differing levels of wood in the forest. The questions are: What are the optimum levels of CWD that will maintain the productivity and diversity of B.C.'s forests and still allow forestry activities to continue? How can these levels be maintained throughout a rotation? Natural levels are a reasonable target, as the underlying premise of the *Biodiversity Guidebook* states that, "[t]he more that managed forests resemble the forests that were established from natural disturbances, the greater the probability that all native species and ecological processes will be maintained" (p. 4). Natural levels themselves are extremely variable and will therefore allow for variability in recommendations and variability through time. Appendix 2 shows some known natural levels of CWD in forests throughout the province.

7 SUMMARY

- The importance of CWD to forest biodiversity and ecosystem function has been established.
- Variability is found among and between the ecosystems in NDTs for all factors determining CWD volumes and decay classes in a forest stand.
- In spite of the variability, patterns are discernible and should be verified through inventory.
- Management recommendations can be made on the basis of our current understanding and refined as new data become available.
- Input/retention of CWD should mimic the natural patterns shown in figures 2 to 5.
- Size is an important consideration when leaving woody debris. Large pieces will be part of the ecosystem for much longer than small pieces.
- CWD recommendations are closely linked to wildlife tree patch recommendations.

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S. Chatwin, Ministry of Forests, Victoria, B.C.
Telephone conversation.

M. Harmon, Department of Forest Sciences,
Oregon State University, Corvallis, Oregon.
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J.P. Kimmins, Department of Forest Sciences,
University of British Columbia, Vancouver, B.C.
Comments made at a CWD workshop in Victoria. Dec. 8, 1995.

D. Luoma, Department of Forest Sciences,
Oregon State University, Corvallis, Oregon.
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T. Trofymow, Pacific Forestry Centre, Victoria, B.C.
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S. Taylor, Pacific Forestry Centre, Victoria, B.C.
From review comments on this paper.

APPENDIX 1a Mammals closely associated with CWD (modified from Lofroth 1995)

Species	Life history role of CWD	Status
Dusky shrew	cover, foraging, reproduction	
Water shrew	cover, foraging, reproduction	
Vagrant shrew	cover, foraging, reproduction	
Shrew mole	cover	
California myotis	foraging	
Snowshoe hare	cover	trapped
Southern red-backed vole	cover, foraging	Red-listed (*occidentalis* subspecies)
Northern red-backed vole	cover, foraging	
Beaver	dam construction	trapped
Cascades golden-mantled ground squirrel	cover	
Deer mouse	cover	
Douglas squirrel	cover	trapped
Marten	denning, foraging	
Fisher	denning	Blue-listed, trapped
Ermine	denning, foraging, cover	Red-listed (*haidarum* subspecies), Blue-listed (*anguinae* subspecies), trapped
Long-tailed weasel	denning, foraging, cover	Red-listed (*altifrontalis* subspecies), trapped
Grizzly bear	denning, feeding	Blue-listed, hunted
Black bear	denning, feeding	Blue-listed (*emmonsii* subspecies)
Mule deer	feeding in winter (lichens)	

APPENDIX 1b Birds closely associated with CWD (from Lofroth 1995)

Species	Life history role of CWD	Status
Pileated woodpecker	foraging	
Ruffed grouse	drumming	hunted

APPENDIX 1c Herpetofauna closely associated with CWD (from Lofroth 1995)

Species	Life history role of CWD	Status
Pacific giant salamander	reproduction	Blue-listed
Clouded salamander	cover, reproduction	
Couer d'Alene salamander	cover, reproduction	Red-listed
Western red-backed salamander	cover	
Western skink	cover	
Rubber boa	cover	Blue-listed
Sharp-tailed snake	cover	Red-listed

APPENDIX 1d Vascular plants closely associated with CWD (after Lofroth 1995)

Species	Life history role of CWD	Status
Western hemlock	germination	commercially harvested
Sitka spruce	germination	commercially harvested
Red huckleberry	germination, growth	
Gnome plant (*Hypopitis congestum*)	growth	
Candystick (*Allotropa virgata*)	growth	Blue-listed

APPENDIX 1e Nonvascular plants, fungi and lichens closely associated with CWD (from Lofroth 1995)

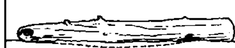
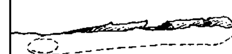
162 species of bracket or shelf fungi/conks
364 species of other macrofungi (some of them commercially harvested e.g., oyster mushroom)
epiphytes (lichens in drier habitats and bryophytes in wetter habitats)

APPENDIX 2 Natural levels of CWD in B.C. forests

Natural disturbance type	Zone	Moisture	N	Average total volume (m^3/ha)	Range (m^3/ha)
1	CWH	DRY	–	–	–
1	CWH	MESIC	55	868.13	12.76–1788.05
1	CWH	WET	106	573.47	40.88–1428.25
1	ESSF	DRY	–		
1	ESSF	MESIC	35	212.07	3.92–373.38
1	ESSF	WET	–		
1	ICH	DRY	–		
1	ICH	MESIC	12	398.87	157.56–557.29
1	ICH	WET	–		
1	MH	DRY	5	198.77	20.57–353.52
1	MH	MESIC	20	329.56	15.94–381.28
1	MH	WET	8	157.0	9.58–433.94
1	SBPS	DRY	–		
1	SBPS	MESIC	16	125.64	19.90–325.70
1	SBPS	WET	–		
1	SBS	DRY	–		
1	SBS	MESIC	18	244.46	83.23–332.12
1	SBS	WET	–		
2	CWH	DRY	–		
2	CWH	MESIC	–		
2	CWH	WET	30	338.96	55.52–440.28
2	ICH	DRY	16	451.5	46.96–492.05
2	ICH	MESIC	179	97.56	8.89–582.92
2	ICH	WET	3	416.34	277.16–546.19
3	BWBS	DRY	–		
3	BWBS	MESIC	64	81.23	4.01–151.49
3	BWBS	WET	1	94.94	
3	ESSF	DRY	5	59.93	4.95–84.94
3	ESSF	MESIC	6	80.63	33.95–200.59
3	ESSF	WET	6	111.84	80.18–281.8
3	MS	DRY	–		
3	MS	MESIC	17	89.69	22.90–103.60
3	MS	WET	12	116.16	60.10–219.20
3	SBS	DRY	64	120.54	4.17–387.08
3	SBS	MESIC	954	222.78	1.37–932.14
3	SBS	WET	129	230.67	3.64–661.04
4	IDF	DRY	–		
4	IDF	MESIC	64	170.93	13.30–299.88
4	IDF	WET	8	54.44	32.10–427.5

Source: Coarse Woody Debris volumes by size class and decay class for B.C. forests, June 1997, Qiwei Lang.

APPENDIX 3 Coarse woody debris classification (Bartels et al. 1985)

	Decay Class				
	I	II	III	IV	V
Characteristics of fallen Douglas fir[1]	 Log class 1	 Log class 2	 Log class 3	 Log class 4	 Log class 5
Bark	intact	intact	trace	absent	absent
Twigs	present	absent	absent	absent	absent
Texture	intact	intact to partly soft	hard, large pieces	small, soft blocky pieces	soft and powdery
Sharp	round	round	round	round to oval	oval
Color of wood	original color	original color	original color to faded	light brown to reddish brown	red brown to dark brown
Portion of tree on ground	tree elevated on support points	tree elevated on support points but sagging slightly	tree sagging near ground	all of tree on ground	all of tree on ground
Invading roots	none	none	in sapwood	in heartwood	in heartwood

[1] Characteristics of other tree species may differ. For other species use texture, shape and invading roots to determine decay class.