

Woody Debris in the Forests of British Columbia: A Review of the Literature and Current Research

C.L. Caza

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EXECUTIVE SUMMARY

Forest managers in the northwestern United States are currently concerned about the retention of adequate amounts of coarse woody debris (CWD) on sites after harvesting. This concern has stimulated interest in the role of CWD in British Columbia's forests.

Some information is available on CWD quantities in forests of the northwestern United States, and research on the ecological significance of woody debris is under way in the region. In comparison, it is not clear what information exists on quantities of woody debris in the forests of British Columbia, or what information is available to assist the evaluation of management strategies for woody debris in the province. We therefore undertook this project with several objectives: to review the published literature on the ecology of woody debris; to determine what data are available on amounts of woody debris in British Columbia forests; to identify proposed or ongoing research on woody debris within the Ministry of Forests; and to discuss the research needed to fill the gaps in our qualitative and quantitative understanding of the role of woody debris in British Columbia forests. An annotated bibliography with abstracts was also prepared as part of the final report and is included as Appendix 3 in this report. Information was gathered from computerized reference collections, review articles, and discussions with university researchers and government and industry personnel in British Columbia and the United States.

A literature review on the ecology of woody debris is presented in Section 2. General information on the structural and functional characteristics of woody debris (primarily CWD) is easily obtained from the literature, but publications of quantitative studies and detailed field studies are scarce. Most of our knowledge comes from forests in Oregon, Washington, California, Colorado, Idaho, and Montana. There is also some data from single studies in other regions (e.g., Alaska and Alberta). Few data have been collected in British Columbia, and what little information is available has come from fire and wildlife studies. We found no published work of field studies that focused on woody debris in forests in the province.

Among the many important roles of CWD in forest ecosystems are the following:

- It is a major element of the structural diversity of old-growth forests.
- It is a major component of the habitat of many forest plants, animals (both vertebrates and invertebrates), and microorganisms.
- It may serve as a major refugium for organisms after disturbance, and through its persistence across disturbances.
- It influences hillslope and stream geomorphology.
- It influences forest floor microtopography and microclimate.
- It is important in the nutrient and organic matter dynamics of forest ecosystems.

Unfortunately, the data do not yet exist to permit us to evaluate how important these functions are to the stability or sustainability of forest ecosystems, nor of how they are affected by changes in levels of CWD above or below those that occur naturally in forests. With respect to harvesting, most concern is focused on the long-term impacts of intensive utilization (e.g., whole-tree harvesting) and reductions in rotation length on CWD contributions to site nutrient capital and organic matter accumulation. Research on these questions is currently constrained by a lack of empirical data and theoretical understanding of the role of CWD in forest floor and soil development.

Data on input rates and quantities of CWD are presented in Section 3. Again, most of the available information for forest types in British Columbia comes from studies done in similar forests in the northwestern United States. Data on input rates and volumes of CWD exist for low-elevation coastal forests in the Pacific Northwest, and for some interior pine and spruce-fir forests, but differences in stand characteristics and sampling methodologies make comparisons among the few published estimates difficult. In addition, differences in climate between British Columbia and the U.S. states to the south of the province are likely to be reflected in differences in rates and patterns of accumulation of CWD between forests in the two regions. Estimates from studies in drier or warmer climatic regions are likely inadequate to represent the characteristics of CWD in British Columbia for management purposes. Further, studies of CWD rarely include estimates of fine woody debris, or forest floor and soil organic matter (particularly the wood component). To assess the relative importance of CWD to the ecosystem detrital pool, estimates of other detrital components are required.

A review of the existing sources of data on woody debris is presented in Section 3.3. Nine potential provincial data inventories are discussed, including: the timber inventory; the biogeoclimatic classification database; the prescribed fire assessment data; residue and waste survey information; the cruising summary compilations; the growth and yield sampling plot data; and the provincial insect and disease damage summaries. Although all of these sources contain some data on CWD, none of them provides comprehensive information. Each lacks data on one or more important characteristics, such as species, decay stage, size, amounts of standing dead, non-merchantable species, small woody debris, or buried wood. The accessibility of the data varies from good to very poor and, in the latter case, considerable time and expense would be required to extract the useful information.

Proposed and ongoing research projects on woody debris in British Columbia are discussed in Section 4. This information was obtained mostly through conversations with Ministry of Forests research personnel in Victoria and the regional offices, from research scientists at Forestry Canada's Pacific Forestry Centre, and from professors at several Canadian and American universities. The Ministry of Forests currently has no ongoing or proposed projects dealing specifically with woody debris. A research program is being developed at the Pacific Forestry Centre to study the biological dynamics of forest ecosystems, and projects on CWD are a component of this program (including one project which began in 1991 and involves estimates of CWD on coastal sites on Vancouver Island). The British Columbia Ministry of Environment, Lands and Parks has a project under way in the Sub-Boreal Spruce biogeoclimatic zone on pine marten ecology, and extensive data on CWD have been collected for the habitat characterization component of this study. Three projects under way by researchers at the University of British Columbia will include estimations of CWD on coastal sites as components of studies on old-growth forest structure and biodiversity. Apart from these few studies, there is at present little research activity in British Columbia dealing with the topic of woody debris.

Section 5 contains recommendations for areas of research on woody debris in British Columbia. Three major areas were identified (in no particular order of importance):

- the functional importance of CWD in moisture retention and habitat development in disturbed and undisturbed forests in British Columbia (e.g., diversity and abundance of organisms, properties of decaying wood and its role in regeneration and as refugia);
- the impacts of woody debris accumulations on the physical and chemical properties of the soil and forest floor (e.g., effects on nutrient availability, thermal regimes, and soil development); and
- the quantitative and qualitative role of woody debris in forest floor and soil organic matter dynamics (e.g., rates of transfer from logs to soil, turnover times, and impacts of changes in amounts).

To manage explicitly for woody debris in British Columbia, an inventory of levels of CWD in British Columbia forests is required. This inventory should include information on:

- natural volumes of CWD for major forest types requiring active management in British Columbia;
- decay class distribution patterns;
- size class distribution patterns; and
- spatial and temporal variation in amounts and distribution.

To manage for CWD, the following information is also necessary:

- input rates, including some data on variations in rates with forest succession; and
- turnover rates of bolewood.

To manage for conservation of soil and forest floor wood, in addition to CWD, the following additional information is necessary:

- amounts of wood in forest floor and soil; and
- turnover rates of soil and forest floor wood.

These information requirements may seem overwhelming, but much of this information is also needed to improve our understanding of other aspects of forest function, such as carbon cycling, old-growth ecology, biodiversity, and long-term forest sustainability. The high level of interest in all these topics provides an excellent opportunity to integrate many related research objectives into a comprehensive, long-term, multi-scale research program.

Given the lack of both quantitative and qualitative information on the ecological significance of woody debris in British Columbia forests, it makes little sense at this time to set standards for the retention of CWD on sites after harvesting. Nevertheless, the removal of large amounts of CWD from sites is not an environmentally sound practice. Activities that are known to reduce or increase the amount of woody debris on a site to levels outside the normal range for that forest type should not be accepted without some understanding of the impacts of such practices and how these impacts can be mitigated if necessary.

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1 INTRODUCTION

The current interest in the role of woody debris in forest ecosystems has its recent origins in the rise of “New Forestry” in the northwestern United States. Many of the ideas for this holistic approach to forest management, and much of the debate on the merits of its major tenets, have been presented in recent issues of *Forest Watch*, a magazine published by Cascade Holistic Economic Consultants in Eugene, Oregon. (See, for example, the March 1988, July 1989, and January 1990 issues.)

Proponents of “New Forestry” have argued vehemently for the need to retain adequate amounts of coarse woody debris (CWD) on sites after harvesting to preserve the many important ecological functions fulfilled by this component of natural forests (Maser 1988). Although exactly what amount is “adequate” remains difficult to define, it is clear that past harvesting practices, such as YUM (yarding unmerchantable material) and PUM (piling unmerchantable material) operations, have resulted in the loss of large amounts of organic matter from sites in the northwest. Chief among the concerns raised by these practices is the question of the long-term impacts of organic matter losses on site productivity.

Most of the research on the ecological significance of CWD in the northwestern United States is relatively recent. Nevertheless, forest managers in some areas have already responded to concerns by instituting guidelines for the retention of CWD on sites after logging. An example of these retention standards are those developed in the Blue River District of Oregon for the Willamette National Forest. These standards are presented in Appendix 1 (see also Eubanks 1989).

In contrast to the policy shift towards CWD retention in the United States, the British Columbia Ministry of Forests recently implemented a “zero waste tolerance policy” as part of its Utilization Standards. These standards are presented in Appendix 2. To minimize the amount of wood left on sites after harvesting, licencees are billed at the average stumpage rate for all avoidable waste wood which they fail to remove from a block during logging operations. Unfortunately, this new zero waste tolerance policy is being implemented at a time when the political focus in British Columbia is shifting from a concern over unacceptably large amounts of post-harvesting woody slash, to a new awareness of the importance of woody debris in forest ecosystems. Thus, the question has arisen: Do current harvesting and silvicultural activities in the province leave too much, too little, or just the right amount of woody debris on sites to ensure forest sustainability and to protect non-timber resource values?

In the northwestern states, concerns that too little woody debris has been retained after logging have focused on warm, dry sites where moisture retention by CWD is ecologically important, and where temperatures and excess moisture do not severely limit wood decomposition (see Section 2). In general, the climate of the forests of British Columbia is wetter and cooler than that of the northwestern states (Alaska, of course, being the exception). The larger accumulations of woody debris observed in the province, particularly on the coast, may be a consequence of much slower decomposition rates (M.E. Harmon, pers. comm., Oregon State University, College of Forestry, 1991). Despite possible differences in the characteristics and dynamics of woody debris between British Columbia forests and southern forests, very little research has been done on this topic in the province. At present, it is unclear what information exists on the quantity of woody debris in British Columbia forest types, and what information is available to assist in the development or evaluation of

management strategies for dead wood.¹ This project was therefore undertaken to address the following objectives.

1.1 Objectives

1. To review the published literature on the ecological role of woody debris in temperate forest ecosystems, with particular emphasis on methods of estimating amounts and turnover rates, and the effects of logging and silvicultural activities on the amounts and behaviour of woody debris in terrestrial ecosystems.
2. To identify proposed or ongoing research within the Ministry of Forests related to the role of woody debris in the forests of British Columbia.
3. To determine what information is available on quantities of woody debris for the forest types of British Columbia.
4. To identify forest types for which information on quantities or functions of woody debris is lacking, and to discuss the research required to fill these gaps.
5. To prepare an annotated bibliography with abstracts, and copies of references relevant to the role of woody debris in the forests of British Columbia.

The following activities were undertaken to meet the objectives specified above.

Objective 1

References on woody debris were obtained from the following sources:

- the BIOSIS, AGRICOLA, CAB, and CCOD computerized reference collections;
- the University of British Columbia library catalogue;
- review article on woody debris by Harmon et al. (1986);
- annotated bibliography on old-growth forests prepared by Cadrin et al. (1991) for the British Columbia Ministry of Forests; and
- published articles on woody debris.

The roles of woody debris in aquatic ecosystems, fish and wildlife habitat, fire ecology, and soil and forest floor dynamics are addressed in other reviews, either published or currently in preparation (see Section 2 for references), and were not treated in depth in this review. The article by Harmon et al. (1986) on the role of CWD in temperate ecosystems was used as a starting point for the literature review. Most of the articles used to extend the information contained in Harmon et al. (1986) were published after 1985, or, if published before 1985, were not included in the Harmon et al. article. However, several papers which were extensively quoted in the woody debris literature were also included in the present review.

Objective 2

Researchers with the British Columbia Ministry of Forests, Research Branch and Silviculture Branch, both in Victoria and in the regional offices, were contacted about ongoing and proposed research on woody debris. Researchers with the United States Department of Agriculture Forest Service and several Canadian and American universities, as

¹ Trofymow, JA. and W.J. Beese. 1990. Quantities of coarse woody debris in old-growth forests. A brief to the Old-growth Project Research Working Group, Sept. 1990. Unpublished report.

well as consultants and researchers working with industry, were also solicited for information and commentary.

Objective 3

The potential for several large provincial inventories to provide information on woody debris in British Columbia's forests was discussed with individuals familiar with the databases. These databases included:

- the timber inventory database— both the data from temporary plots sampled in the 1970's, and the permanent growth and yield plots (Joe Braz, Inventory Branch, Victoria);
- the prescribed fire assessment data (John Parminter, Protection Branch, Victoria);
- the biogeoclimatic classification program database (Del Meidinger, Research Branch, Victoria);
- the insect and disease survey summaries (Wood and Van Sickle 1989);
- residue and waste surveys information (Jim Gowriluk, Timber Harvesting Branch, Victoria);
- cruising summary compilations (Maarten Prinsze, Forest Valuation Branch, Victoria);
- research growth and yield installations (Stephen Omule, Research Branch, Victoria); and
- permanent growth and yield sampling plots of MacMillan Bloedel (Kim Iles, Woodland Services Division, Nanaimo).

1.2 Organization of Report

Sections 2–5 contain the literature review on the ecology of woody debris, published information on quantities of woody debris and potential data sources for British Columbia's forests, the review of proposed and ongoing research in British Columbia, and information needs and research priorities. The annotated bibliography with abstracts is presented in Appendix 3, and additional unreviewed references with relevant information are included in Appendix 4. Several of the references cited in the review also contain extended bibliographies, in particular Cadrin et al. (1991); Franklin and Waring (1979); Harmon et al. (1986); Maser and Trappe (1984); and Maser et al. (1988b).

1.3 Comments on Definitions

As described in Harmon et al. (1986), CWD includes snags (dead standing trees), logs (dead downed trees), chunks of wood, large branches, and coarse roots. Most of the references included in Section 2 deal with coarse woody debris, as much of the recent interest in the role of wood in forests has focused on its importance as habitat for plants, microbes, and animals. Harmon et al. (1986) considered CWD to include any material >2.5 cm in diameter.

Fine woody debris (FWD) generally includes small woody roots, small branches, twigs and cones, and, in some cases, tree bark. Studies on the role of FWD are less common than studies on larger materials, possibly because the contribution of FWD to the detritus pool in forests is much less than that of CWD, at least in terms of biomass (Harmon et al. 1986). However, FWD is very important in nutrient cycling and accumulation of organic matter in forests.

In this report, the type of woody debris (e.g., bole wood, twigs, and cones) considered in a study will be discussed more commonly than the size of the wood, unless size was examined as a factor influencing function. However, where used, the term “coarse woody

debris” refers to material >2.0 cm in diameter, and the term “fine woody debris” refers to smaller material.

2 LITERATURE REVIEW

2.1 Introduction

Although woody debris is an integral part of forest ecosystems, we have only a general understanding of its importance in forest function and structure. Coarse woody debris is a significant structural element of old-growth forest ecosystems (Franklin and Spies 1989; Franklin et al. 1981), but large volumes of woody debris may be found in most seral stages (e.g., see Table 3.1). Dead downed and standing trees are critical components of the habitat of many forest plants, animals and microbes. However, for many species the relationship may not be obligatory (Fischer and McClelland 1983; Christy and Mack 1984; Harmon et al. 1986; Harvey et al. 1987; Scott and Murphy 1987; Aubrey et al. 1988; Maser et al. 1988b; Harmon and Franklin 1989).

The roles of insects and microorganisms (chiefly fungi and bacteria), and abiotic factors such as moisture and substrate quality, in the processes of wood decomposition have been qualitatively described (Kaarik 1974; Swift et al. 1979). Decay and input rates of woody debris have been estimated for a number of forest types and numerous studies have described the nutrient content and organic matter composition of wood at various stages of decay in natural stands (Grier 1978; Graham and Cromack 1982; Harmon et al. 1986; Edmonds 1987; Sollins et al. 1987; Fahey et al. 1988; MacMillan 1988; Prescott et al. 1989; Arthur and Fahey 1990). The importance of woody debris in hillslope and stream geomorphology is also well recognized, if still only partly understood (Wilford 1984; Harmon et al. 1986).

Although we know that woody debris plays many roles in forests, we do not yet understand how important these functions are to the stability or sustainability of forest ecosystems. Although some functions are exclusive to snags and CWD (e.g., habitat for cavity-nesting birds and substrate for wood-boring insects), many of these may be fulfilled by other forest components under certain conditions (e.g., the relative importance of CWD versus forest floor materials in the nutrient-supplying capacity of a site). Estimates of the quantity of woody debris (usually CWD) have been made for several forest types in the northwestern states. However, very little is known about the relationship between naturally occurring quantities of woody debris and healthy forest functioning, or about the impacts of levels of woody debris above or below that documented in natural stands on long-term forest productivity, biodiversity, microbial decomposition, and other forest processes. It is in these areas that research efforts must be concentrated if our objective is to establish guidelines for managing woody debris in British Columbia's forests.

In this section, current knowledge about the role of woody debris in forests is reviewed. Emphasis has been placed on what is known about the relationship between site factors (both biotic and abiotic) and the structural and functional characteristics of woody debris in forest types related to those found in British Columbia. For the purposes of this review, CWD refers to materials ≥ 2.0 cm in diameter and FWD to materials < 2.0 cm in diameter, unless otherwise specified. References were obtained from the sources described in Section 1. Additional references can be found in the annotated bibliography (Appendix 3), the supplemental list of references (Appendix 4), and the bibliographies mentioned in Section 1.

2.2 Characteristics of Woody Debris

2.2.1 Structural characteristics

The functional importance of woody debris is influenced by structural characteristics of the dead downed and standing trees in a forest. These characteristics include the volume of woody debris (discussed in Section 3), degree of decay, size, position (standing or down), spatial arrangement, orientation, and the species (Harmon et al. 1986).

The decay class distribution of woody debris is influenced by the size of logs, the decay resistance of the log species, the residence time of logs in each decay stage, the decay organisms present, climatic factors, and the disturbance regime of the stand. Means et al. (1985) estimated residence times on the forest floor for Douglas-fir logs in five decay classes, where logs in class 1 were the least decayed and those in class 5 were the most decayed. Residence times were 7, 17, 33, 82, and 219 years from class 1 to 5. This geometric increase in residence times results in the highest volumes of woody debris in intermediate decay classes, as is commonly observed in forests of the Pacific Northwest (Harmon et al. 1986).

McFee and Stone (1986) have estimated that decayed wood may persist in soils for >1000 years, and Harvey et al. (1981b) estimated lag times of 100–300 years for the replacement of soil wood losses, the result of harvesting in Rocky Mountain forests. However, even calculations of turnover times for bole wood alone are difficult, and are complicated by such factors as the temporal variability in inputs. Many estimates of turnover time are based on steady-state assumptions and, as a consequence, are of dubious value (Lang 1985). Very little is known about the residence times of FWD in northwestern forests. Prescott et al. (1989) estimated mean residence times of 2–3 years for cones, twigs, and bark in the litter layer of pine, spruce, and fir forests in the Rocky Mountains. In general, the decay rate of woody debris decreases with increasing size, and it can be assumed that turnover times of smaller material are typically shorter than those of CWD. However, important exceptions to the general trend in decay rates have been observed. Some of these exceptions, and the factors influencing decay rates, are discussed in Section 2.4.

There have been few studies on the size class distribution of woody debris. Typically, the frequency of logs decreases as the size class increases. According to Harmon et al. (1986), CWD frequently constitutes >80% of the biomass in the terrestrial woody detritus pool, and the majority of this biomass may be contained in only a few, large logs. Some work on the size class distribution of FWD has been done in Japanese and Malaysian forests by Yoneda (1982). The relationship between diameter and frequency was log-log linear in the stands studied.

Large variation with little pattern occurs within and among forest types in the relative distribution of woody debris between snags and logs (Harmon et al. 1986). The cause of mortality and the frequency of disturbance are two factors affecting the input rates of standing and downed dead trees (see Section 2.2.2 for discussion of input rates). In an attempt to develop a definition of old-growth Douglas-fir stands, Franklin and Spies (1989) tested a number of criteria for their ability to discriminate among differently aged stands. Two of the criteria were related to structural characteristics of CWD: the size and number of snags in the stand, and the biomass of logs (both on a per hectare basis). However, the authors found that the set of characteristics with the best classification success used only overstory (i.e., live tree) attributes and that a large number of mature (80–199 years) stands were classified as old growth when both the live tree and CWD attributes were used.

Little is known about the spatial distribution of CWD in forests. Aggregation does occur, as factors such as insects, disease, and blowdown tend to cause localized mortality rather than random death throughout the stand. Taylor and Fonda (1990) found that twice as much woody debris (all sizes) accumulated around the base of trees in a subalpine fir stand in Washington than accumulated throughout the stand as a whole. They contrasted this with the

pattern of accumulation in a fire-stable ponderosa pine stand, where woody debris levels around trees were not significantly different from those throughout the stand.

The orientation of logs in a stand is also an important structural characteristic which affects habitat use and geomorphic processes, as well as sampling designs (Harmon et al. 1986). Orientation is influenced by topography, slope, and prevailing wind direction. For example, Wilford (1984) described the sediment build-up behind CWD on steep slopes in coastal British Columbia. Trees dropped perpendicularly to the slope by storms in this region catch wash materials, such as silts and fine organics, and form terraces that can be very productive sites for tree growth. Disturbance of these terraces, by harvesting for example, may reduce the stability and productivity of these sites through the removal of fine particles, increased drainage from coarse soils, and increases in the water table from reduced uptake by trees.

2.2.2 Input characteristics

Harmon et al. (1986) give input rates of CWD for coniferous forests in the United States ranging from 0.17 to 30 Mg ha⁻¹yr⁻¹, although most values are <5 Mg ha⁻¹yr⁻¹. Input rates for deciduous forests vary from 0 to 14.5 Mg ha⁻¹yr⁻¹, with most rates <1–2 Mg ha⁻¹yr⁻¹. Values from Harmon et al. (1986) and other sources are presented in Table 3.2. Methods of estimating inputs are discussed in Section 3.1.1. In general, input rates for CWD are higher in coniferous forests than in deciduous forests, and the highest input rates in North America are in the coastal coniferous forests of the Pacific Northwest.

Much less information is available on FWD inputs in northwestern forests. Prescott et al. (1989) estimated annual litter inputs from non-woody, CWD, and FWD sources in a clearcut, a 90-year-old lodgepole pine stand, a 120-year-old white spruce stand, and a 350-year-old subalpine fir stand in the Rocky Mountains. Non-woody litter dominated the inputs on all sites, but annual inputs of cones, bark, twigs, and branches exceeded those of trees in the spruce and fir stands. Litterfall of large woody debris was similar to that of smaller material in the pine stand.

Prescott et al. (1989) estimated input rates for each of three consecutive years, and found that annual input rates were similar from year to year. Most estimates of input rates are based only on short-term (1–2 years) measurements and do not give an adequate picture of the large year-to-year variation that occurs. Harmon et al. (1986) discuss a hypothetical pattern of change in CWD input over time. They suggest that steady-state input levels are typically low, and that annual inputs which fluctuate about this long-term mean are characterized by occasional spikes due to sudden, catastrophic events, or by longer-term increases in input due to gradually increasing disturbances (such as a disease). In the development of a probabilistic model to predict inputs of CWD to streams, Van Sickle and Gregory (1990) found that the assumption of a constant input rate was inadequate to simulate observed inputs from natural stands. In general, catastrophic events such as insect epidemics or wind storms can dramatically alter the pattern of long-term changes in woody debris (Lang 1985; Harmon et al. 1986).

The characteristics of CWD inputs to forests are influenced by factors that cause tree mortality, such as wind, insects, diseases, suppression and competition, and fire (Harmon et al. 1986). Wind is a major factor that causes both chronic and catastrophic damage to stands. Catastrophic damage is generally caused by wind storms, whose importance varies regionally. For example, in a coastal spruce-hemlock stand, 70% of tree mortality was caused by wind and <1% by insects (Harmon et al. 1986). In contrast, only 18% of the mortality in a Rocky Mountain lodgepole pine stand was wind-related, in comparison to the 40% due to insects and disease. Diseases, mostly fungal, typically result in small inputs, but may also contribute to the mortality caused by other factors, such as wind and insects. Suppression and competition create snags and are important causes of mortality in closed-canopy stands. Suppression results in a spatially random input of CWD, unlike most other mortality factors. Fire, though

less common than wind, insects, and disease, is an important long-term cause of mortality, and may help keep levels of CWD below those that impede forest function (Covington and Sackett 1984). The effect of fire on levels of woody debris varies greatly with the characteristics of a particular fire. The literature is extensive on the effects of fire on forest ecosystems (e.g., see Feller 1982). This topic is not discussed here.

Input rates also differ among species, because of differences in longevity. Raphael and Morrison (1987), for example, in a study of the decay and dynamics of snags in a fir-pine forest in California, found that rates of mortality caused by herbivory were higher in Jeffrey pine than in either red or white fir, due to differences among species in endemic levels of pine beetle. In addition, dead pines fell to the forest floor faster than did the firs. Franklin and DeBell (1988) found very different mortality rates among several conifer species during a 36-year period of population change in an old-growth Douglas-fir/western hemlock stand in Washington. Rates of mortality were much higher for amabilis fir than for Douglas-fir or western hemlock. Similarly, in high-elevation stands of Engelmann spruce and subalpine fir, the fir typically dies at a younger age and a smaller size than the Engelmann spruce does (Veblen 1986).

In addition to the ecological importance of the amounts of woody debris that enter forests, the process of tree death itself affects ecosystem structure and function. In the process of dying, a tree releases resources such as light and moisture, and microsites are created through both understory and overstory disturbance (Franklin et al. 1987). This process influences competitive interactions among advanced regeneration, as well as the establishment and recruitment of new individuals. The uprooting that is often a component of this process mixes forest soils and creates microtopography, thereby influencing nutrient cycling and regeneration (Falinski 1978; Schaetzl et al. 1989). It is important to note that these processes are not conserved simply by the retention of CWD on the forest floor after harvesting.

2.3 The Role of Woody Debris as Habitat

2.3.1 Plants

In many mature and old-growth forests, tree seedlings are most commonly found rooted in or on fallen logs (Harmon et al. 1986). In the northwest, this phenomenon of “nurse logs” occurs in coastal Douglas-fir, cedar-hemlock, and Sitka spruce forests, high-elevation Engelmann spruce–subalpine fir forests, and northern white spruce forests (McCullough 1948; McKee et al. 1982; Christy and Mack 1984; Harmon et al. 1986; Harmon et al. 1987; Scott and Murphy 1987; Harmon and Franklin 1989). McKee et al. (1982) found that 88–97% of the tree seedlings in an alluvial spruce-hemlock stand in Olympic National Park grew on logs, although these logs represented only 6–11% of the ground cover on the site. Christy and Mack (1984) also found that western hemlock seedlings occurred almost exclusively on decaying logs in the Cascades, where woody debris typically covered from 10 to 30% of the forest floor. They did not find a relationship between decay stage and emergence, but did observe higher seedling survival on Douglas-fir logs with rotten heartwood. In contrast, Scott and Murphy (1987) found no relationship between survival and stage of log decomposition. In the eastern white cedar forest they studied, higher seedling survival was correlated with larger canopy openings. Harmon (1987) also found that greater growth of Sitka spruce and western hemlock seedlings was associated with larger canopy openings.

Plant species in general, and tree seedlings in particular, are not restricted to nurse logs, but these logs appear to provide the largest source of safe sites for early establishment in mature and old-growth stands. There have been few detailed studies of the factors responsible for greater establishment of seedlings on nurse logs. One factor that is important in coastal

Sitka spruce–western hemlock forests of the Pacific Northwest is competition from other plants. Harmon and Franklin (1989) studied the effects of pathogens, predation, the presence of standing water, and competition from herbs and mosses on seed germination and seedling survival in four conifer species. Seeds were unable to penetrate moss mats >5 cm in depth, and when ground-layer vegetation was removed from around seedlings, survival increased significantly. The authors concluded that competition with herbs and mosses on the forest floor restricted seedlings to logs.

Other factors which may result in higher establishment on logs include a longer snow-free period in elevated microsites, amelioration of environmental factors, lower litter loads on logs (although growth may increase with increases in litter loads; see below), and higher moisture levels in rotten wood. Water availability may be a particularly important factor on drought-prone or xeric sites. Amaranthus et al. (1989) found higher levels of root and mycorrhizal activity in logs than in the soil on post-fire sites in southwestern Oregon; they suggested that decaying logs can be important reservoirs for moisture after fires.

Despite the apparent importance of logs as sites of establishment, early growth may be limited in these microsites, due to the low nutrient supplying capacity of decaying wood. Harmon and Franklin (1989) found that the growth of Sitka spruce and western hemlock seedlings increased as the litter-humus accumulation on logs increased, suggesting that low nutrient levels may limit growth in the woody substrate. It is likely that seedlings must rely heavily on root mycorrhizae to exploit decaying wood early in growth, and that logs are important reservoirs of these fungi (Maser and Trappe 1984). Harvey et al. (1987) found a positive correlation between the presence of soil wood and the establishment of conifer seedlings on drier sites in old-growth forests of western Montana. Results from other studies suggest this may be strongly influenced by the amount of mycorrhizae in soil wood (Harvey et al. 1981a), but the relationship between soil organic matter and seedling establishment is not well understood. While some studies have shown a positive association between soil wood and establishment (Turner and Franz 1985; Harvey et al. 1987), others have found the opposite (Taylor 1935).

As decay proceeds, the nutrient supplying capacity of logs also increases (see Section 2.4), but Harmon et al. (1986) have suggested that logs are not stable long-term substrates for tree establishment. Logs collapse as decay proceeds, and this physical instability, plus the typically low surface cover of logs in forests, suggest that logs may not be as important to regeneration as early patterns of establishment suggest. For example, Scott and Murphy (1987) found that only 1% of all the seedlings on logs in an old-growth white cedar stand were >25 cm in height. They attributed the low survival to low light levels, however, rather than to an unstable substrate.

2.3.2 Animals

Vertebrates

Woody debris is an important component of the habitat of many forest species. Trees that fall into forest streams, or are carried down from upper reaches, influence channel hydraulics and create rearing habitat for fish (British Columbia Ministry of Forests 1990). Snags provide essential habitat for many forest birds, in particular cavity-nesting birds, as reflected in the extensive literature on this topic. The bibliography prepared by Fischer and McClelland (1983), for example, contains 1700 references on cavity-nesting birds alone. Most of the studies on the role of woody debris in fish and bird habitat relate to old-growth forests, and a number are reviewed in the Ministry of Forests “Old-growth Forests: Problem Analysis” (1990). Few detailed studies have been done on the importance of woody debris to other types of vertebrates (Harmon et al. 1986). This work does not cover the literature on wildlife and woody debris.

The functional importance of CWD to vertebrates changes as logs decay. Vertebrates use CWD for cover, feeding, reproduction, resting, preening, bedding, lookouts, drumming, sunning, bridging (runways and tunnels), roosting, and hibernating (Thomas 1979). In the early stages of decay, when logs are hard and sound, use is primarily external. As decay proceeds and wood decomposes, use becomes internal. The size, species, orientation, quantity, and decay stage of CWD all influence how it is used, but little is known about the nature of these relationships. As an example, the frequency, length, and orientation of logs on a site will determine the capacity of the downed woody debris to provide a network of runways that allow animals to move through an otherwise hostile environment.

Little is known about the importance of woody debris to reptiles and amphibians. Aubrey et al. (1988) observed differences in CWD use by Plethodontid salamanders in Douglas-fir forests of Washington. One species was found under pieces of bark and another under logs. Individuals occurred in stands of all ages, but abundance was greatest in the youngest stands. Bury and Corn (1988) also found that salamanders varied in their use of CWD in Douglas-fir stands, although their abundance was more strongly related to the availability of breeding habitat in adjacent areas than to the forest conditions. In their study, lizards were found mainly in dry stands and clearcuts. Raphael and Barrett (1984) also reported that the abundance and diversity of reptiles were highest in young stands of Douglas-fir. They sampled a number of stands ranging in age from 55 to 315 years and found no correlation between seral stage and the diversity of birds, mammals, or amphibians, although amphibian and mammal abundance was highest in the older stands. (Of the 150 species recorded, 15 showed a positive correlation with stand age and 18 showed a negative correlation.)

Harmon et al. (1986) list 20 species of small mammals that are known to use CWD. Of these 20, 13 use downed wood for the primary life processes of reproduction, feeding, and cover, and 8 of the 20 species also use standing dead wood. The fruiting bodies of mycorrhizal-forming fungi that colonize wood have been shown to be a component of the diets of small mammals such as shrews, mice, and voles, and these species may be important dispersal agents of the fungi (Maser et al. 1978; Rhoades 1986). Attempts have been made to establish a quantitative relationship between volumes of CWD and small mammal abundance in forests. Harmon et al. (1986) suggest that abundance increases with increasing volumes of wood, and some researchers have shown positive correlations between these two factors (Goodwin and Hungerford 1979). However, it has not always been possible to establish such a correlation, at least not within a single seral stage, and it may be that the relationship depends on other forest conditions, or that use changes functionally with changes in volume and is not necessarily reflected in differences in density (Nowotny et al. 1990). Larger mammals, such as bears, also use logs as cover and for dens, and prey on insect colonies in decayed woody debris (Harmon et al. 1986). Their scavenging activities may have a large impact on rates of fragmentation in individual pieces of wood.

Invertebrates

Many invertebrates use woody debris and have specialized to use particular species, decay stages or wood components (Maser and Trappe 1984; Harmon et al. 1986). Insects not only exploit woody debris as habitat, they are also essential to the process of wood decomposition. They use wood for protection and food, as well as for hibernation, nesting, breeding, and reproduction sites. They influence decay rates by the processes of consumption, excavation, and defecation, and through mortality. They also introduce microorganisms into wood, and by their presence attract predators to debris. As decay proceeds, the invertebrate fauna change in a well-known succession of species that characterizes invertebrate use of woody debris (Harmon et al. 1986). Coarse woody debris is also extremely important habitat for aquatic invertebrates, and its role in aquatic ecosystems is reviewed by Harmon et al. (1986).

The major taxa involved in invertebrate succession on terrestrial CWD are bark beetles, wood borers, termites, carpenter ants, other Hymenoptera (especially horntail wasps and carpenter bees), several members of the Lepidoptera, Diptera, and mites. Wood decomposition is often initiated by bark beetles, which attack weakened or recently dead trees. These beetles create entrance points for other insects, as well as transporting microbes themselves into trees. Wood borers typically use woody debris after the initial attack by bark beetles. They feed on the cambium and phloem, and tunnel into the heartwood of the tree. Carpenter ants and termites have specific moisture and decay state requirements, and typically use woody debris after decay has proceeded beyond its earliest stages. Members of the Hymenoptera, Lepidoptera, Diptera, and mites are generally found only in very decayed wood. Although invertebrate succession on CWD has been described, there is little known about quantitative relationships between invertebrate abundance or diversity, and volumes and decay class distribution of woody debris, or the significance of these relationships to the dynamics of woody debris in forests.

2.4 Decomposition of Woody Debris

2.4.1 Decay rates

Harmon et al. (1986) provide a long list of decay rates for tree species that occur in the northwest. Some of these numbers, plus additions from recent published studies, are presented in Table 2.1. Only one study was found on rates of root decay. Fahey et al. (1988) compared the rates of decay and nutrient flux in roots of four dominant species (three deciduous species and one conifer) in a northern hardwood forest after whole-tree harvesting. Rates of decay differed little among species, but decreased with increasing root diameter and were much slower than rates for twigs and branches above the ground.

TABLE 2.1 *Decomposition rates of snags and logs in temperate forest ecosystems (from Harmon et al. 1986)*

Species	dbh (cm)	Study length (year)	Lag time (year)	Decay rate constant	Type	References
<i>Abies lasiocarpa</i>	<7.50	15	2	0.317	Snag-bole fragmentation	Lyon 1977 ^a
<i>Picea engelmannii</i>	7.5—24	25	10	0.015	Snag-bole fragmentation	Mielke 1950 ^a
<i>P. engelmannii</i>	25—39	25	10	0.012	Snag-bole fragmentation	Mielke 1950 ^a
<i>P. engelmannii</i>	>40	25	10	0.009	Snag-bole fragmentation	Mielke 1950 ^a
<i>P. engelmannii</i>	12	22 ^b	4	0.023	Snag-bole fragmentation	Hinds et al.
<i>Picea glauca</i>	—	7	0	0.012	Snag-bole fragmentation	Riley and Skolko 1942 ^a
<i>Pinus contorta</i>	7.5—30	15	2	0.089 ^c	Snag-bole fragmentation	Lyon 1977 ^a
<i>P. contorta</i>	<25.00	8	2	0.318 ^c	Snag-bole fragmentation	Bull 1983 ^a
<i>P. contorta</i>	>25	8	3	0.133 ^c	Snag-bole fragmentation	Bull 1983 ^a
<i>P. contorta</i>	—	17 ^b	<4	0.021	Snag-bole fragmentation	Hinds et al. 1965 ^a
<i>Pinus ponderosa</i>	<25.00	8	3	0.283	Snag-bole fragmentation	Bull 1983 ^a
<i>P. ponderosa</i>	25—49	8	3	0.113	Snag-bole fragmentation	Bull 1983 ^a
<i>P. ponderosa</i>	>50	8	5	0.161	Snag-bole fragmentation	Bull 1983 ^a
<i>P. ponderosa</i>	>20	22	<9	0.073 ^c	Snag-bole fragmentation	Dahms 1949 ^a
<i>P. ponderosa</i>	>25	29 ^b	1	0.197 ^c	Snag-bole fragmentation	Keen 1955 ^a
<i>P. ponderosa</i>	>25	29 ^b	2	0.112 ^c	Snag-bole fragmentation	Keen 1955 ^a
<i>P. ponderosa</i>	>25	9 ^b	1	0.189 ^c	Snag-bole fragmentation	Keen 1955 ^a
<i>Pseudotsuga menziesii</i>	10—18	25 ^b	4	0.354 ^c	Snag-bole fragmentation	Cline et al. 1980 ^a
<i>P. menziesii</i>	29—31	60 ^b	6	0.109 ^c	Snag-bole fragmentation	Cline et al. 1980 ^a
<i>P. menziesii</i>	32—46	40 ^b	11	0.033 ^c	Snag-bole fragmentation	Cline et al. 1980 ^a
<i>P. menziesii</i>	47—71	45 ^b	17	0.055 ^c	Snag-bole fragmentation	Cline et al. 1980 ^a
<i>P. menziesii</i>	<40	50 ^b	<5	0.026	Snag-bole fragmentation	Graham 1982 ^a
<i>P. menziesii</i>	>65	30 ^b	<6	14	Snag-bole fragmentation	Graham 1982 ^a
<i>Tsuga heterophylla</i>	>25	30 ^b	<2	0.067	Snag-bole fragmentation	Graham 1982 ^a
<i>Pseudotsuga menziesii</i>	>20	250 ^b	80	0.008	Log-bole fragmentation	Graham 1982 ^a
<i>Tsuga heterophylla</i>	>15	50 ^b	>50	0	Log-bole fragmentation	Graham 1982 ^a
<i>Pinus contorta</i>	>1	20 ^b	12	0.006	Snag-bole mineralization	Fahey 1983 ^a
<i>Pseudotsuga menziesii</i>	<40	50 ^b	—	0.027	Snag-bole mineralization	Graham 1982 ^a
<i>P. menziesii</i>	40—65	30 ^b	—	0.013	Snag-bole mineralization	Graham 1982 ^a
<i>P. menziesii</i>	>65	30 ^b	—	0.003	Snag-bole mineralization	Graham 1982 ^a
<i>Tsuga heterophylla</i>	<25	30 ^b	—	0.017	Snag-bole mineralization	Graham 1982 ^a

TABLE 2.1 *Decomposition rates of snags and logs in temperate forest ecosystems (from Harmon et al. 1986) — Continued.*

Species	dbh (cm)	Study length (year)	Lag time (year)	Decay rate constant	Type	References
<i>T. heterophylla</i>	>25	30 ^b	—	0.016	Snag-bole mineralization	Graham 1982 ^a
<i>Picea sitchensis</i>	>15	100 ^b	—	0.011	Log-bole mineralization	Graham and Cromack 1982 ^a
<i>Pinus contorta</i>	>1	40 ^b	—	0.012	Log-bole mineralization	Fahey 1983 ^a
<i>Populus tremuloides</i>	>2	5	0	0.049	Log-bole mineralization	Miller 1983 ^a
<i>P. tremuloides</i>	17	5	0	0.070	Log-bole mineralization	Gosz 1980 ^a
<i>Pseudotsuga menziesii</i>	<40	200 ^b	—	0.004	Log-bole mineralization	Graham 1982 ^a
<i>P. menziesii</i>	40—65	200 ^b	—	0.004	Log-bole mineralization	Graham 1982 ^a
<i>P. menziesii</i>	>65	250 ^b	—	0.006	Log-bole mineralization	Graham 1982 ^a
<i>P. menziesii</i>	>15	320 ^b	—	0.007	Log-bole mineralization	Means et al. (unpubl.) ^a
<i>Tsuga heterophylla</i>	<25	50 ^b	—	0.012	Log-bole mineralization	Graham 1982 ^a
<i>T. heterophylla</i>	>25	50 ^b	—	0.024	Log-bole mineralization	Graham 1982 ^a
<i>T. heterophylla</i>	>25	38 ^b	2	0.008	Log-bole mineralization	Grier 1978 ^a
<i>T. heterophylla</i>	15	50 ^b	—	0.010	Log-bole mineralization	Graham and Cromack 1982 ^a

The decay rate constant, k , is most commonly derived from a single exponential model of the form (Olson 1963):

$$Y_t = Y_0 e^{-kt}$$

Where Y_0 = initial quantity of material

and Y_t = amount left at time t

The decay rate constant, k , can be used to calculate the time to decompose half of a quantity of wood, (where $t_{0.50} = 0.693/k$), or its turnover time, which is equal to $1/k$. The single exponential model treats decayed wood as a homogeneous substrate. Double and multiple exponential models allow for several wood components to be modelled, and have also been used to estimate decay rates, but all three models assume that detritus is not transformed during the decomposition process into substances with different decay rates. According to Harmon et al. (1986) this assumption is probably invalid. Means et al. (1985) recommended the use of the single exponential model for the calculation of mineralization rates due to high variability in the decay process within species, but they recommended the use of a multiple exponential model to study the dynamics of carbon components in decaying wood.

In the calculation of k values, Harmon et al. (1986) distinguished between rates of snag and log decay, between mineralization losses (losses due to respiration and leaching) and fragmentation losses, and between bark decay and bole decay. Rates (k) for northwestern conifers range from 0.009 to 0.354 yr⁻¹ for snag-bole fragmentation, 0 to 0.060 yr⁻¹ for log-bole fragmentation, 0.003 to 0.04 yr⁻¹ for snag-bole mineralization, and 0.004 to 0.024 yr⁻¹ for log-bole mineralization. Snag-bark fragmentation rates are similar to those for snag-boles, whereas log-bark rates are higher than those for log boles. No published information is available on bark mineralization rates. Comparisons of rates within species suggest large variation, but this may be partly a consequence of differences in methodologies, study objectives, and stand conditions, which make it difficult to analyze the limited information available. Mineralization rates are typically derived from changes in wood density or specific gravity caused by microbial respiration and leaching processes. Density is usually calculated from dry mass and volume estimates (Lambert et al. 1980), but the assumption of constant volume, the dependence of density on moisture content, and variations in the initial density of wood can all cause problems in the use of wood density to estimate decay rates. Decay rates are also influenced by the many factors discussed in the following section (Lambert et al. 1980; Boddy and Swift 1984; Means et al. 1985).

As illustrated by Table 2.1, decay rates are available for coastal conifers, high-elevation species, interior pines, and several common hardwoods, but are lacking for northern species and mid-elevation interior trees. For coastal conifers in the Pacific Northwest, comparative studies have shown higher decay rates of bole wood and FWD for western hemlock than for other species (Erickson et al. 1985; Edmonds 1987; Sollins et al. 1987). Edmonds (1987) found that decay rates of FWD were similar for Douglas-fir and amabilis fir, but Erickson et al. (1985) found that Douglas-fir wood (<12 cm in diameter) decayed faster. Edmonds et al. (1986) observed higher rates of decay in red alder than in Douglas-fir on clearcut sites.

Most decay processes are characterized by lag times (Table 2.1). For example, most snags fall within the first 3 years after tree death, but lag times for tree fall may be as long as 20 years, and for log mineralization >25 years (Harmon et al. 1986). However, there is little information available on the factors influencing lag times or their ecological significance.

2.4.2 Processes of decomposition

The major processes involved in wood decomposition are (Harmon et al. 1986):

- leaching, the percolation of water through woody debris, which dissolves materials and causes weight loss;
- fragmentation, the physical break-up of wood and bark;
- transportation of material in streams or downslope;
- collapse and settling of wood that occurs as decay proceeds and structural strength declines;
- seasoning, the aging of wood in a dry environment;
- respiration, the evolution of CO₂ primarily by microbes;
- biological transformation, the metabolism of wood by decomposers and its transformation into new compounds.

The major factors controlling decay processes are temperature, moisture, oxygen and carbon dioxide, substrate quality, size of woody debris, and the characteristics of the decomposers. The role of most of these factors has been described only in qualitative terms, and detailed studies have been largely restricted to the laboratory. There is at present little understanding of how these factors interact to determine decay patterns in natural environments, or how they are affected by disturbances such as harvesting or site treatment.

Temperature has been shown to affect the distribution of fungi and insects in wood (Harmon et al. 1986). Most wood-decaying fungi have a temperature optimum of 25–30°C, and cannot grow above 40°C (Kaarik 1974). Species with higher tolerances tend to occur in the outer portions of CWD that are exposed to sunlight, while those with lower tolerances inhabit the lower portions of logs. Temperature also affects microbial and insect activity through its effects on relative humidity, moisture, and oxygen and carbon dioxide levels. Few field studies have examined the importance of temperature relative to other factors affecting decay rates, but Edmonds (1987) observed that minimum litter temperature explained more variation in the decay rates of twigs, cones, and branches of Douglas-fir than substrate moisture content in several closed-canopy forest types in the Pacific Northwest. However, under open conditions moisture may be the more important factor.

Optimum moisture levels for microbial decomposition vary according to the organisms involved in the decay process. Whereas basidiomycetes (fungi) can grow in wood with moisture contents ranging from 30 to 160% (dry weight basis), the ascomycetes and fungi imperfecti that cause soft rots can tolerate moisture contents up to 240% (Kaarik 1974). Much less is known about insect tolerances, although some species can live in very dry wood (Harmon et al. 1986).

Most studies indicate that, as decay proceeds, the moisture content of wood increases (Harmon et al. 1987; Sollins et al. 1987). The water-holding capacity of decayed wood may be very important in maintaining levels of biological activity under drought conditions (Harvey et al. 1987). Erickson et al. (1985) found that the FWD of several western conifer species decayed more slowly than the CWD on clearcut sites in Washington. They attributed the differences to very low dry-season moisture contents in the smaller-diameter wood. Edmonds et al. (1986) found that elevated wood of Douglas-fir decayed more slowly than surface or buried wood on similar clearcut sites in the Pacific Northwest. They concluded that lower moisture contents, as well as larger temperature fluctuations in the elevated wood, were responsible for the differences. In contrast to Erickson et al. (1985), however, decay rates of FWD were higher than those for CWD in their study and the authors were not able to explain the conflicting results of the two studies.

Chemical heterogeneity among tree species and within individual boles has a significant effect on decomposition of woody debris. Edmonds et al. (1986) found that initial wood chemistry, particularly soda solubility, was the major factor influencing the decomposition of

red alder in Douglas-fir clearcuts, whereas moisture and temperature were the dominant factors in the decomposition of Douglas-fir wood.

Invertebrates use the four major components of wood — the outer bark, the inner bark (cambium and phloem), the sapwood, and the heartwood — in very different ways. For example, bark beetles do not attack the heartwood of a bole, but consume only the inner bark, which has a much higher nutrient content. The wood borers of the family Cerambycidae will attack the wood only after feeding extensively on the inner bark (Harmon et al. 1986). In general, the concentration of nutrient elements in wood is much lower than that in other plant components such as leaves, flowers, and fruits; and organisms using this substrate are adapted to low nutrient levels. Harmon et al. (1986) note that the nitrogen content of wood appears to be suboptimal for fungi, and that additions of nitrogen generally increase the rate of wood decay. The nutrient content of decayed wood is discussed further in Section 2.5.

Competition among microorganisms for the nutrients in dead wood may affect the rate of decomposition. Gadgil and Gadgil (1975) found that the suppression of litter decomposition in the presence of external mycelia of mycorrhizal fungi on the roots of radiata pine did not appear to involve either moisture or pH as the mechanisms of suppression, and they suggested that competition for nutrients may have been involved.

In conifers, cellulose accounts for 38–53% of the dry weight of undecayed wood, hemicellulose constitutes 17–31%, and lignin, 26–34% (Harmon et al. 1986). The wood of deciduous species has more hemicellulose and less lignin on average than does conifer wood. The non-uniform distribution of cellulose, hemicellulose, and lignin within wood cells and the variation in the anatomical structure of wood have a large influence on microbial colonization (Harmon et al. 1986). Of the three major cell wall constituents, lignin is the most chemically and structurally complex and is the most difficult for microbes to break down and use. Lignin content is negatively correlated with decay rates in leafy litter, but its relationship to rates of wood decay is less clear (Harmon et al. 1986). The lignin content of wood generally increases as decay proceeds (MacMillan et al. 1977; Lambert et al. 1980; MacMillan 1988). However, higher lignin levels are not always associated with lower decay rates (Edmonds 1987; MacMillan 1988). Edmonds (1987) found that branches had both lower lignin contents and lower decay rates than twigs of the same species in several western conifers. He suggested that nitrogen concentrations, which are lower in the branches, were more important than lignin content in determining decomposition rates. Preston et al. (1990) studied changes in the organic compounds of decomposing logs of Douglas-fir, western hemlock, and western redcedar, using ^{13}C nuclear magnetic resonance spectroscopy. They observed changes that were consistent with the breakdown of hemicellulose and cellulose over time, and with increasing concentrations of lignin, waxes, and resins. Patterns were similar for Douglas-fir and western hemlock, although the latter passed through decay stages more quickly. Cedar, in contrast, showed little change in organic compounds until the decay process was well advanced, despite earlier changes in physical appearance and log density. The lack of chemical changes in cedar was attributed to slow fungal colonization, possibly due to the presence of thujaplicins in the cedar wood. There was, however, little degradation of lignin in the most decayed wood of all three conifer species. The relationship between structural and chemical composition of wood components and decomposition processes is reviewed in detail by Harmon et al. (1986).

Decay rates generally decrease with increasing bole size (Yoneda 1982; Edmonds et al. 1986; Harmon et al. 1986). However, other factors such as decreases in surface area:volume ratios, increasing proportions of heartwood with increasing size, and colonization patterns of decomposers (as influenced by environmental conditions, for example) can all confound this relationship. Not all studies have been able to establish a significant correlation between tree size and decay rate (Boddy and Swift 1984; Erickson et al. 1985; Harmon et al. 1986).

2.4.3 Classification of decayed logs

In most studies decay rates are estimated from the changes in mass or volume that occur as logs decay. On a particular site an array of aged pieces, representing a chronosequence of logs, may be selected to determine the residence times and decay rates of logs in various

stages of the decomposition process. To determine the age of the logs, historical records can be examined for the dates of catastrophic mortality events, the age of seedlings rooted on the logs can be determined, or the scars on living trees adjacent to the downed wood can be aged (Harmon et al. 1986). (Decay rates can also be estimated from the ratio of woody debris input to woody debris biomass present on a site, but this is done less commonly.)

Rather than determining the age of logs, which is often difficult to do with any precision, researchers often place logs into one of three or five decay classes based on observations of field characteristics such as degree of bark retention, presence of invading roots or fungal hyphae, or configuration or fragmentation of logs (Triska and Cromack 1980). Classification is sometimes based on the depth to which a metal rod will sink into a decaying bole (Lambert et al. 1980). Triska and Cromack (1980) describe a five decay class system (in which the level of decay increases from class 1 to class 5) that is widely used in studies in the Pacific Northwest. Definitions of the five classes are given in Appendix 5. Hope (1987) tested this classification system using multivariate analysis to study the ability of visual, chemical, and physical wood properties to discriminate amongst *amabilis* fir logs in both three- and five-decay classes. The results indicated that wood density, cellulose content, and lignin content were all good indicators of the amount of decay, and that field characteristics were not. The author recommended the use of a three-class system for a clearer separation of decay stages. However, a five-class system may be more appropriate for species that decompose more slowly than *amabilis* fir.

2.5 The Role of Woody Debris in Carbon and Nutrient Cycling

Heilman (1990) suggests that CWD is unimportant relative to other detrital pools for nutrient cycling in the forests of the Pacific Northwest because of the low concentration of nutrients in wood and bark. However, the large biomass of woody debris in these forests may make CWD more important than a relative comparison of nutrient concentrations would suggest. Table 2.2 is modified from Harmon et al. (1986) and shows for several forest types the relative contribution of nitrogen and phosphorus from CWD compared to other biomass components. Published studies have shown that CWD in western coniferous forests makes up between 8 and 19% of the total above- and belowground dry weight and between 18 and 45% of the aboveground-only dry weight. Coarse woody debris also contains 0.3–4.4% of the nitrogen and 4.2–10.6% of the phosphorus in stands. Even where annual inputs of woody debris are high, however, a greater proportion of nutrients is returned to the forest floor from foliage than from woody debris, because of the higher nutrient concentrations and shorter turnover time of leafy litter (Harmon et al. 1986; Prescott et al. 1989). As the data in Table 2.2 illustrate, the importance of woody debris to energy and nutrient cycles in forests depends to a great extent on the size and dynamics of other organic pools. Harmon et al. (1986) reviewed the few studies that contain measurements or estimates of the relative sizes of organic pools in forest ecosystems, and only a few additional studies were found during the searches undertaken for this review (Sprugel 1985; Boone et al. 1988; Alaback 1989; Prescott et al. 1989; Harmon et al. 1990).

Although the large biomass of CWD represents the largest pool of detrital carbon in many forests (Fahey 1983; Boone et al. 1988; Alaback 1989), the amount of nitrogen stored in CWD is generally small compared to the amount stored in the forest floor or in the soil (Sollins et al. 1980; Prescott et al. 1989; Arthur and Fahey 1990; Table 2.2). In a study of nutrient content of decaying boles in a subalpine forest in Colorado, however, high base cation contents in decayed wood led Arthur and Fahey (1990) to conclude that decaying boles might be important storage sites for cation nutrients, especially calcium. On sites with coarse soils that have a low cation exchange capacity, woody debris may serve a very important role in nutrient retention because of its high cation exchange capacity (J.P. Kimmins, pers. comm., University of British Columbia, Faculty of Forestry, 1991). Arthur and Fahey (1990) also observed that the highest relative nitrogen storage in dead boles was in a lodgepole pine forest where nitrogen availability was lowest.

Coarse woody debris has been described as a short-term sink and a long-term source of nutrients in forest ecosystems (Harmon et al. 1986). Nutrients accumulate over time through litterfall, throughfall, nitrogen fixation, and fungal and root colonization (Grier 1978; Jurgensen et al. 1984, 1987). These processes result in inputs of nutrients into CWD. They are distinctly different from the increase in nutrient concentrations that also occur as decay proceeds due to a decrease in wood mass and due to microbial activity. Harmon et al. (1986) suggest that colonization is probably the most important source of inputs, but only nitrogen fixation has been quantitatively assessed. Although recent studies have determined that decaying wood is a site of high levels of mycorrhizal activity, the contribution of this activity to the nutrient dynamics of woody debris is still unknown (Harvey et al. 1987). Average rates of nitrogen fixation by asymbiotic bacteria have been estimated to be in the order of $1 \text{ kg ha}^{-1} \text{ yr}^{-1}$ for several forest types in the northwest (Silvester et al. 1982; Jurgensen et al. 1987; Sollins et al. 1987). Input levels from this source are low, but may be significant in the long term or on sites where inputs from other sources, such as precipitation or cyanolichens, are equally low. Most estimates of nitrogen fixation have been based on the acetylene reduction method, which employs a theoretically derived ratio of 3:1 for acetylene reduction to fixed nitrogen. The accuracy of this method is questioned in Harmon et al. (1986) on the basis of the effects of experimental conditions on the validity of the 3:1 ratio (see also Silvester et al. 1982).

TABLE 2.2. Biomass, nitrogen, and phosphorus storage in fallen logs, snags, and other ecosystem components (modified from Harmon *et al.* 1986)

Stand type	Item ^a	Vegetation						CWD			References ^b (in Harmon <i>et al.</i> 1986)
		Fallen logs	Snags	Above-ground	Below-ground	Litter	Soil	System total	(% of above-ground)	(% of system total)	
Mixed deciduous	DW	1.60	—	121.0	35.0	3.20	120.0	280.8	1.27	0.57	Duvigneaud and Denaeyer-DeSmet 1970
	N	11.0	—	406.0	127.0	33.0	4 480.0	5060.0	2.44	0.22	
	P	0.50	—	32.0	12.0	1.4		45.90	1.47	1.09	
Mixed deciduous	DW	3.90	—	122.0	34.0	25.60		185.00	2.57	2.10	Henderson and Harris 1975
	N	9.00	—	388.0	104.0	265.0	5 080.0	5 850.0	1.36	0.15	
Coastal <i>Tsuga heterophylla</i> (26 years old)	DW	90.0	—	193.00	38.00	22.0	770.0	1113.0	29.50	8.09	Grier 1976
	N	95.00	—	335.00	32.00	171.0	33	34	15.80	0.28	
	P	11.00	—	54.00	3.00	42.0	800.0	400.0	10.30	8.87	
Coastal <i>Tsuga heterophylla</i> (121 years old)	DW	212.0	—	920.0	187.0	34.0	776.0	2130.0	18.20	9.96	Grier 1976
	N	180.0	—	780.0	157.0	265.0	34	36	14.70	0.50	
	P	33.0	—	188.0	13.0	65.0	900.0	300.0	11.50	10.60	
Old growth <i>Pseudotsuga menziesii</i>	DW	190.0	25.0	718.0	152.0	51.0	133.0	1 270.0	21.90	1690	Sollins <i>et al.</i> 1980
	N	190.0	25.0	539.0	197.0	260.0	3 720.0	4 930.0	21.20	4.36	
	P	6.7	0.8	89.1	22.6	50.2	13.00	177.0	5.11	4.24	
<i>Abies amabilis</i> (23 years old)	DW	200	63.0	53.0	25.0	48.0	220.0	429.0	45.10	19.30	Grier <i>et al.</i> 1981
<i>Abies amabilis</i> (130 years old)	DW	75.0	165.0	447.0	138.0	149.0	273.0	1 247.0	28.70	19.20	Grier <i>et al.</i> 1981

^a DW=biomass dry weight (Mg ha⁻¹); N=nitrogen (kg ha⁻¹); P=phosphorus (kg ha⁻¹).

^b Note that the references cited from Harmon *et al.* (1986) are not included in the reference list for this report. Readers should refer to the Harmon *et al.* review for the complete citation.

Nutrients are lost from decaying wood through processes such as fragmentation and leaching. Fragmentation may be the more important of the two, particularly for losses of nitrogen, but it has been less studied (Harmon et al. 1986). MacMillan (1988) observed that fragmentation was the major factor in the disappearance of downed trees of several hardwood species in an old-growth stand in Indiana. Nitrogen losses may be greater through fragmentation because both fragmentation and the nitrogen concentration of wood increase as decay progresses. This accumulation of nitrogen in decaying wood (including in the roots) has been measured in numerous studies and, as mentioned before, may be due to both nitrogen inputs and changes in nitrogen concentrations with decay (Graham and Cromack 1982; Fahey 1983; Sollins et al. 1987; Edmonds 1988; Fahey et al. 1988; Arthur and Fahey 1990). Mineralization of nitrogen has been associated with a critical carbon-to-nitrogen (C/N) ratio of approximately 100 in several studies, suggesting that mineralization is limited by nitrogen at ratios greater than 100 (Edmonds 1987; Sollins et al. 1987; MacMillan 1988). Edmonds (1987), however, observed that the critical C/N ratio for twigs, cones, and branches of four northwestern conifers was not constant, but increased with increasing decomposition rates. Ratios of nitrogen-to-phosphorous also increase as decay proceeds, converging to values of 20 for a number of species in the northwest (Sollins et al. 1987; Arthur and Fahey 1990). Harmon et al. (1986) present a set of curves showing patterns of accumulation and loss of major nutrients in dead wood over time. In the absence of large inputs in precipitation, the results of a number of studies have shown net accumulation in CWD of nitrogen and calcium over time, and net loss of potassium and phosphorus (Grier 1978; Fahey 1983; Edmonds 1987). There are, however, many exceptions to this trend, particularly with respect to the behaviour of phosphorus (Sollins et al. 1987; Arthur and Fahey 1990).

Coarse woody debris is also a source of humus and soil organic matter. Little and Ohmann (1988) found that 9–68% of the forest floor in Douglas-fir/western hemlock clearcuts in the Pacific Northwest was derived from decayed wood. Woody debris may be important in stabilizing the pool of organic matter in forests. For example, a large amount of woody material is a relatively inert mass, slowing down soil processes and buffering against rapid changes in soil chemistry (L. Lowe, pers. comm., University of British Columbia, Department of Soil Science, 1991). However, little is known about the quantitative contribution of wood to the processes of humus formation or soil development, and opinions differ widely on the importance of this contribution to long-term site productivity (Harvey 1982; McFee and Stone 1986; L. Lowe, pers. comm., 1991). The incorporation of wood into soil organic matter may, nevertheless, take several centuries (McFee and Stone 1986; Harvey et al. 1987), suggesting the importance of long-term planning in management of CWD.

As previously mentioned, there has been almost no research done on the impact of woody debris on long-term site productivity in conifer forests of the northwest. Apart from the possibility of negative impacts associated with the loss of woody debris from ecosystems, accumulation of wood can also have adverse impacts on soil properties. In cool climates, the insulating properties of wood may result in lower soil temperatures beneath logs, which in turn may affect chemical weathering rates and organic matter mineralization (K. Klinka, pers. comm., University of British Columbia, Faculty of Forestry, 1991). In addition, the observation of greater Ae horizon development beneath wood suggests that organics from the wood solution washed down through the soil may cause greater leaching of nutrients beneath decayed wood. The result may be increased rates of podzolization, as have been observed beneath organic matter accumulations in cool, moist climates (Ugolini and Mann, 1979; M.E. Harmon, pers. comm., Oregon State University, College of Forestry, 1991; K. Klinka, pers. comm., 1991).

In some of the colder and wetter biogeoclimatic zones in British Columbia, organic matter accumulation may lead to declining site productivity, as shown by the work of Van Cleve in taiga forest ecosystems in Alaska (Van Cleve et al. 1983). Although no analogous

research has been done in the forests of British Columbia, Van Cleve's results are relevant because similar forests do occur extensively in the province. In contrast, these forests are not found in Oregon and Washington, where much of our current understanding about CWD comes from. Periodic disturbances, such as fire or windthrow, may be important processes for maintaining productivity in forests with slow rates of decomposition, primarily because of temperature limitations.

The ecological consequences of large accumulations of CWD are not well known, except perhaps as they affect the fire stability of forests (Covington and Sackett 1984; Habeck 1985). Some other possible impacts include (Covington and Sackett 1984; J.P. Kimmins, pers. comm., 1991; K. Klinka, pers. comm., 1991):

- increased soil acidification and podzolization;
- slowed or conservative nutrient cycles;
- increased disease and insect infestations;
- decreased seedling recruitment;
- reduced tree growth; and
- decreased forage quality and quantity.

2.6 The Impacts of Forest Management on Woody Debris

Factors affecting the amount of woody debris on a site after harvesting include the harvesting method, the degree of utilization of cut trees, the amount of damage from logging operations, and the extent of salvage of downed wood. Several examples of the amounts of CWD on sites after harvesting are given in Table 3.2. No studies were found that compared pre- and post-harvest levels of CWD on sites, although such data might exist in the harvesting literature. Many fire studies have documented the effects of prescribed burning on fuel loads (see Feller 1982), but this information is not reviewed here.

Much of the concern over the impacts of harvesting methods, and whole-tree harvesting in particular, has focused on the loss of nutrients from sites with the removal of biomass destined to become CWD, and the consequences of this removal for long-term site productivity (Stark 1979; Clayton and Kennedy 1985; Sachs and Sollins 1986; Hendrickson 1988). The removal of bole wood in any harvest represents a large export of nutrients from a site. Clayton and Kennedy (1985) estimated that from 4% of the total ecosystem nitrogen to 21% of the potassium were removed in boles harvested from a mature ponderosa pine/Douglas-fir forest in southwestern Idaho.

Gholz et al. (1985) studied nutrient uptake by recovering vegetation and watershed solution losses in clearcuts in Oregon. They concluded that the nitrogen removed in boles (57 gm^{-2}) greatly exceeded the combined uptake and streamflow losses ($< 5 \text{ gm}^{-2}$) during the 3 years following logging. In another study, Clayton and Kennedy (1985) speculated that inputs of nutrients from precipitation, primary mineral weathering, and nitrogen fixation would restore the nutrient status of a ponderosa pine/Douglas-fir ecosystem to pre-harvest conditions within 50 years of logging. Similarly, Stark (1979) suggested that nutrient losses would be easily replaced by precipitation and weathering inputs in a Douglas-fir/western larch forest in Montana, even under the most intensive of harvesting and site preparation treatments. Although this may be the situation for interior forests, where the amount of nitrogen removed through harvesting is low relative to precipitation inputs, the same may not hold true for coastal forests, where levels of rainfall are much higher.

Sachs and Sollins (1986) used an ecosystem simulation model, FORCYTE-10, to determine the impact of harvesting intensity on nitrogen and site productivity in coastal

western hemlock forests. They found that model results were very sensitive to the calibration data used for the decomposition rate and nitrogen mineralization pattern of large and medium-size roots and woody debris. Our lack of information on these and other aspects of the ecology of woody debris indicates that field studies to collect calibration data will be necessary before the potential of simulation models can be adequately explored. Nevertheless, the results of the FORCYTE-10 application suggested that, on the rich sites in the study, there would be little reduction of nitrogen capital or site productivity over six successive 90-year rotations with conventional harvesting.

FORCYTE-11, a further development of the FORCYTE model, has also been used to simulate CWD requirements for a medium site in the Coastal Western Hemlock zone of British Columbia (Bieber 1990). Based on a 75% utilization standard of stemwood and bark, the results of the simulation suggested a retention level of $165 \text{ m}^3 \text{ ha}^{-1}$ of CWD to maintain ecological conditions over four 60-year rotations on the site. Although the model requires more calibration and testing to be widely applied, it contains a number of very useful features for studying the dynamics of CWD on sites. These include, as examples, the modelling of different organic matter pools, different wood components, input decay rates, and site conditions. The model is described in detail in Kimmins et al. (1990).

These studies indicate that the impacts of bole wood export on the nutrient status of a site depend on the nutrients stored in the forest floor and the soil. For example, Hall (1984) studied the effect of site preparation on nutrient capital in radiata pine plantations in Australia. The plantation soils contained large reserves of nitrogen, and the author concluded that raking operations, which removed only woody debris, but not fine litter or topsoil, would have little impact on the nitrogen status of the site.

Woody debris must play an extremely important role in the development of forest floor and soil organic matter, although many aspects of this relationship are poorly understood (McFee and Stone 1986; Jurgensen et al. 1990). Sprugel (1985), for example, found that the forest floor of a balsam fir forest in the northeastern United States was derived mainly from woody tissue and its decay products; < 25% came from foliage. As mentioned in the previous section, Little and Ohmann (1988) found that 9–68% of the forest floor in clearcuts in the Pacific Northwest was derived from decayed wood. Aber et al. (1978) used a simulation model to study the impacts of different rotation lengths and harvesting intensities on the characteristics of a northern hardwood forest floor. They found that rotation length had a greater impact than harvesting intensity on reductions in mass and nitrogen availability. Clearcutting on a 30-year rotation reduced the biomass to one-half that under a 90-year rotation. A rotation length of 90 years yielded stable production and soil organic matter levels when the ecosystem simulation model FORCYTE-10 was used to predict the impacts of harvesting on growth and nutrient cycling of western hemlock stands (Sachs and Sollins 1986). More intensive utilization—that is, shorter rotations, whole-tree harvesting, and commercial thinning—caused depletion of soil and forest floor nitrogen. On the nitrogen-rich site, the result of the depletion was only a small decline in long-term productivity (5%). The authors noted, however, that the effects on an infertile site might be much greater.

Shorter rotation lengths and/or more intensive utilization (over current practices) will not only reduce the amount of woody debris on sites, it will also affect its structural characteristics, such as the size class distribution (Gore and Patterson 1986). These changes could have significant impacts; for example, on the role of woody debris as habitat. Accumulation of woody debris on forest floors creates animal habitat that might be conserved in the conversion of old-growth to first-rotation forests (because of the depth of the forest floor), but not be preserved through subsequent rotations (J.P. Kimmins, pers. comm., 1991).

Woody residue management guidelines that focus on the amount and size of woody debris to be retained on sites do not address the problem of the effects on woody debris of changes in rotation lengths. Harvey et al. (1981b) suggested lag times of 100–300 years

between the time wood is produced on a site and the time it becomes incorporated into soil organic matter. They also observed that, whereas woody debris on a cool-moist site in the inland northwest accumulated mainly as surface woody residues, on a warm-moist site most of it was present as decayed wood in the soil. Changes in rotation length may have large impacts on the amount and rate of incorporation of decayed wood into soil wood, impacts which will vary with site conditions, and which will have consequences for the many roles played by woody debris in forest ecosystems (Harvey 1982).

3 QUANTITIES OF WOODY DEBRIS

This section presents information from the literature on volumes, masses, and rates of input of woody debris for coniferous forest ecosystems similar to those in British Columbia. The methods used to estimate standing volumes and biomass and rates of input are reviewed, and some of the problems associated with obtaining these estimates are discussed.

3.1 Methods for Inventory

A wide variety of methods have been used to estimate input rates and standing amounts of woody debris in coniferous forests. In developing an appropriate sampling strategy to estimate a parameter of interest, such as mean timber volume in a forested area, a number of factors must be considered. Among these are the pattern of variability within the population, the desired level of confidence in the estimate, and the resources available to undertake the survey. The methodology is well described in texts such as DeVries (1986); a detailed discussion of sampling theory is not presented in this report. In general, the high level of natural variability in the rates of input and amounts of woody debris in unmanaged forests (on which most studies have been based) means that a large number of units must be sampled to obtain estimates with reasonable precision. The nature of the material of interest (i.e., large logs lying on the ground in various angles of repose) also leads to a high potential for measurement error, and some of the sampling problems associated with CWD are further discussed below.

3.1.1 Estimating inputs

Harmon et al. (1986) refer to four ways of measuring inputs of woody debris

1. Determination of tree mortality in permanently marked plots

Tree mortality is the major source of large woody debris, and measurements of tree size at death provide estimates of the contribution of CWD to the debris pool over time. This method has been used in recent studies by DeBell and Franklin (1987) and Harcombe et al. (1990). These studies consisted of measurements made at 5-year intervals on plots established 35–55 years ago for growth and yield or ecological monitoring. The technique underestimates input rates, because branches and dead tops falling from live trees are not included. Unless the time of treefall is noted, separating the rate of input into dead standing and down material is not possible.

2. Measurement of input on cleared plots

This method is analogous to the use of litter traps for foliage. An area is initially cleared of debris and then downed woody material is collected at given time intervals. This method is commonly used for quantifying fine debris. For example, in their study in the Kananaskis Valley, Prescott et al. (1989) used plots 3 × 3 m in size from which all woody debris, 1–4 cm in diameter, was removed annually.

Plot size, or total plot area, must be larger for larger material. Instead of clearing plots, researchers can mark trees with paint at the beginning of a study and collect information on those that fall during the study period. Lang (1985) used this method in 0.4-ha plots on several sites which were monitored for 8 years. Similarly, Prescott et al.

(1989) used this method in 0.06-ha plots, although this area is probably too small for an accurate estimate of input rates to be obtained. It is suggested that a minimum of 5 hectare-years is necessary to obtain a reasonable initial estimate of CWD inputs.

3. Measurement of inputs along line transects

Instead of using plots, Tritton (1980, as cited in Harmon et al. 1986) measured input rates along lines. Lines are, in effect, one-dimensional plots and are an efficient way of sampling for CWD, as long as the appropriate precautions for line intersect sampling are taken into account (see Section 3.1.2).

4. Stand reconstruction and other disturbance history studies

Disturbance is the major determinant of tree mortality in many forest ecosystems, and therefore the pattern of input of woody debris will often be strongly related to disturbance history. Lorimer (1985) presents a review of the methodology for analyzing forest disturbance history, including age-class analysis, fire scars, forest floor studies, growth increment patterns, and structural characteristics of wood. These methods can provide an indication of the past pattern of disturbance and tree mortality, and can be used to estimate the input of woody debris into forest stands.

3.1.2 Estimating volume, surface area, and projected area

The volume of CWD can be estimated in two ways: by measuring dimensions of woody material on a number of fixed-area sample plots; or by using the line intersect method. Both approaches have been used extensively to estimate amounts of woody debris.

Two standard formulas are used to obtain volume estimates of logs from measurements of length and diameter: Smalian's formula, which uses length and small- and large-end diameter; and Huber's formula, which uses length and diameter at the mid-point. Smalian's formula is more appropriate where the log shape approximates a segment of a cone; Huber's is better when the taper of the logs approximates the frustrum of a second-degree paraboloid.

Fixed-area plots

Fixed-area plots vary in size and shape, and plot number and size depend on population variability and the desired sampling error for the study. Most recent studies have used rectangles or squares, ranging in size and number from eighteen 0.0016-ha plots per stand (Mattson et al. 1987) to a complete inventory of 2.5 ha (Harmon et al. 1987).

Circular plots present some problems with measurement error. It is difficult, for instance, to determine the portion of a log to include when it is only partly in the plot. Consequently, rectangles or squares are the preferred shape for fixed-area plots. However, Spies et al. (1988) used 0.1-ha circular plots in their extensive study of the characteristics of old-growth Douglas-fir forests in Washington and Oregon.

Fixed-area plots are the only way to map pieces of CWD, or to estimate projected log cover. The volume of standing dead trees can be estimated by using fixed-area plots, or by using variable-radius plots where an estimate of basal area is made based on a count of trees with a basal-area wedge. The basal-area estimate is multiplied by an estimate of the mean height of the dead trees and a taper factor to obtain an estimate of volume.

Line intersect sampling

An alternative to measuring the volume of material in a quadrat is to sample using the line intersect method. This method has been used extensively in the field to estimate the volume of woody fuel in fire studies (Brown 1974; Pickford and Hazard 1978) and the volume of logging residues (Van Wagner 1982). Lines, rather than plots, are randomly located within a target survey area, with each line representing one cluster. The total for the variable of interest, which is measured on all items that intersect the line, is equal to the sum

of all the measurements, divided by their corresponding probabilities of intersecting the line. If the variable of interest is log volume, then:

$$Y_i = \sum_{j=1}^{m_i} \frac{V_{ij}}{P_{ij}}$$

In equation (1), Y_i is the total volume of all logs measured on line i , V_{ij} is the volume of log j on line i , and P_{ij} is the probability of log j intersecting line i . By obtaining the log volume and determining the probability of intersection, Y_i can be used as a sample to estimate mean volume per hectare, or total volume on a target area. If a number of lines are measured, the associated variances and confidence interval of the sample can be obtained. The probability of intersection is a function of the line length and the target area.

There are three possible approaches to calculating volume using the line intersect method: (1) the diameter of intercepted logs can be measured at both ends and the volume calculated using Smalian's formula; (2) logs can be measured for diameter at the mid-point and volumes calculated using Huber's formula; or (3) the diameter of logs can be measured at the point of intersection, and Huber's formula used (which assumes that the average point of intersection is the log mid-point). Van Wagner and Wilson (1976) compared volumes from these three schemes and the time needed to obtain measurements. They concluded that the third method was the most time-efficient, with no loss of accuracy when compared with the other two approaches. However, the method depends on the number of crossings being large enough that the variability in the point of crossing is accounted for.

With the third method, equation (1) becomes:

$$Y_i = \frac{\pi^2 \leftarrow A}{8 \leftarrow L} \sum_{j=1}^{m_i} \frac{d_{ij}^2}{10\,000}$$

This will yield a volume in cubic metres for an area of size A in square metres. If the area is 1 ha, then:

$$Y_i = \frac{\pi^2}{8 \leftarrow L} \sum_{j=1}^{m_i} d_{ij}^2$$

Other factors that need to be considered are:

- the development of a correction factor for logs not lying flat on the ground;
- the establishment of measurement rules for irregularly shaped pieces that are crossed twice;
- the degree to which logs approximate a cylinder, or the frustrum of a second-degree paraboloid, which allows for the correct application of Huber's formula; and
- the orientation of the logs and the sampling pattern of the lines.

There is a trade-off between line length and the number of lines required to obtain a desired sampling precision. This is similar to the relationship between plot size and number of plots in a plot-based survey. The line length should be long enough to satisfy the requirement that, on average, the mid-point diameter is measured. Brown (1974) suggests that for larger

pieces (e.g., > 7.5 cm diameter), a length of at least 10 m should be used. Systematic location of randomly oriented lines is probably the most efficient approach, as long as precautions are taken against bias in the systematic layout.

The general evidence from the literature indicates that the line intersect method can be more efficient than fixed-area plots (Van Wagner 1982; Hazard and Pickford 1984, 1986). However, for logging residue and fire fuel surveys, the sampling effort required to obtain estimates within $\pm 10\%$ of the mean may be high using either method. The line intersect method reduces much of the measurement error associated with determining whether pieces are in or out of fixed plots.

A number of recent studies of fuel loadings, following harvesting and in natural stands, have used a variation of the line intersect method. This method employs an equilateral triangular transect with three 30-m sides (for details see Trowbridge et al. 1986). The triangular layout is used to minimize bias in situations where the logs are not randomly oriented (e.g., after cable logging or a wind storm) and to cover the variation in fuel distribution. This approach is also more efficient than laying out three randomly located transects. In a recent evaluation of the method in natural lodgepole pine stands, Delisle et al. (1988) compared the estimates obtained from measurements on just one side of the triangle, with measurements on two sides and all three sides. They found that, regardless of the number of sides measured, the standard error for fuels < 7.0 cm was at most 20% of the mean, while the standard error for fuels > 7.0 cm was always more than 20% of the mean. For the larger fuels, more sampling was needed to achieve a lower standard error, but because of the correlation between different sides of the same triangle, additional sampling using the triangular sampling pattern did not provide a great reduction in standard error of the mean. Delisle et al. (1988) suggested that, rather than laying out triangles, Brown's (1974) approach of using independently located transects was more efficient in the types of stands relevant to their study.

3.1.3 Estimating mass

Mass can be estimated independently of volume if all the woody debris collected on a sample plot is weighed. This is obviously impractical for large pieces of debris, and the most common approach for obtaining biomass estimates of woody debris is to convert volume to mass by using an estimate of wood density for different decay classes. Density varies considerably between tree species and between logs in different stages of decay, and is more difficult to determine accurately than is volume. Decay classifications using visually identifiable properties of logs are now quite common (see, for example, Arthur and Fahey 1990). Typically, in studies where mass is calculated, mean wood density is first determined for a subsample of logs from each decay class and this figure is then multiplied by the volume estimate for each class. To determine the volume of individual pieces of wood, samples can be immersed in water and the displacement volumes measured. Pieces at an advanced stage of decay can be dipped in liquid paraffin before being immersed in water (Prescott et al. 1989).

There are methodological problems associated with the determination of both species and decay class for CWD. Once the bark of logs has sloughed and the structure becomes crumbly, the identification of species requires microscopic examination of wood structure, and may be impossible in highly decayed material. Also, logs do not decay uniformly, and one part of a large log, typically the portion in contact with the ground, may be at a more advanced stage of decay than aboveground portions. In general, estimates of density should be interpreted conservatively, as should the estimates of mass derived from them.

3.1.4 Statistical considerations

The frequency distribution of measurements of CWD volume or mass do not typically conform to those of a normally distributed population. Instead, distributions tend to be

skewed, with higher numbers of plots containing small volumes of material, and large-sized pieces contributing greatly to volume and mass estimates. Because of high spatial variability, sample variances associated with biomass estimates for large-sized pieces are high. This means a large number of samples must be collected to obtain a standard error within 20% of the mean. This may be reduced by stratifying the target population on the basis of factors that contribute to variability in biomass.

3.2 Estimates of Input Rates and Biomass for Forest Types Found in British Columbia

3.2.1 Rates of input

Aboveground input rates of woody debris are shown in Table 3.1. For forests of the northwest, these range from 0.17 Mg ha⁻¹yr⁻¹ in lodgepole pine stands in Colorado, to 30 Mg ha⁻¹yr⁻¹ in Douglas-fir stands in Oregon. Factors affecting variation in input rates among forest types include stand productivity, individual tree sizes, and the characteristics of disturbances that occur during the measurement period (which can markedly influence the overall input rate, as illustrated by the very high input rate for Douglas-fir in the Wright and Lauterbach study [1958 study, as cited in Harmon et al. 1986]).

Data from studies with longer measurement periods (e.g., Harcombe et al. 1990) are more representative of long-term input rates in coastal coniferous systems. Their data indicate that the rate of input varies with stand age, remaining below 2 Mg ha⁻¹yr⁻¹ until age 85, and increasing to 6 Mg ha⁻¹yr⁻¹ at 138 years in these forests. The increase between ages 85 and 138 is explained by increased tree mortality from windthrow. Lang (1985) also observed increases in input rates with increasing stand age in a subalpine fir forest in the eastern United States. With one exception, no information was obtained on input rates for deciduous species in the northwest and, as is evident from Table 3.1, values are available for only a few of the coniferous forest types in the province. All of the values in Table 3.1 are from studies outside British Columbia, and it is not known how similar the input rates in the province's forests are to rates in related forest types in other areas of the northwest.

3.2.2 Volume and mass

Data on volumes and masses of CWD taken from published sources for forest types within British Columbia, for related forest types in the United States and Alberta, and for several representative types from other localities are presented in Table 3.2. Volumes of standing and downed material for similar forest types to those found in British Columbia range from approximately 60 m³ha⁻¹ in pine and Douglas-fir stands in Montana and Idaho, to over 1400 m³ha⁻¹ in coastal Douglas-fir stands in Oregon. Mass varies from 10 Mg ha⁻¹ in montane spruce forests in Alberta, to over 580 Mg ha⁻¹ in coastal Douglas-fir stands in Oregon. Harmon et al. (1986) discuss the little that is known about quantities of CWD in natural forests. Additional estimates of volume and mass have been added to the literature since the publication of their review, but these have not added much to our understanding of the ecological significance of the amount of woody debris in forests.

TABLE 3.1. Aboveground input of CWD for temperate coniferous ecosystems. Includes data from Table 1 of Harmon et al. (1986) and additional recent studies. Footnotes follow Table 32.

Relevant BGC zone ^a	Major species	Location	Stand age	Sample Period (yr)	Sample Area (ha)	Biomass Input m ³ ha ⁻¹ yr ⁻¹	Reference
CDF/CWH	<i>Pseudotsuga menziesii</i> (old)	Oregon and Washington	450	2	10.2	7.0	Grier and Logan 1977 ^b
		Washington	500	29	41.6	4.54	Sollins 1982 ^b
	<i>Pseudotsuga menziesii</i> (mature)		—	10	80–265	0.5–30	Wright and Lauterbach 1958 ^b
CWH	<i>Pseudotsuga menziesii</i> , <i>Tsuga heterophylla</i>	Washington	110	16–46	0.2–2.8	1.55–4.25	Sollins 1982 ^b
			450	36	3.0	2.4 ^c	De Bell and Franklin 1987
CWH	<i>Picea sitchensis</i> , <i>Tsuga heterophylla</i>	Oregon	121	40	0.4	2.8	Grier 1978 ^b
		Washington	125	43	4.5	3.11	Sollins 1982 ^b
			—	6	4.0	4.1	Harmon, unpublished ^b
CWH	<i>Picea sitchensis</i> , <i>Tsuga heterophylla</i>	Washington	37	53	3.6	0–2	Harcombe et al. 1990
			85	53	3.6	2.0	
			138	53	3.6	6.0	
CWH/MH	<i>Abies amabilis</i> (second growth)	Washington	—	5	0.13	0.3	Grier et al. 1981 ^b
PP	<i>Pinus ponderosa</i>	Arizona	—	50	15.8	0.25	Avery et al. 1976 ^b
IDF	<i>Pseudotsuga</i> , <i>Abies</i> , <i>Picea</i>	Arizona	—	5	—	–3.8	Gottfried 1978 ^b
ICH/ESSF	<i>Pinus contorta</i>	Colorado	—	12	8.0	0.17 ^c	Alexander 1954 ^b
ESSF	<i>Abies lasiocarpa</i> , <i>Picea engelmannii</i>	Alberta	200	3	0.06–0.18	0.76	Prescott et al. 1989
ESSF	<i>Picea engelmannii</i> , <i>Abies lasiocarpa</i>	Colorado	—	11	12.8	0.18	Alexander 1956 ^b
MS	<i>Pinus contorta</i>	Alberta	90	3	0.06–0.18	0.93	Prescott et al. 1989
MS	<i>Picea abies</i> , <i>Pseudotsuga menziesii</i>	Alberta	120	3	0.06–0.18	0.75	Prescott et al. 1989
N/A	<i>Picea rubens</i> , <i>Abies balsamea</i>	Maine	—	20	—	1.45 ^c	Frank and Blum 1987 ^b
N/A	<i>Picea abies</i> , <i>Carpinus betulus</i>	Poland	400	10	1.0	~1.6 ^c	Falinski 1978 ^b
N/A	<i>Pinus banksiana</i>	Minnesota	—	30	—	~2.3 ^c	Jensen and Zasada 1977 ^b
N/A	<i>Pinus strobus</i> , <i>Acer saccharum</i>	Minnesota	—	26	0.48	1.1 ^d	Peet 1904 ^b
N/A	<i>Populus tremuloides</i>	New Mexico	—	5	3.4	0.45	Gosz 1980 ^b
N/A	<i>Abies balsamea</i> , <i>Betula</i> sp.	Eastern USA	44	8	0.4	0.25	Lang 1985
			78	8	0.4	0.82	

Footnotes follow Table 3.2.

Successional patterns in quantities were discussed in Section 2.2.2. Briefly, the evidence indicates that the amount of CWD is high early in the development of a stand following a disturbance, declines during the stem exclusion phase (which occurs at stand ages 100–150 years [Oliver 1981]), and increases again as a stand develops to the old-growth stage late in the successional sequence. These observations are supported by the recent study of Spies et al. (1988) for Douglas-fir stands of Washington and Oregon. The volume and mass data in Table 3.2 also indicate that quantities of woody debris are generally higher in older stands. Brown and See (1981) measured volumes of dead fuels in various forest types in Idaho and Montana. They observed that amounts of CWD were high in old-growth stands but variability was low, whereas in immature and mature stands the variability was much greater.

In general, available data suggest that quantities of downed CWD are higher in coniferous forests than in deciduous forests (see Table 5 in Harmon et al. 1986). For forest types found in the northwest, the highest quantities of wood are found in mature and older coastal forests. The second highest values are for old-growth interior forests of cedar-hemlock, and higher-elevation spruce-fir. Amounts of CWD are lower in interior pine forests, and lowest in the northern mixed spruce-birch-willow forests. High levels of CWD in young stands occur when major disturbances such as logging, fires, or severe wind storms result in large inputs of woody debris. At present, comparisons among forest types can be based on estimates from only a few studies. These studies differed greatly in their objectives, methodologies, and site conditions, and these differences limit the usefulness of comparisons among their results.

As indicated in Table 3.2, data on quantities of CWD are scarce for most of the major forest types in British Columbia. Most values come from coastal stands of Douglas-fir, Sitka spruce, western hemlock, and/or western redcedar. A number of estimates also exist for interior pine-fir, pine-larch, and pure pine stands, and also for high-elevation spruce-fir forests. Data are scarce for other forest types, particularly northern spruce forests, and interior spruce-cedar-hemlock forests. The data currently available are not sufficient to characterize levels of CWD for most of the province's major forest types.

TABLE 3.2. Volumes, biomass and projected area of woody debris for various temperate ecosystems, summarized by relevant British Columbian biogeoclimatic zone

Relevant BGC zone ^a	Major species	Location	Stand age (years)	Lower diameter limit (cm) ¹⁰	Volume (m ³ ha ⁻¹)		Biomass (Mg ha ⁻¹)		Projected area (%) (total)	References
					logs	snags	logs	snags		
					CDF/CWH	<i>Pseudotsuga, Tsuga</i>	Oregon	450		
CDF/CWH	<i>Pseudotsuga, Tsuga</i>	Washington	450	15.0	396	270	81.0	54.0	—	Sollins 1982 ^b
CWH	<i>Abies amabilis</i>	Oregon	23	10.0	—	—	20.0	60.0	—	Grier et al. 1981b
			130	10.0	—	—	75.0	157.0	—	
CWH	<i>Picea, Abies</i>	Oregon	+200	7.50	416	—	97.0	—	—	Harmon unpubl. ^b
CWH	<i>Picea, Tsuga</i>	Washington	+200	15.0	—	—	93.0	26.0	6.2	Graham and Cromack 1982 ^b
	<i>Tsuga, Picea</i>		+200	15.0	—	—	167.0	40.0	11.4	
CWH	<i>Pseudotsuga, Tsuga</i>	Oregon	100	15.0	491	153	108.0	34.0	15.3	Franklin et al. unpubl. ^b
			130	15.0	309	167	65.0	42.0	15.1	
			250	15.0	488	339	93.0	80.0	24.5	
			450	15.0	490	349	82.0	84.00	20.3	
			750	15.0	554	635	97.0	105.0	25.1	
CWH	<i>Pseudotsuga, Tsuga</i>	Oregon	+1000	15.0	574	376	115.0	81.0	23.7	
			3	20.0	673	—	249.0	1255.0	—	Huff 1984 ^b and Agee and Huff 1987
			19	20.0	981	—	342.0	301.5	—	
			110	20.0	389	—	138.0	45.2	—	
			181	—	376	—	130.0	40.8	—	
			515	—	1421	—	490.0	93.5	—	
CWH	<i>Tsuga heterophylla</i>	Oregon	130	15.0	—	—	212.0	—	—	Grier 1978 ^b
CWH	<i>Pseudotsuga menziesii</i>	Oregon	-65	10.0	248	175	43.0	35.0	9.8	Spies et al. 1988
		Washington	-121	10.0	148	101	20.0	23.0	6.5	
			-404	10.0	313	221	66.0	57.0	9.3	
CWH	<i>Tsuga heterophylla, Picea sitchensis</i>	Alaska	—	small	—	—	74.3	—	—	Larson 1991 unpubl. ^f
CWH	<i>Thuja plicata</i>	Alaska	—	small	—	—	117.5	—	—	Larson 1991 unpubl. ^f
CWH	<i>Pinus contorta</i>	Alaska	—	small	—	—	1.2	—	—	Larson 1991 unpubl. ^f
CWH	<i>Populus</i>	Alaska	—	small	—	—	7.6	—	—	Larson 1991 unpubl. ^f

Relevant BGC zone ^a	Major species	Location	Stand age (years)	Lower diameter limit (cm) ¹⁰	Volume (m ³ ha ⁻¹) logs	Biomass (Mg ha ⁻¹) snags	Projected area (%) (total) logs	References snags		
CWH	<i>Alnus rubra</i>	Alaska	–	small	–	–	62.3	–	–	Larson 1991 unpubl. ^f
CWH	<i>Pseudotsuga menziesii</i>		22	–	–	–	0.60	–	–	Turner 1975 ^g
			30	–	–	–	1.40	–	–	
			36	–	–	–	6.30	–	–	
			42	–	–	–	3.50	–	–	
			49	–	–	–	7.40	–	–	
			73	–	–	–	56.4	–	–	
			95	–	–	–	37.2	–	7	
			450	–	–	–	55.2	–	–	
CWH	<i>Chamaecyaris nootkatensis</i>	Alaska	–	small	–	–	62.1	–	–	Larson 1991 unpubl. ^f
ESSF	<i>Picea engelmannii, Abies lasiocarpa</i>	Colorado	300–500	–	243.1	54.3	70.0	18.5	9.0	Arthur and Fahey 1990
ESSF	<i>Abies lasiocarpa, Picea engelmannii</i>	Montana	old growth	7.6	–	–	145.7	–	–	Jurgensen et al. 1987
ESSF	<i>Picea engelmannii, Abies lasiocarpa</i>	Montana	wide range	7.5	79.8–255.5 ^h	–	53.00	–	–	Brown and See 1981 ^b
ESSF	<i>Abies lasiocarpa, Picea engelmannii</i>	Alberta	200	small	–	–	20.0	–	–	Prescott et al. 1989
ESSF	<i>Picea engelmannii, Abies lasiocarpa</i>	Montana	mature	7.5	60.50	15.40	–	–	–	Bensen and Schlieter 1980
ICH	<i>Tsuga heterophylla, Pseudotsuga menziesii</i>	Montana	old growth	7.6	–	–	83.2	–	–	Jurgensen et al. 1987
ICH	<i>Tsuga heterophylla, Thuja plicata</i>	Idaho	old growth	7.6	–	–	154.3	–	–	Jurgensen et al. 1987
		Montana		7.5	102.2–273.7 ^h	–	66.0	–	–	Brown and See 1981
ICH	<i>Abies grandis</i>	Montana	mature	7.5	174.7	19.6	–	–	–	Bensen and Schlieter 1980
IDF/ICH	<i>Tsuga heterophylla, Larix occidentalis, Pseudotsuga menziesii</i>		mature	small	254.2	–	–	–	–	
IDF	<i>Pinus contorta</i>	Montana	mature	0-7.5	–	–	9.00	–	–	Bensen and Schlieter 1980
			mature	7.50	77.7	60.5	–	–	–	

Relevant BGC zone ^a	Major species	Location	Stand age (years)	Lower diameter limit (cm) ¹⁰	Volume (m ³ ha ⁻¹) logs	Biomass (Mg ha ⁻¹) snags	Projected area (%) (total) logs	References snags		
	<i>Larix occidentalis</i>		mature	7.50	10.4	63.7	–	–	–	
	<i>Pseudotsuga menziesii</i> (moist)		mature	7.50	59.7	22.4	–	–	–	
IDF	<i>Pseudotsuga menziesii</i> (dry)		mature	7.50	53.8	7.0	–	–	–	
	<i>Pinus contorta</i>	S.E. Wyoming	105	small	–	–	20.80	3.00	–	Fahey 1983
IDF	<i>Pseudotsuga menziesii</i> , <i>Larix occidentalis</i>	Montana	240	small	–	–	1.50	41.30	–	Harvey et al. 1981 ^b
IDF	<i>Pseudotsuga menziesii</i> , <i>Larix occidentalis</i>	Montana	mature	7.60	–	–	45.10	–	–	Jurgensen et al. 1987
IDF	<i>Larix occidentalis</i>	Montana	–	7.5	82.6-163.8 ^h	–	40.0	–	–	Brown and See 1981 ^b
IDF	<i>Pinus contorta</i>		7.50	69.3-127.4 ^h	–	32.00	–	–	–	
IDF	<i>Pinus contorta</i> , <i>Larix occidentalis</i>	E. Washington	–	2.50	–	–	17.40	29.40	–	Gower and Grier 1989
IDF/MS	<i>Abies lasiocarpa</i> , <i>Pseudotsuga menziesii</i> , <i>Larix occidentalis</i>		mature	small	430.3	–	–	–	–	
MH	<i>Tsuga mertensiana</i> , <i>Pinus contorta</i>	Oregon	225	1 m (log length)	–	–	25.0	–	–	Boone et al. 1988 ⁱ
			0-30	1 m (log length)	–	–	130.00	–	–	
			30-60	1 m (log length)	–	–	60.00	–	–	
			~90	1 m (log length)	–	–	25.0	–	–	
MH	<i>Abies lasiocarpa</i>	Washington	mature	small	–	–	35.0	–	–	Taylor and Fonda 1990
MH	<i>Tsuga mertensiana</i>	Alaska	–	small	–	–	28.40	–	–	Larson 1991 unpubl.
MS	<i>Pinus contorta</i>		90	small	–	–	16	–	–	Prescott et al. 1989
MS	<i>Picea</i> , <i>Abies</i> , <i>Pseudotsuga menziesii</i>		120	small	–	–	10.10	–	–	Prescott et al. 1989
MS	<i>Pseudotsuga</i> , <i>Abies</i> , <i>Picea</i>	Montana	–	7.50	125	–	42.00	–	–	Sackett 1979b
PP	<i>Pinus ponderosa</i>	Arizona	200	small	–	–	23.30	–	–	Covington and Sackett 1984

Relevant BGC zone ^a	Major species	Location	Stand age (years)	Lower diameter limit (cm) ¹⁰	Volume (m ³ ha ⁻¹) logs	Biomass (Mg ha ⁻¹) snags	Projected area (%) (total) logs	References snags		
PP	<i>Pinus ponderosa</i>	Montana/ Idaho	old growth	7.60	–	–	20.0	–	–	Jurgensen et al. 1990
PP	<i>Pinus ponderosa</i>	E. Washington	mature	small	–	–	11.35	–	–	Taylor and Fonda 1990
PP	<i>Pinus ponderosa</i>	Montana/ Idaho	–	7.50	54	–	18.00	–	–	Sackett 1979 ^b
SBS	<i>Abies lasiocarpa, Pinus contorta</i>	Smithers	1-2 (post-harvest)	small	–	–	50.50	–	–	Macadam 1987
			1-2 (post-harvest and burn)	small	–	–	26.10	–	–	Macadam 1987
SBS	<i>Pinus contorta, Abies lasiocarpa</i>	Smithers	1-2 (post-harvest)	small	–	–	59.6	–	–	Macadam 1987
			1-2 (post-harvest and burn)	small	–	–	39.8	–	–	Macadam 1987
SBS		Prince George	6-12	small	148.6	–	–	–	–	Nowotny et al. 1990 unpubl. ^k
					210.7	–	–	–	–	
					20.0	–	–	–	–	
SWB	<i>Populus, Betula, Alnus, Picea</i>	Alaska	–	small	–	–	12.8	–	–	Larson 1984
SWB	<i>Salix, Betula, Ericaceae</i>	Alaska	–	small	–	–	41.1	–	–	Larson 1984
BWBS	<i>Picea glauca, Picea mariana</i>	Alaska	–	–	–	–	4.5	–	–	Larson 1984
N/A	<i>Sequoia sempervirens, Pseudotsuga menziesii, Tsuga heterophylla</i>	California	old growth	25	957.00	–	200.00	–	–	Bingham and Sawyer 1988
N/A	<i>Acer saccharum, Betula alleghaniensis,</i>	Eastern USA	1 (cut)	small	–	–	86.40	–	–	Gore and Patterson 1986

Relevant BGC zone ^a	Major species	Location	Stand age (years)	Lower diameter limit (cm) ¹⁰	Volume (m ³ ha ⁻¹) logs	Biomass (Mg ha ⁻¹) snags	Projected area (%) (total) logs	References snags		
	<i>Fagus grandifolia</i>		15 (cut)	–	–	–	32.4	–	–	
			50 (cut)	–	–	–	32.10	–	–	
			100 (cut)	–	–	–	54.40	–	–	
			>250 (uncut)	–	–	–	29.90	–	–	
			selectively cut	–	–	–	21.50	–	–	
N/A	Uplands <i>Sequoiadendron giganteum</i>	California	old growth	15	340.00	80.9	110.7	27.4	6.9	Harmon et al. 1987
	Riparian <i>S. giganteum</i>			–	1104.50	55.9	383.0	16.60	9.3	
	Dry <i>Abies concolor</i> , <i>Pinus lambertiana</i>			–	151.0	130.4	32.6	42.90	6.4	
	<i>Abies concolor</i> , <i>Abies magnifica</i>			–	151.0	178.3	48.7	51.90	9.6	
	Riparian <i>P. lambertiana</i> , <i>Abies concolor</i>			–	242.9	68.2	67.1	22.50	7.0	
	<i>Pinus jeffreyi</i>			–	340.0	80.9	110.7	27.40	7.0	
N/A	<i>Abies balsamea</i> , <i>Betula papyrifera</i>	New Hampshire	44	5	–	–	21.0	–	–	Lang 1988
			78	5	–	–	14.0	172.0	–	
N/A	<i>Quercus</i> , <i>Carya</i> , <i>Fagus</i> , <i>Acer</i>	Indiana	mature	5	–	–	17.9	–	–	MacMillan 1988
N/A	Mixed hardwoods	Appalachians	post-harvest	small	–	–	129.7	–	–	Mattson et al. 1987
			1	–	–	–	96.1	–	–	
			6	–	–	–	60.8	–	–	
N/A	Mixed pine	Tennessee	50+	7.5	~30	–	7	–	–	Harmon unpubl. ^b
			–	–	–	–	11	–	–	
N/A	<i>Picea mariana</i> , <i>Cladonia stellaris</i>	N. Quebec	0	–	–	0	27.5	–	–	Auctair 1985
			1	–	–	0	24.0	–	–	
			3	–	–	0	13.5	–	–	
			4	–	–	0	23.1	–	–	
			5	–	–	0	23.3	–	–	

Relevant BGC zone ^a	Major species	Location	Stand age (years)	Lower diameter limit (cm) ¹⁰	Volume (m ³ ha ⁻¹) logs	Biomass (Mg ha ⁻¹) snags	Projected area (%) (total) logs	Referenc es	
								logs	snags
			7	–	–	8.00	21.7	–	–
			15	–	–	21.00	17.0	–	–
			47	–	–	25.0	3.5	–	–

^a References cited from Harmon et al. (1986) are not included in the reference list for this report. Readers should refer to the Harmon et al. review for the complete citation. a Relevant BGC zone describes what the authors feel is the nearest related biogeoclimatic zone in British Columbia to those forests studied. N/A indicates no relevant British Columbia zone.

Forested biogeoclimatic zones of British Columbia

1.	BWBS	Boreal White and Black Spruce
2.	CDF	Coastal Douglas-fir
3.	CWH	Coastal Western Hemlock
4.	ESSF	Engelmann Spruce–Subalpine Fir
5.	ICH	Interior Cedar–Hemlock
6.	OF	Interior Douglas-fir
7.	MH	Mountain Hemlock
8.	MS	Montane Spruce
9.	PP	Ponderosa Pine
10.	SBPS	Sub-Boreal Pine–Spruce
11.	SBS	Sub-Boreal Spruce
12.	SWB	Spruce–Willow–Birch

^b This information was taken from tables in Harmon et al. 1986. Input data were presented in Table 1 and quantities data were presented in Table 5.

^c Note in Harmon et al. 1986: assumes density of 0.4 Mg m⁻³.

^d Note in Harmon et al. 1986: converted data from Figure 1 to biomass using equations in Ker (1980) and Tritton and Hornbeck (1982).

^e Calculated from volume assuming a density of 0.4 Mg m⁻³.

^f Unpublished data from F. Larson, U.S. Dep. Agric. For. Serv. PNW Research Station, Anchorage, Alaska.

^g From J. Turner. 1975. Nutrient cycling in a Douglas-fir ecosystem with respect to age and nutrient status. Ph.D. thesis. University of Washington, Seattle, Wash. Data provided by P. Comeau, British Columbia Ministry of Forests, Research Branch, Victoria, British Columbia

^h Additional information calculated from the article.

ⁱ Estimated from Figures 1 and 3.

^j Small = < 2 cm diameter.

^k From Nowotny, C., T.P. Sullivan, and A.S. Harestad. 1990. Woody debris and abundance of rodents on clearcuts in sub-boreal spruce forest. Unpublished manuscript.

3.3 Review of Existing Sources of Data on Woody Debris

In general, there is little information available on woody debris in existing inventories in the province. Timber inventories contain some data, but non-merchantable material is not included and dead material is not a sampling priority. The fuel load data are useful but restricted to post-harvest sites and forest types in which burning is used as a management tool. The biogeoclimatic classification (BGC) data do not include measurements of downed wood, so quantities cannot be estimated. None of the inventories contain information on soil or forest floor wood (apart from a general description in the BGC information) and, except for size class estimates in the fuel inventory, none contain information on fine woody debris. Nevertheless, some general information may be obtained from these sources and each one is reviewed below for its potential usefulness and the accessibility of data on woody debris.

1. Timber inventory database

Contact: Joe Braz, Inventory Branch, Victoria.

Number of plots: approximately 65 000.

Location (range of BGC zones if known): widely distributed throughout the province for commercial forest types.

Potentially useful information: contains volume information on dead standing trees >10 cm dbh; wood is classified as sound, dead potential (>50% usable), and dead useless (<50% usable); downed wood is included if potentially useful.

Condition of data: data have been summarized by inventory region (geographically defined) and are in the Stand and Stock Tables for the province; data are stored on plot sheets in files with the Inventory Branch.

Evaluation: the database is unwieldy, and considerable time would be needed to access and extract the useful information; the quality of the data is questionable because inventorying of dead material was not a sampling priority; decayed downed wood and non-merchantable species were not inventoried.

2. Timber inventory database – permanent growth and yield sample plots

Contact: Joe Braz, Inventory Branch, Victoria.

Number of plots: 2500.

Location (range of BGC zones if known): well distributed in commercial forest types throughout the province.

Potentially useful information: contains information on mortality in stands ranging in age from 20 to 140 years; data for some plots have been collected since the 1920's, but most plots were established in the 1960's; plots are remeasured every 10 years for volume increments.

Condition of data: data have been summarized by inventory region and are stored in a computerized database that is currently being reorganized; plots are being classified into BGC zones, so that ultimately the relationship between productivity and zone can be examined.

Evaluation: reorganization will make the data more accessible; the mortality data will be useful for estimating input rates in regrowth stands; input rates could then be correlated with stand age and productivity; decay rates might be estimated using mortality data and current condition of dead trees.

3. Prescribed fire assessment data

Contact: John Parminter, Protection Branch, Victoria.

Number of plots: approximately 50.

Location (range of BGC zones if known): Engelmann Spruce–Subalpine Fir, Sub-Boreal Spruce, Interior Cedar–Hemlock, Montane Spruce, Interior Douglas-fir, Coastal Western Hemlock, Coastal Douglas-fir.

Potentially useful information: volumes of post-harvest woody debris <7 cm in diameter (by size class) and >7 cm in diameter (individual measurements) before and after burning, by species or decay (if wood is sound but species unknown, classification is “U”; if unidentified and decayed, then classified “D”).

Condition of data: database is computerized and easy to access; the hard-copy format is also useful and additional information on species and decay could be easily obtained.

Evaluation: the database contains useful summaries of the post-harvest volumes of downed woody debris; volumes of unidentified and decayed wood might provide a rough indication of pre-harvest volumes; if plots could be relocated, then long-term dynamics could be investigated; standing dead is inventoried separately; there are problems with the sampling method—only pieces that are >50% above ground are measured; sampling intensity within the target area is low; estimates of the mean may have large standard errors.

4. Biogeoclimatic classification ecoplots

Contact: Del Meidinger, Research Branch, Victoria.

Number of plots: approximately 4 000.

Location (range of BGC zones if known): the information from these plots was used in the development of the BGC system; all forested zones have been sampled.

Potentially useful information: the number of dead standing and downed trees/plot by species, vegetation layer and snag class (1 = dead, 2 = loose bark, 3 = clean, 4 = broken, 5 = decomposed, 6 = down material, 7 = stump); estimate of % decayed wood as a surface substrate (only if >10 cm in thickness if <10 cm thick, then classified as part of the humus type); humus classification for mors containing >50% decaying wood by volume.

Condition of data: most of the data are on file in Victoria, although some of the environmental data are still in the regional offices; accessibility is unknown.

Evaluation: the data are of limited use as the only information available on CWD is number of stems per plot and it is of questionable quality because inventorying snags and downed material is not a priority; although a complete dataset has not yet been assembled, summarized, or organized into an easily accessible database, these data do contain the only information available on forest floor wood.

5. Residue and waste survey information

Contact: Jim Gowriluk, Timber Harvesting Branch, Victoria.

Number of plots: many (historically few blocks were surveyed for waste, but surveys are now required for all harvested areas).

Location (range of BGC zones if known): will eventually have information for all forest types that are harvested.

Potentially useful information: volumes of post-harvest CWD.

Condition of data: a new policy on residue and waste surveying has recently been implemented by the Ministry (the standards and definitions of this policy, known as the “zero waste tolerance policy”, are presented in Appendix 2); collection of the new data has just begun; the surveys are kept in the site opening files in district offices; the extent to which data are summarized or analyzed is unknown.

Evaluation: these data are of limited usefulness: they include only currently merchantable timber; they exclude non-commercial species, smaller woody debris, and decayed wood; information is available only for recently harvested sites; and considerable effort would be required to summarize the information for different forest types.

6. Cruising summary compilations

Contact: Maarten Prinsze, Valuation Branch, Victoria.

Number of plots: many.

Location (range of BGC zones if known): all commercial forests throughout the province.

Potentially useful information: the data that are collected are similar to those described for the timber inventory (see (1) above) (i.e., potential and useless dead standing trees, and potential downed trees >3 m in length and 10 cm dbh).

Condition of data: cruising is done primarily by companies such as Reed-Collins, Timberline, and IFS; original data are kept by them and may be difficult to access; the district offices receive compilations (on paper) with estimates of potential material.

Evaluation: these data are not very useful for estimating total amounts of woody debris for the reasons discussed in (1) above: only merchantable material is inventoried, dead material is not a sampling priority, and sampling standards may vary by product requirement (i.e., lumber or pulp).

7. Research growth and yield installations

Contact: Stephen Omule, Research Branch, Victoria (coast) and Wayne Johnstone, Kalamalka Research Station, Vernon (interior).

Number of plots: approximately 2000 on the coast; number in the interior unknown, distributed in over 100 experimental projects.

Location (range of BGC zones if known): mostly Coastal Western Hemlock on the coast, mostly Sub-Boreal Spruce, Interior Cedar–Hemlock, Montane Spruce, and Interior Douglas-fir in the interior (one or two experiments are in the Engelmann Spruce–Subalpine Fir, Ponderosa Pine, and Boreal White and Black Spruce zones).

Potentially useful information: the following data on mortality may be available: average height, total volume, merchantable volume, number of stems per hectare, basal area, and average dbh of dead trees.

Condition of data: data are in a computerized database; mortality information is available in summary output; additional information may be in the database, but it would have to be extracted; the entire database might be obtained from S. Omule.

Evaluation: the potential of this database is similar to that of the permanent growth and yield sampling plots described above in (2), with the exception that these stands have been experimentally manipulated by fertilization and herbicide applications, so rates of mortality or input are not natural (however, the data from the control plots would be natural).

8. Growth and yield permanent sample plots (MacMillan Bloedel)

Contact: Kim Iles, Woodland Services Division, MacMillan Bloedel, Nanaimo.

Number of plots: 1850 in second-growth stands originating from harvest, 150 in old-growth stands.

Location (range of BGC zones if known): MacMillan Bloedel privately owned lands and Tree Farm Licence on southern Vancouver Island (Coastal Western Hemlock and Coastal Douglas-fir zones).

Potentially useful information: all plots have been classified by BGC zone; the information collected is similar to that collected in the Ministry's growth and yield plots (see (2) above); data from old-growth stands sampled for approximately 15 years may also be of use.

Condition of data: data are in a computerized database and are easier to access than the Ministry's growth and yield data, but their use would be subject to approval from the company.

Evaluation: with permission from the company, the data are in a condition that would make them fairly easy to access, but the information is only on mortality (from which input rates might be derived).

9. Insect and disease survey summaries

Contact: see Wood and Van Sickle (1989).

Comments: the original database from which these summaries were prepared was not investigated, but there is information in these summaries on number of trees and volumes killed or damaged by major pests throughout the province; summaries are presented by region and pest, not by BGC zone, but maps are included that show areas of mortality or defoliation; it is not known whether more detailed information is available in the original data (believed to be held at Forestry Canada); this information is only marginally useful, but it might be used to determine the magnitude and frequency of woody debris inputs from catastrophic events; it is not known how much work would be required to extract this information.

4 PROPOSED AND ONGOING RESEARCH ON WOODY DEBRIS IN FOREST ECOSYSTEMS IN BRITISH COLUMBIA

4.1 Ministry of Forests

To determine the research on woody debris that is currently under way or is planned within the Ministry, researchers in Victoria and regional Forest Science Officers were contacted for information. Their responses are summarized below. Although no projects now deal specifically with woody debris, several projects described below contain (or will contain) information relevant to this topic.

4.1.1 Research Branch (Victoria)

1. **Phil Comeau, Technical Advisor, Vegetation Management, and Dave Spittlehouse, Research Scientist, Research Branch; Tony Trofymow and Hugh Barclay, Research Scientists, Forestry Canada.**

Projects: Development of carbon budgets for northern mixedwood and coastal old-growth forest types.

Comments: The objective of this project is to examine the effects of harvesting on CO₂ emissions. A literature review on soil organic matter is currently under way. Estimates of quantities and turnover rates of carbon are being obtained from published and unpublished sources (the latter include the ecoplots used in the biogeoclimatic classification program, and the prescribed fire assessment data). Field work to collect additional data was scheduled for the summer of 1991. Estimates of CWD have been obtained from several published papers, PhD theses, and the prescribed fire database. These estimates are included in this report.

The project is being funded as FRDA II Integrated Resources Management Sub-Program Project #IR14.

2. **Alison Nicholson, Research Vegetation Ecologist, and Evelyn Hamilton, Research Ecologist, Research Branch.**

Projects:

1. Old-growth Problem Analysis and Annotated Bibliography (completed).
2. Report on definitions of old growth (proposed).

Comments: Information in the problem analysis on the role of CWD in old-growth forests was very general, and most of the cited references are reviewed in this report. There are many references with information relevant to CWD in the annotated bibliography. Work has not yet begun on the definitions report.

3. **Steve Chatwin, Research Branch, and Dan Hogan, Vancouver Forest Region.**

Project: The role of large woody debris in old-growth forest streams: a spatial analysis of biogeoclimatic zones.

Comments: This project deals specifically with CWD, but in aquatic ecosystems. It is being funded as FRDA II Integrated Resources Management Sub-Program Project #IR17. The objectives of the project are:

- to regionalize British Columbia into zones of homogeneous hydrologic, biogeoclimatic and physiographic types, called biogeohydrologic regions;
- to develop the appropriate field methods required to evaluate the function of large organic debris (LOD) in a range of stream sizes in each biogeohydrologic region;
- to compare and contrast the role of LOD in each stream size and biogeohydrologic region; and
- to contribute hydrological criteria to the development of regionally appropriate riparian zone management guidelines.

4.1.2 Regional Offices

1. Kamloops Region—Alan Vyse, Forest Science Officer.

Projects: No ongoing or proposed research specifically on woody debris.

Comments: Vyse felt that the work A.E. Harvey (U.S. Dep. Agric. For. Serv., Forest Sciences Laboratory, Moscow, Idaho) has done in the inland northwest is applicable to some forest types in the Kamloops Region. Vyse suggested that after one rotation, too little CWD was unlikely to be a problem in wet-belt forests in the region, although the long-term effects of reductions are not known. The role of CWD in contributions to soil organic matter may be more important in dry-belt forests.

2. Cariboo Region—Craig Sutherland, Forest Science Officer.

Projects: No ongoing or proposed research specifically on woody debris.

Comments: The question of the role of CWD has been raised as a concern for whole-tree harvesting in the dry Chilcotin pine region, but no research is planned to address this issue. Sutherland said that most of the concern with CWD has been with the problems of too much woody debris for mechanical site preparation.

3. Prince Rupert Region—Jim Pojar, Forest Science Officer.

Projects: No ongoing or proposed research specifically on woody debris.

Comments: Estimates of CWD are a component of a current study by Eric Lofroth (Wildlife Research Biologist, Ministry of Environment, Smithers) on habitat use and the population biology of pine marten. Lofroth is developing a habitat suitability model to predict the relative value of areas for marten habitat. Coarse woody debris provides critical habitat for winter dens, and Lofroth has collected data on characteristics (including size measurements for the estimation of volumes) of CWD from 450 plots in the SBSmc and SBSdk Sub-Boreal Spruce subzones. He has also collected data on stocking and condition of snags. He has used a modification of the methodology of Trowbridge et al. (1986) for sampling woody debris. Lofroth also mentioned that Judy Baker (Victoria) was collecting similar information on CWD for a study of marten habitat on Vancouver Island.

Like Sutherland, Pojar also commented on the fact that CWD has more commonly been raised as an issue related to mechanical site preparation. In his opinion, the problem of too little CWD is more of a concern with later rotations than in the initial conversion of old-growth stands, at least in the SBS.

4. Vancouver Region—Fred Nuzdorfer, Research Ecologist, and Dale Seip, Research Wildlife Ecologist.

Projects: No ongoing or proposed research specifically on woody debris.

Comments: According to Seip, information on characteristics of CWD has been collected for both old-growth and second-growth (40–80 years) stands in the Queen Charlotte Islands and in Vancouver's north shore watersheds as part of a broader study of the relationship between wildlife populations and habitat characteristics. The method used to collect the

information on CWD was modified from that of Trowbridge et al. (1986). Similar data will be collected in stands on Vancouver Island.

Nuszdorfer commented on the large site-to-site variability in amounts of CWD in coastal forests. Although quantities seem to be large, questions of long-term site productivity still need to be addressed.

5. Nelson Region—John Pollack, Forest Science Officer.

Projects: No ongoing or proposed research specifically on woody debris.

6. Prince George Region—Les Herring, Forest Science Officer, and Marty Osberg, Research Pedologist.

Projects: No ongoing or proposed research specifically on woody debris.

Comments: The Site Degradation and Rehabilitation Committee is currently preparing a working plan for a project to study the relative importance of soil compaction and organic matter levels on long-term site productivity, on a number of sites to be set up this summer in the Sub-Boreal Spruce zone. According to Osberg, the experimental design will be modified from that used by Powers et al. (1990) in a similar study in northern California. Three levels of soil compaction and three levels of organic matter removal (bole-only harvest, whole-tree harvesting, and whole-tree harvesting with removal of forest floor) will be incorporated into a split-plot (vegetation control/no vegetation control) factorial design. It is unclear at this point to what extent measurements of CWD will be incorporated into the study, but the study has large potential for research in this area.

4.1.3 District Offices

1. Port Alberni District—Rick Brand, Inventory/Planning Resource Officer.

Comments: The Port Alberni District is experimenting with leaving CWD on sites in the Tofino Creek area after logging in volumes that are similar to pre-logging estimates of avoidable waste (see Appendix 2 for Ministry policy on utilization standards). Estimates of this volume are highly variable, and range from about 40 to 170 m³ha⁻¹ for stands in the Tofino Creek area. An amount of about 60 m³ha⁻¹ has been chosen to be left on sites, and the success at achieving this level has been variable. Brand said the district would like to monitor the ecological impacts of this level of CWD retention, as well as increasing its inventory activities, but no formal research plan has been developed.

4.1.4 Other

There are currently a number of fire studies under way in the province, in which estimates of fuel loading, and slash and nutrient losses associated with prescribed burning may provide some information on CWD. These studies are not reviewed here, but some of the researchers involved in fire studies include:

- Rick Trowbridge—Pedologist, Prince Rupert Region
- Mike Curran—Pedologist, Nelson Region
- Bob Mitchell—Pedologist, Kamloops Region
- Evelyn Hamilton—Research Ecologist, Research Branch, Victoria
- Steve Taylor—Pacific Forestry Centre, Forestry Canada, Victoria

4.2 Forestry Canada, Pacific Forestry Centre

1. Tony Trofymow, Research Scientist.

Project: Effects of converting coastal old-growth forests to managed forests: changes in site carbon and nutrient contents during post-harvest succession.

Comments: This 3-year project has received some funding from the ENFOR program and from the FRDA II Integrated Resources Management program. The objectives of the project, as stated in the funding proposal are to: “establish how the amounts and distribution of carbon and nutrients on a site change during post-harvest succession and how closely they recover to pre-harvest levels, by retrospective study of a chronosequence of stands in two coastal forest types (Coastal Douglas-fir CDFb or Coastal Western Hemlock CWHa1 subzones, and the CWHb1 subzone). Such information is critically needed in order to develop options for safeguarding carbon retention and calibrating and testing models such as FORCYTE-11”.

Measurements of CWD are an integral component of this study and, according to the project proposal, will be based on the methods of Trowbridge et al. (1986) and Brown (1974) with the modifications suggested by Delisle et al. (1988). Work on the project was scheduled to begin in the summer of 1991.

2. Doug Pollard, Research Scientist and Program Head.

Project: Biological dynamics of forest ecosystems.

Comments: This is a large research program that has just begun with several components relating to CWD. Funding is also from the FRDA II program. One of the components is Tony Trofymow’s project described above. In broad terms, the program will address the role of carbon cycling in ecological processes and biodiversity in forests. One of the objectives is to establish links between habitat development, substrate development, and biodiversity. There will be a number of researchers involved in the program including Caroline Preston (soil chemistry) and Val Marshall (soil zoology), as well as Tony Trofymow and Doug Pollard (who will be looking at physical processes of CWD breakdown). Other researchers will be looking at stump decay and soil organisms, mycorrhizae, and small invertebrates and insects in woody debris. For more information, contact Doug Pollard. Site selection was to take place during 1991. Four sites are to be selected for study in the Coastal Douglas-fir zone on southern Vancouver Island.

4.3 Other

4.3.1 University

1. Hamish Kimmins, Rod Keenan, and Cindy Prescott, Ecologists, Forest Sciences, University of British Columbia.

Project: Biomass and carbon storage in the forest floor and woody debris of old-growth western redcedar and western hemlock forests on northern Vancouver Island.

Comments: This project is being funded by the Ministry of Forests with monies from the FRDA II agreement (Integrated Resources Management Sub-Program Project #IR15). The objective of the project is to obtain an estimate of the total biomass and carbon content of woody debris and forest floor material in old-growth cedar-hemlock forests by:

- estimating the biomass and carbon content of CWD (dead standing trees and stumps and down boles and branches); and

- estimating the biomass and carbon content of the forest floor, by forest floor component.

This work is being carried out in the Coastal Western Hemlock CWHvm1 subzone using the methods of Brown (1974) and will be completed by March 1992.

2. Shannon Berch, Department of Soil Science, University of British Columbia.

Project: Macrofungi of old-growth forests: saprophytes and biotrophs and their correlation to biogeoclimatic zones and humus forms.

Comments: This is a 5-year project, which has received approval for funding in 1991/92 under FRDA II Integrated Resources Management Sub-Program (Project #IR09). The first-year objectives of the project are:

- to predict, from extensive literature and herbarium searches, macrofungi of old-growth forests in coastal British Columbia, with emphasis on the biogeoclimatic zone and site(s) selected for a joint study of biodiversity;
- to carry out limited on-site collections to establish protocols for more extensive studies to follow; and
- to compare findings to predictions.

The study will provide an inventory of the diversity of macrofungi present in woody debris in old-growth coastal forests.

3. Mike Feller, Fire Ecologist, Forest Sciences, University of British Columbia.

Comments: Feller has measured volumes of woody debris on both old growth and clearcut sites in the Engelmann Spruce–Subalpine Fir ESSFwc subzone as part of an ongoing study into the impacts of prescribed burning on the ecology of subalpine forests. The old-growth data were collected using a modification of the method described by Trowbridge et al. (1986). This information is unpublished.

4. Dale Seip mentioned several wildlife projects that have been suggested as topics for graduate student research. The status of these projects is unknown but the students and the general subject areas are listed below.

1. Vanessa Craig (supervisor: Fred Bunnell, Forestry, UBC). The relationship between forest floor characteristics and small mammal and salamander populations in Vancouver's north shore watersheds.
2. Linda Dupuis (supervisor: Jamie Smith, Zoology, UBC). Salamander populations in the Campbell River area. Vancouver Island.
3. Andre Arsenault (supervisor: Gary Bradfield, Botany, UBC). Structural characteristics of old-growth forests.

4.3.2 United States

Although it was not an objective of this work to review current research on CWD in the United States, there are several researchers who are involved in long-term projects that may yield information with relevance to British Columbia forest types. These researchers and some of their research topics are briefly mentioned here:

1. Paul Alaback, U.S. Dep. Agric. Forest Service, Pacific Northwest Research Station, Juneau, Alaska.

Comments: About 30 permanent plots, 1/4 ha in size, have been established in Alaska for long-term monitoring of inputs and quantities of CWD. Most of the plots are in the productive hemlock stands of the coastal area, but plots will also be established in reference stands of yellow cypress and redcedar. Approximately 20 of the plots have been

mapped, and data on CWD (>10 cm) have been collected but not yet analyzed. Measurements of diameter, length, height above ground, species, position, and age will be collected every 10 years. There are also plans to study the carbon dynamics in these reference stands, but not much has been done on this so far.

Alaback also mentioned the nutrient cycling work of Keith Van Cleve (University of Alaska, Fairbanks, Alaska) and his long-term ecological project in the taiga (an area for which there is very little information in British Columbia). In general, Van Cleve's work does not separate woody debris from other organic pools, making it difficult to isolate the overall contribution of this component to cycling in taiga forests. However, several references are included in Appendix 4, as this work does provide some indication of the importance of woody debris in this forest type.

2. Mark Harmon, Forest Sciences, Oregon State University, Corvallis, Oregon.

Comments: A long-term study of conifer log decomposition has been set up in old-growth fir-hemlock forests at the H.J. Andrews Experimental Forest in Oregon. A time-series approach is being used to investigate the changes that take place in fresh woody debris of all size classes as decay progresses. The project is only a couple of years old and few results have been published (see Carpenter et al. 1988). Harmon also mentioned that there is a great deal of inventory work being carried out to assess levels of CWD in various forest types in the Pacific Northwest. In addition, periodic remeasurements of mortality in permanent plots in a spruce-hemlock forest at Cascade Head Experimental Forest in Oregon are being used to study forest turnover rates and the population dynamics in these coastal forests (see Harcombe et al. 1990). Harmon referred to Bruce McComb (Oregon State University) as another researcher interested in CWD, specifically with respect to the effects of snag characteristics on birds and on strategies for retention of standing dead wood.

5 RECOMMENDATIONS

5.1 Information Needs

As illustrated by the data in Table 3.2, there is information from the United States and Alberta on amounts of woody debris in a number of forest types similar to those found in British Columbia, but almost no information for stands in this province. The available information suggests that differences in input rates and turnover times of CWD between forests in British Columbia and those farther south are large enough to warrant a separate inventory for forests in this province. If we intend to manage explicitly for CWD, then such an inventory is imperative. This inventory should include information on:

- natural volumes of CWD for all major forest types requiring active management in British Columbia;
- decay class distribution patterns;
- size class distribution patterns; and
- spatial and temporal variation in amounts and distribution.

To manage for CWD, the following information is also necessary:

- input rates, including some data on variations in rates with forest succession; and
- turnover rates of snags and logs.

Turnover rates should be related to environmental parameters such as temperature and moisture.

To manage for conservation of soil and forest floor wood, in addition to CWD, this additional information is necessary:

- amounts of wood in forest floor and soil loss; and
- turnover rates of soil and forest floor wood.

In addition to quantifying the amount of CWD in forests, it is also necessary to quantify the dynamics of the woody debris component of these ecosystems. Given that there is little quantitative data available, the best approach at present would be to develop and calibrate computer models that include, for example, the quantitative effects of temperature and moisture on decomposition rates.

Although inventory information is required for most forest types in British Columbia, we recommend that the highest priority be given to forests of economic importance, those with extensive harvesting activities, and those in which environmental factors have a large impact of CWD dynamics.

5.2 Suggested Areas for Research

Past and present research, mainly in the northwestern United States, has provided considerable insight into the role of CWD in forest ecosystems. Most of our current

understanding, however, is general and based on studies of only a few forest types that are environmentally or economically prominent in the northwest. Ongoing research activities in the United States focus on quantifying the amount of CWD in forests and establishing long-term studies into the nutrient and organic matter dynamics of woody debris (see Section 4).

Very little information exists on either quantities or functions of CWD in British Columbia's forests. Existing inventories for merchantable timber, fuel loads, forest community composition, logging residues, and insect and disease mortality contain some data on woody debris, but in all cases these inventories can provide only partial information on amounts of dead wood, and in many cases considerable effort would be required to extract this information. Since this information is likely insufficient for management purposes, efforts would be better directed towards a research program designed specifically to address relevant questions concerning the role of woody debris in British Columbia's forests. Based on the information presented in the previous sections, we recommend that such a program focus on the following areas of research.

- Studies of the functional importance of CWD in moisture retention and habitat development in those forest types in British Columbia where moisture is known to be a major limiting factor (e.g., the Coastal Douglas-fir and Ponderosa Pine zones, or xeric sites in other zones).

Rationale:

A great deal of what we know about woody debris comes from experiences in the northwestern States, experiences which have indicated an important role for CWD in moisture retention and as habitat for forest species. Disturbances, such as logging or fire, may further enhance the functional importance of wood. The climate of British Columbia is generally wetter and cooler, especially on the coast, than that of the States to the south of the province, and it is appropriate to ask whether or not the climatic differences are reflected in different patterns and rates of accumulation of woody debris in British Columbia forests. Consequently, it can be hypothesized that retention of CWD will not be as critical for keeping moisture in areas that do not experience drought, or where forests are characterized by deep humus layers and cool soils.

Suggested research topics (not in order of priority):

1. The diversity, abundance, and distribution of animals and microbes (especially those important to wood decomposition) in CWD, in comparison to those of other substrates in disturbed and undisturbed forests.
 2. The functional use of CWD by species, and changes in use with seral stage, habitat quantity and quality, and disturbance.
 3. Physical properties of decaying wood, especially moisture content and availability.
 4. The importance of CWD in both early seedling establishment and long-term patterns of regeneration, particularly in relation to availability of other substrates, the role of soil wood, and factors limiting early recruitment and long-term survival on logs.
- Studies of the impacts of woody debris accumulations on the physical and chemical properties of the soil and forest floor, particularly with respect to effects on nutrient availability and thermal regimes.

Rationale:

Most of the concern over CWD in the United States has focused on the consequences of the loss of significant amounts of debris from sites (although actual studies on site responses to the removal of woody debris have just begun). There has been much less interest in the ecological impacts of accumulations of debris in areas where conditions are less favourable for organic matter decomposition. In parts of British Columbia (e.g., the Sub-Boreal Spruce and Engelmann Spruce–Subalpine Fir biogeoclimatic zones), wet and

cold soils are believed to be factors limiting the establishment and growth of trees. It can be hypothesized that, in the short term at least, reductions in levels of CWD below those in natural stands will benefit organisms in the areas rather than harm them. (In fact, this is one of the rationales for the use of prescribed burning after harvesting in these zones.)

Suggested research topics:

1. The effects of woody debris on soil thermal properties.
2. The effects of woody debris on soil and forest floor chemical properties, particularly on the leaching of nutrients from upper soil horizons; the acidification of soils; and nutrient availability within the sphere of log influence.
3. The short- and long-term effects of changes in the amounts and distribution of woody debris on microclimatic and soil physical and chemical properties.
4. The quantitative and qualitative role of woody debris in forest floor and soil organic matter dynamics.

Rationale:

The work that has been done on the role of woody debris in nutrient dynamics suggests that the importance of wood (in storage and turnover functions) is strongly related to the availability and storage of nutrients in other organic and inorganic pools. In many cases, the amounts or rates of nutrient turnover in CWD are low relative to other sources. However, very little is known about how much of the forest floor and soil are derived from woody debris. One could hypothesize that the long-term contributions of woody debris must be significant where woody debris accumulations are high, rates of decomposition and soil development slow, and plants are conservative in their use of nutrients. In addition, if lag times for the incorporation of woody debris into soils are as important in CWD management as has been suggested (Harvey et al. 1981b), then these must be determined for different management scenarios.

Suggested research topics:

1. The determination of rates of transfer of wood from logs to buried soil wood, and the characteristics of buried wood (e.g., amounts, sizes, and chemical composition)
2. The determination of turnover rates for various woody debris components, and the effects of site and environmental conditions on turnover rates.
3. The wood composition of the forest floor, the effects of this wood on forest floor conditions, and the impacts of changes in levels of woody debris to this relationship.

5.3 Recommendation for the Development of a Research Strategy

The above “shopping list” for information on woody debris seems daunting, given the fact that almost nothing has been collected in British Columbia to date. However, we also need much of this data to answer pressing questions about the impacts of harvesting and other human activities on carbon cycling, the degradation of long-term site productivity, and the conservation of old-growth forests. There is currently considerable interest in all of these areas, providing an excellent opportunity to integrate many related research objectives into a comprehensive, long-term, multi-scale research program. Consequently, we recommend that studies of woody debris be undertaken as part of more comprehensive studies on the characteristics and processes of British Columbia’s forests.

5.4 Management Guidelines

It seems premature to be setting provincial standards for the retention of CWD after harvesting or site preparation. Standards in the United States, such as those set out in the Blue River Residue Guidelines (Appendix 1), were developed largely from professional experience with particular forest types, rather than from a quantitative analysis of the ecological importance of woody debris. Managers in British Columbia lack both quantitative and qualitative information on the role of woody debris in natural forests, or the impacts of changes in naturally occurring levels of debris. We do not know the ecological significance of the large spatial and temporal variability that characterizes the distribution of CWD in forests. We do know, however, that simply leaving CWD on sites does not mimic the ecologically important processes of tree death or treefall. It is also clear, nevertheless, that the removal of large amounts of CWD from sites is not an environmentally sound practice. Activities that reduce or increase the amount of CWD on a site to levels outside the normal range for that forest type should not be accepted (except in an experimental project) and the “zero waste tolerance” policy of the Ministry of Forests should be re-examined from this point of view. We do not yet know what that range is for most forest types in British Columbia, or whether harvesting alone will lead to reductions in CWD over time, and so we cannot ensure that standards based on available data will achieve conservation of the role of woody debris in the forest of British Columbia.

APPENDIX 1. *Blue River Ranger District: guidelines for managing large woody debris*

United States	Forest	Willamette	Blue River Ranger District
Department of	Service	National	Blue River, OR
Agriculture		Forest	97413

Caring for the Land and Serving People

Reply to: 2430 Commercial Timber Sales	Date: July 28, 1986
2410 Plans	
Subject: Guidelines for Managing Large Woody Material	
To: District Resource Management Guidelines	

BACKGROUND

Increasing levels of wood fiber utilization, coupled with evidence that productivity may decrease over time at high levels of utilization, indicate a need to address the issue of long term site productivity and maintenance of large, woody material. “The Seen and Unseen World of the Fallen Tree” (Maser, Chris; Trappe, James M., Oen. Tech. Rep. PNW-164, Portland, OR. USDA Forest Service, PNW Exp. Sta. 1984) is an excellent reference document for this issue.

A long standing land management objective of the Forest Service is to maintain the long term productivity of the site. Regional and National Policies reflect this concern. The Blue River District convened an interdisciplinary team to develop a strategy to insure that the productivity of our intensively managed timber stands will be preserved over time, through the application of recent research findings, and the following plan to implement the management of large woody materials on all harvested areas.

The following describes the efforts of the District and the resulting plan, which is intended to be dynamic and responsive to new information or changes.

DISTRICT PROCESS

The District Residue Management task force evaluated the existing situation, regarding the status of large, woody material.

- A. Fire Hazard: Current situation in most areas of the District is “no risk” following treatment. Residue levels are treated to fire potential rather than incorporation of ignition probability. There is little analysis of area specific ignition probability. Cost of fuels treatment has not included YUM costs, but only actual burning costs.
- B. Post harvest residues: Mature, second growth, 50–75 tons/acre after PUM 8x10. Old growth (clean), 90–120 tons/acre after PUM 8x10. Old growth (dirty), 150 tons/acre after PUM 8x10.
- C. Small mammal and avian habitat: Current prescription is two logs, 12"x40'. Most of these prescriptions have not been put on the ground yet. The current situation is deficient in producing habitat. Replacement may depend on standing wildlife trees, which are also deficient in number. There is no satisfactory range of decay classes (LV) of down woody material. There are no guidelines yet on what species to manage for, and what percentage of viable populations to manage for. 40% is the absolute minimum.
- D. Reforestation/Site preparation: The current situation does not limit the establishment of an adequate number of seedlings to meet stocking objectives.
- E. Soils: Effective ground cover requirements are being met most of the time following residue treatment; scorch is minimal (less than 5%).
- F. Long term productivity: Status is questionable. Current research indicates that long term productivity decreases as utilization of wood increases.
- G. Silviculture project costs: Residues on sites are not a significant contributing factor to any project costs at this time.
- H. Firewood: Demand appears to be met most of the time.

The District then hosted a field trip which included scientists from OSU, PNW, along with Forest and District specialists (Field Trip 6/85). The participants represented all disciplines, and agreed on what proper large, woody debris levels looked like (Inventory of woody debris, Green Mountain unit 1303-51), but not on specific amounts or numbers.

Hal Legard (Soils, Water, Fish and Wildlife Staff, SO) recommended using the Fuels Management Photo Series, page 20 (“Photo Series for Quantifying Forest Residues in the Coastal Douglas-fir/Hemlock Type.” Maxwell and Ward, USDA Forest Service General Technical Report, PNW-51, 1976), which was selected as a good example of woody debris levels by a consensus of specialists during a different exercise, in 1984.

An inventory of the site of the field trip was completed in spring 1986, and the results are shown below.

Sound		
Size Class	Tons/Acre	Cubic Feet/Acre
3.1” - 9.0”	5.73	459.1
9.1” - 20.0”	7.89	632.2
20.1”+	37.34	2991.9

Rotten		
Size Class	Tons/Acre	Cubic Feet/Acre
3.1”– 9.0”	3.27	349.3
9.1”–20.0”	11.59	1238.2
20.1”+	14.0	1495.7

Sound: 34 pieces, average diameter of 9.20”

Rotten: 27 pieces, average diameter of 10.07”

RESIDUE MANAGEMENT GUIDELINES

Very little research has been completed to date on the amount of large, woody material needed to maintain a functional ecosystem in a managed forest. Therefore, it is necessary to choose a point at which to begin; a “reasonable” estimate of quantities of logs, based on all of the information gleaned from the exercise. It must be understood that the following recommendations are intended to be dynamic, similar to most of the other Resource Management Guidelines for the Blue River Ranger District. As new information becomes available, the guidelines will change.

In order to meet the objectives of maintaining long term site productivity, the following measures will be included in all timber harvesting activities, unless otherwise dictated by over-riding resource management needs:

1. Leave all class III, IV, and V logs on the site following harvest, unless there are other documented, over-riding concerns.
2. For sound material that does not meet utilization standards, 10–15 pieces per acre will be left on the ground. Longer pieces are preferred. When class III logs are not available on the site, 15 class I and II pieces will be left. When class III’s are available, leave 10 class I and II pieces per acre. The integrated resource management prescription should include both an estimate of the existing pre-harvest inventory, and a site specific plan to manage large, woody debris on the site, including an analysis of the effects of a YUM requirement.
3. The table below shows the number of pieces to leave by diameter class, with minimum lengths which consider that pieces must be a minimum of 40 cubic feet to be effective.

POST HARVEST OBJECTIVE FOR LARGE WOODY MATERIAL		
If diameter is:	Pieces per acre:*	Minimum length:
16”–22”	10–15*	30’
22”–32”	10– 15*	16’
32”–42”	10– 15*	8’
42”– 60’	8 (+ 2–7 smaller)*	8’
60+	5 (+ 5–10 smaller)*	8’

(* Depending on the availability of Class III logs on the site.)

4. To aid in field estimation, the average spacing of 10 pieces per acre would be 66’. 15 pieces would be spaced at 54’.

5. We will need to negotiate changes in existing contracts, or buy-out YUM requirements as necessary to ensure that these guidelines are met.
6. As adopted, this guide becomes a part of the Blue River District Resource Management Guidelines. As with the other District Guidelines, when better data becomes available, or when monitoring shows a need to make a change, the guidelines will be updated.

APPENDIX 2. *British Columbia Ministry of Forests policy: utilization standards*



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PURPOSE:

The purpose of this Policy is to establish minimum required utilization standards for timber harvesting operations on the Coast.

SCOPE OF APPLICATION:

This Policy is applicable to timber harvesting operations authorized under the FOREST ACT on the British Columbia Coast. This Policy is effective from January 1, 1989.

DEFINITIONS:

Coast: that part of the Province of British Columbia where log-based appraisal is used; predominantly the geographic area of British Columbia west of the Cascade Mountains.

Allowable Annual Cut (AAC): the rate of harvest determined by the Chief Forester for Timber Supply Areas (TSAs) and Tree Farm Licences (TFLs), and by the District Manager for Woodlot Licences (WLs), and the rate of harvest specified in a licence or in a Management & Working Plan.

Waste: the volume of timber which should have been removed from the logged area by the Licensee, based on the minimum cutting and utilization standards stated in the cutting authority, but which has been left on the harvested area.

Unavoidable Waste: that component of the waste which cannot be removed with a reasonable effort because of physical impediments and safety reasons.

Avoidable Waste: the waste minus the unavoidable waste.

Residue: the volume of timber that is below the required standard of utilization but is part of the AAC for cut control purposes (includes grade Y logs from live trees).

Residue and Waste Reporting Unit: the area for which the waste is measured and reported. It may be either a cut block or licence, or parts of a licence.

Coast Old Growth: a stand of timber which has an average age of greater than 120 years.

Coast Second Growth: a stand of timber which has an average age of 120 years or less.

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DEFINITIONS: cont'd.

Minimum Utilization Standards: the standards of timber cutting and log utilization specified in the cutting authority.

Log Grade: those log grades which are defined in the Scaling Regulation.

POLICY STATEMENT:

It is the Policy of this Ministry that minimum cutting and utilization standards shall be specified in all documents authorizing timber harvesting.

CONDITIONS:

1. Except for deciduous species, salvage logging and selection cutting, the minimum cutting standards will be as follows:

	<u>Old Growth</u>	<u>Second Growth</u>
- maximum stump height, cm *	30.0	30.0
- minimum top diameter inside bark, cm	15.0	10.0
- minimum slab thickness, Cedar only	15.0	
- log length, m	3.0	3.0

* measured on the side adjacent to the highest ground.

2. Cutting specifications for deciduous species, salvage logging and selection cutting will be set by the District Manager on a site-specific basis.
3. All coniferous logs, except logs designated Grade Y and Grade Z, must be utilized.
4. The cutting and utilization standards described in Conditions 1, 2 and 3 above will be assumed on cruise-based cutting authorities, but residue and waste measurements will not be required. Where the standard of utilization expected to be practiced is of major concern, cruise-based cutting authorities will not be issued.

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CONDITONS: cont'd.

5. Scale-based cutting authorities under Tree Farm Licences (TFLs), Timber Licences (TLs) outside TFLs, Forest Licences (FLs) and Timber Sale Licences (TSLs)(Major) with an Allowable Annual Cut (AAC) over 10 000 m³ will require the holder to have the residue and waste measured in accordance with the "Vancouver Region Depletion Survey Manual" during 1989, and the "Forest Service Residue and Waste Measurement Manual" from January 1, 1990. Licensees will report the results, under the seal of an R.P.F., to the Forest Service within 60 operative days (when field work is reasonably possible) of completion of logging, unless the time limit is extended by the District Manager. Licence holders will be encouraged to have the residue and waste measurement and reporting done by an independent party. This work will be done at the expense of the Licensee.
6. All residue and waste volumes will be added to the scaled volume for cut control purposes, and will be charged to the AAC for the licence.
7. All scale-based cutting authorities will specify that all avoidable waste will be billed monetarily at stumpage or royalty rates, described under Conditions 8, 9, 10, 12 and 13 below. Volumes billed will be determined from sample plot measurements made within all cut blocks logged during the calendar year (as described in Condition 8 below) or from a sampling of cut blocks logged during the calendar year (as described in Condition 9 below), in which case the average waste volume determined will apply to all cut blocks logged in the identified reporting unit for the calendar year.
8. Licensees, at their option, may choose a cut block as the residue and waste reporting unit, and have the residue and waste measured for every cut block of their licence. Billing for avoidable waste will immediately follow reporting, and will be at the average billed stumpage (or royalty) rates over the preceding 12-month period for the timber mark.
9. Subject to Condition 10 below, Licensees, at their option, may choose a licence or part of a licence as the residue and waste reporting unit, and if so, will have the average residue and waste (m³/ha) measured for the unit(s) applied to all cut blocks harvested within the reporting unit during the calendar year. Billing for avoidable waste will be by timber mark at the average billed stumpage (or royalty) rate over the preceding 12-month period for the timber mark.

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10. Notwithstanding Condition 9 above, the District Manager may require that the waste be measured and reported to him for one or more cut blocks, if and where he considers the waste excessive. The avoidable waste will be billed at the average stumpage (or royalty) rates over the preceding 12-month period for the timber mark. Such cut block(s) will be excluded from the determination of, and billing for, the average avoidable waste for the relevant licence.
11. The option of Condition 8 or 9 above, elected by the Licensee, has to be formally approved by the District Manager.
12. For scale-based licences or cutting authorities under the Small Business Forest Enterprise Program, the Licensor will have the residue and waste measured. Billing for the avoidable waste will be at the average stumpage rate over the preceding 12-month period for the licence.
13. For scale-based cutting authorities under Woodlot Licences (WLs), the Licensor may require the Licensee to have the residue and waste measured and the results reported to the Forest Service, or the Licensor may have the residue and waste measured. Billing for avoidable waste will be at the average stumpage rate over the preceding 12-month period for the licence.
14. Subject to Condition 15, grade Y logs will be considered as part of the cut for cut control and AAC purposes, and where utilized, will have a stumpage charge as defined in the appraisal manual (currently \$.25/m³) or royalty, as prescribed in the Regulation (currently \$.25/m³). There will be no charge for Grade Y logs which are not utilized. Grade Z logs will not be considered as part of the cut, and will not bear stumpage charges.
15. For the period January 1, 1989 to December 31, 1990, grade Y logs from dead trees left on the ground will not be considered part of the AAC. This condition of Policy will be reviewed on or before December 31, 1990.
16. The District Manager may require that Y grade logs of Cedar and Yellow Cedar be yarded or skidded to the landings where, in his opinion, a demand for such logs exists.

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RESPONSIBILITIES:

Chief Forester:

- to determine the AAC for TSAs and TFLs; and
- to ensure that the applicable minimum utilization standards are used in the determination of AACs for TSAs and TFLs.

Director, Timber Harvesting Branch:

- to monitor the administration of this Policy;
- to recommend changes to the Policy, when considered desirable or necessary; and
- to provide technical expertise to the Regions and Districts, as required.

Director, Valuation Branch:

- to develop standards and procedures for estimating the volume of waste and residue timber.

Regional Manager:

- to ensure that Districts adhere to this Policy;
- to recommend modified utilization standards to the Executive through the Director, Timber Harvesting Branch, when considered necessary; and
- to implement the FOREST ACT, Section 56, where required.

District Manager:

- to determine the AAC for WLs;
- to implement and administer this Policy;
- to ensure that the minimum utilization standards are used in the determination of the AAC for a WL;
- to include a clause in cutting permits or TSLs that will allow a billing for waste in accordance with Conditions 8, 9, 10, 12 and 13 above; and
- to initiate waste billing.

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REFERENCES:

FOREST ACT, Part 2, Section 6, 7 and Part 4

Scaling Regulation 563/78 and all amendments.

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Aber, J.D., D.B. Botkin, and J.M. Melillo. 1978. Predicting the effects of different harvesting regimes on forest floor dynamics in northern hardwoods. *Can. J. For. Res.* 8:306–315.

Keywords: logging impacts, modelling, organic matter dynamics, nutrient dynamics, quantities, northeastern U.S.A., hardwood forest, long-term impacts, nitrogen, harvesting methods, rotation length.

Abstract: The effects of different intensities of forest management on forest floor organic matter and nitrogen dynamics in northern hardwoods were simulated with a computer model built from the extensive database of the Hubbard Brook Ecosystem Study. Three cutting intensities and three rotation lengths were tested. In all cases, both nitrogen availability and forest floor organic matter declined for 15–30 years following cutting and required 60–80 years to recover to pre-cut levels. Rotation length had a much greater effect on the forest floor biomass under this treatment and was reduced to roughly one-half of that under clearcutting (90-year rotation).

Agee, J.K. and M.H. Huff. 1987. Fuel succession in a western hemlock/Douglas-fir forest. *Can. J. For. Res.* 17:697–704.

Keywords: quantities, fuel load, *Tsuga heterophylla*, *Pseudotsuga menziesii*, early seral, old growth, mature, decay classes, accumulation.

Abstract: Fuel succession was quantified for a 515-year chronosequence in a *Tsuga heterophylla*/*Pseudotsuga menziesii* forest. Postfire stand ages selected were 1, 3, 19, 110, 181, and 515. After initial reductions due to mortality from fire in the first 3 years, live aboveground biomass in the tree component increased over time to over 1100 t/ha. Shrub and herb layer biomass was highest in year 19 and year 515. Dead aboveground biomass had different trends for different fuel size classes; normalized fuel loadings of five dead and down fuel categories peaked at four different stand ages: 1-h and 10-h timelag (TL) fuels, age 1; 100-h TL fuels, age 19; 1000-h TL fuels, age 110; >1000-h TL fuels, age 515. Surface fire behaviour was highest early in the seral and lowest at ages 110–181. Old-growth forest patches appear to be best buffered against forest fire by mature forest patches rather than old growth or recently burned natural stands.

Alaback, P.B. 1989. Logging of temperate rainforests and the greenhouse effect: ecological factors to consider. *Proc. of Watershed '89: Conference on the Stewardship of Soil, Air, and Water Resources*. E.B. Alexander (editor). March 21–23, 1989, Juneau, Alaska. U.S. Dep. Agric. For. Serv. Alaska Region, pp. 195–202.

Keywords: nutrient dynamics, carbon, accumulation, logging impacts, old growth, Alaska.

Abstract: This is a review of the carbon budget and the principal ecological processes regulating carbon flow in forest ecosystems and includes preliminary data on carbon cycling in temperate rain forest regions. Old-growth forests in Southeast Alaska were estimated to accumulate 150–300 t C/ha on average to productive sites. Second-growth sites were estimated to accumulate 131–227 t C/ha at 110 years of age on average sites. The highest biomass accumulations generally occur at 200–300 years of age. Logs were estimated to contain 20–40 t C/ha in old-growth sites. Southern hemisphere sites had similar carbon storage in second-growth hardwood sites, but had as much as 3 times greater storage in old-growth conifer types. Little information is available on how much soil and forest floor carbon is lost following logging in the temperate rain forest zone.

In temperate forest studied to date, deforestation and subsequent management has resulted in a net emission of carbon to the atmosphere due to lower equilibrium carbon

pools (in trees and soil) and a more rapid turnover of carbon. Disposition of forest products is a key variable in determining the net effect of forest management activities on atmospheric carbon. Because of the small land area involved and the high degree of reforestation following logging, effects of land use practices in the temperate rain forest zone are expected to have little effect on global atmospheric carbon. Basic research on decomposition, microclimate, and soils changes with logging are needed to better understand the productivity potential of the full range of temperate rain forest sites and to more precisely predict what impact land use practices may have on atmospheric carbon.

Arp, P.A. and T.P. McGrath. 1987. A parameter-based method for modelling biomass accumulations in forest stands: theory. *Ecol. Modelling* 36:29–48.

Keywords: decomposition, accumulation, input rate, modelling.

Abstract: A parameter-based method is proposed for modelling annual plant- and soil-biomass increments in forest stands. Model components include foliage, aboveground wood of live and dead trees, forest floor, roots, and the soil beneath the forest floor. Also considered is a leaf-area component to simulate biomass production in stands growing from an open to a fully stocked condition. The annual increments within each component are developed by quantifying processes such as leaf production, photosynthate allocation for wood and root growth, litterfall, and decay.

The approach undertaken leads to a matrix representation, and a method to parameterize the increments of each component in terms of measurable transfer coefficients. Knowledge of these coefficients allows for analytical or numerical simulations of annual biomass accumulations for selected site and species combinations, and for a way to examine existing biomass data in a systematic manner.

Arp, P.A., T.P. McGrath, and J.A. Beck. 1987. A parameter-based method for modelling biomass accumulations in forest stands: an application. *Ecol. Modelling* 36:49–64.

Keywords: decomposition, accumulation, input rate, modelling.

Abstract: The approach developed by Arp and McGrath to assess the production, allocation, and decay of biomass in forest stands is used to examine stand-age data for foliage area, foliage biomass, woody biomass, and forest floor biomass of Northern Tolerant Hardwood stands of medium site quality. From this, information is obtained to simulate the effect of stand-internal nutrient mineralization, and of an epidemic outbreak of gypsy moth (*Lamantria dispar* L.) on the above- and belowground biomass production in Northern Tolerant Hardwoods by way of a representative example.

Arthur, M.A. and T.J. Fahey. 1990. Mass and nutrient content of decaying boles in an Engelmann spruce–subalpine fir forest, Rocky Mountain National Park, Colorado. *Can. J. For. Res.* 20:730–737.

Keywords: nutrient dynamics, Rocky Mountains, *Picea engelmannii*, nutrients, quantities, *Abies lasiocarpa*, nitrogen, bole wood, decomposition.

Abstract: We classified dead bole wood in an old-growth Engelmann spruce – subalpine fir (*Picea engelmannii* Parry–*Abies lasiocarpa* [Hook.] Nutt.) forest in Rocky Mountain National Park, Colorado, into decay classes and measured dead bole surface area, volume, biomass, and nutrient content. Biomass of dead boles was 70 Mg/ha, about half as large as aboveground live biomass in these forests. Net accumulation of N, P, Ca, and Na occurred with increasing decay. The N:P ratio varied little with decay, approaching a value of 20 in the most decayed wood, typical of that found in other studies of dead boles. Loss of K during bole decay exceeded the rate of weight loss, whereas Mg loss followed weight loss. The total pools of nutrients in dead boles and (in parentheses), the amount of nutrients stored in dead boles as a percentage of total above- and belowground living, forest floor, and dead wood nutrients were 92.2 kg N/ha (7%), 4.89 kg P/ha (5%), 67.9 kg K/ha (16%), 156.6 kg Ca/ha (12%), 28.9 kg Mg/ha (17%),

and 0.74 kg Na/ha (9%). Storage of relatively high amounts of Ca in dead wood of most natural forests indicates that management could have a significant effect on its availability in the long term.

Aubrey, K.B., L.L.C. Jones, and P.A. Hall. 1988. Use of woody debris by Plethodontid salamanders in Douglas-fir forests in Washington. *In Proc. Symp. on Management of Amphibians, Reptiles, and Small Mammals in North America*. R.C. Szaro, K.E. Severson, and D.R. Patton (editors). July 19–21, 1988, Flagstaff, Ariz. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. RM-166, pp. 32–37.

Keywords: Pacific Northwestern states, *Pseudotsuga menziesii*, herpetofauna, habitat.

Abstract: *Ensatina eschscholtzii* was found most often under pieces of bark, whereas *Plethodon vehiculum* occurred primarily under logs. Captures of both species were highest in young stands, but occurred in all age classes. Our results suggest that the retention of coarse woody debris in managed forests would provide for the habitat needs of these species.

Auclair, A.N.D. 1985. Postfire regeneration of plant and soil organic pools in a *Picea mariana*–*Cladonia stellaris* ecosystem. *Can. J. For. Res.* 15:279–291.

Keywords: quantities, fuel load, *Picea mariana*, organic matter dynamics, regeneration, decay rate, accumulation.

Abstract: Postfire recovery of biomass and soil organic pools was measured in a sequence of 10 subarctic lichen woodlands aged from 0 to 140 years. Less than one-tenth of total live biomass combusted at the time of burning. Aboveground biomass combustion of species ranged from nil to over 90% depending on plant stature. Although no trees or lichen survived, shrub mortality (6%) was minor. Developmental phases similar to those in northern hardwood forest were apparent. Reorganization was dominated by shrubs over the first three decades. Aggradation resulted in a fourfold increase in total biomass; it was then followed by a 14% decrease occurring at transition (11–140 years postfire). Breakdown of the burnt lichen mat was rapid (1500 kg ha⁻¹ year⁻¹) compared with the disintegration of dead wood. Of an initial 40 000 kg ha⁻¹ in dead boles and branches, 15 000 kg ha⁻¹ remained 110 years later. Little change in soil humus mass occurred during fire and postfire. Total live and dead organic mass remained relatively constant over the 140 years of recovery. However, the live/dead ratio of organic mass showed a gradual but consistent increase.

Bensen, R.E. and J.A. Schleiter. 1980. Woody material in northern Rocky Mountain forests: volume, characteristics, and changes with harvesting. *In Environmental consequences of timber harvesting in Rocky Mountain coniferous forests*. Symp. Proc. Sept. 11–13, 1979, Missoula, Mont. U.S. Dep. Agric. For. Serv., Ogden, Utah. Gen. Tech. Rep. INT-90, pp. 27–36.

Keywords: quantities, decay classes, Rocky Mountains, *Pseudotsuga menziesii*, *Larix occidentalis*, *Abies grandis*, *Abies lasiocarpa*, *Picea engelmannii*, logging impacts.

Abstract: In mature coniferous stands in the Northern Rockies, total volume of wood 3 inches in diameter (7.6 cm) and larger, ranges from 3000 to 8000 ft³/a (210–560 m³/ha). Typically, about half of this volume is removed in logging, and the remaining residues include up to 50 percent or more sound wood, plus material in various stages of decay. In Wyoming, Montana, and Idaho over 450 million ft³ (13 million m³) of residue may be left on site annually, but residue is being utilized to meet demands for wood.

Bieber, W.P. 1990. The application of “New Forestry” in British Columbia and a method of determining coarse woody debris requirements. B.S.F. thesis. Univ. British Columbia, Fac. Forestry, Vancouver, British Columbia

Keywords: management, modelling, long-term impacts, *Pseudotsuga menziesii*, British Columbia, quantities, old growth, partial cut, coastal western hemlock forest.

Abstract: This essay is in two parts. The first discusses the application of “New Forestry” practices to British Columbia, with reference to ecological rotation, forest nutrient cycling, regeneration, and crop risk. The second part discusses the policy regarding coarse woody debris requirements in Oregon and presents a method of determining coarse woody debris requirements in British Columbia, using FORCYTE-11, an ecosystem model, and tables of whole-tree weight for selected U.S. tree species. For a medium site in the Coastal Western Hemlock biogeoclimatic zone of British Columbia, managed for Douglas-fir (*Pseudotsuga menziesii*), it was determined that leaving about 165 m³/ha of coarse woody debris would maintain ecological condition for four 60-year rotations. It is assumed that this amount of debris may produce the habitat and vertical heterogeneity conditions that characterize old-growth stands in this type of forest ecosystem and therefore satisfy this requirement of “New Forestry” prescriptions. In the least, it is a place to start. Subsequent application and long-term analysis of this estimate will assist in determining whether this assumption is met.

Bingham, B.B. and J.O. Sawyer, Jr. 1988. Volume and mass of decaying logs in an upland old-growth redwood forest. *Can. J. For. Res.* 18:1649–1651.

Keywords: quantities, southwestern U.S.A., old growth, *Sequoia sempervirens*, *Pseudotsuga menziesii*, decomposition, decay classes, *Tsuga heterophylla*, bole wood.

Abstract: A line intersect technique was used to determine the volume and mass of dead, naturally fallen logs at least 25 cm in diameter and 4 m in length over an 80-ha, mesic, upland, old-growth redwood forest in northwestern California. Each log was identified to species and placed in one of three decay classes: sound logs, moderately decayed logs, and logs in an advanced state of decay. Only logs of redwood (*Sequoia sempervirens* [D. Don] Endl.), Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), and western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) met the dimension requirements of sampling. Redwood logs in the middle decay class had the greatest volume (528 m³/ha) and mass (116 t/ha). The total volume and mass of all logs were 957 m³/ha and 200 t/ha, respectively. The total volume and mass of decaying logs in this redwood stand exceeded averages typical of other kinds of low-elevation coniferous forests in the Douglas-fir region.

Binkley, D. 1984. Does forest removal increase rates of decomposition and nitrogen release? *For. Ecol. and Manage.* 8:229–233.

Keywords: decomposition, logging impacts, clearcut, nitrogen.

Abstract: Little information is yet available concerning the effects of forest harvest on rates of decomposition and nutrient release. This study examines decomposition and nitrogen availability in adjacent cut and uncut sites by means of cellulose-filled litterbags and ion exchange resin bags located at three elevations on Vancouver Island, British Columbia, Canada. Cellulose weight loss was no greater in clear-cut than in uncut sites at the forest floor interface of litter and fragmented layers, but was 3–5 times greater at the interface of fragmented and humified layers and the interface of the humified layer and mineral soil. Resin-based estimates of nitrogen availability were 7–20 times greater in clearcut sites.

Boddy, L. and M.J. Swift. 1984. Wood decomposition in an abandoned beech and oak coppiced woodland in SE England. III. Decomposition and turnover of twigs and branches. *Holarctic Ecology* 7:229–238.

Keywords: decomposition, hardwood forest, England, decay rate, turnover time, branches, twigs.

Abstract: The rate of litter decomposition is often expressed as a constant decay rate (k ; $\text{g g}^{-1} \text{yr}^{-1}$) or as the time required for a certain percentage (often 95% and estimated as $3/k$) of it to decompose (termed turnover time). Estimates of k may be obtained by determining the weight loss of litter in the field and also by assuming a steady state and obtaining the ratio of litter input:standing crop. Both methods were used to estimate decay rate and turnover times for beech and oak branches and twigs decomposing on the forest floor and these were critically evaluated.

Considerable variation, ranging between 1.8 and 144.5 years, was found between the 95% turnover time estimates of various size components of the two species, obtained from woodfall and standing crop data. Likewise variation in decay rate of 2–2.5 cm diameter beech branches, estimated from field experiments, was large both between and within groups of branches categorized according to initial state of decay and presence or absence of bark. The mean annual decay rate for the various categories ranged between $k = 0.165$ and $k = 0.452 \text{ g g}^{-1} \text{yr}^{-1}$. Branches without bark generally decomposed more slowly than those with bark. Beech twig (<0.5 cm diameter) decomposition rates, from field experiments, ranged between $k = 0.149$ and $0.220 \text{ g g}^{-1} \text{yr}^{-1}$ and variation was relatively low compared with that of branches. No significant differences ($P < 0.05$) were detected between twig decomposition rates obtained from experiments initiated at different seasons although there was a slight decline in decay rate in winter months. Twig and branch decomposition rates fell within the range found in the other comparable studies.

Boone, RD., P. Sollins, and K. Cromack, Jr. 1988. Stand and soil changes along a mountain hemlock death and regrowth sequence. *Ecology* 69(3):714–722.

Keywords: organic matter dynamics, nitrogen, nutrient dynamics, *Tsuga mertensiana*, coastal subalpine forest, structural characteristics, *Phellinus weirii*, carbon, Pacific Northwest, mortality.

Abstract: Stand characteristics, dead wood, and soil carbon (C) and nitrogen (N) pools were measured through a wave-regenerated sequence of mountain hemlock death and regrowth created by *Phellinus weirii*. Stem density increased along the 96-year regrowth sequence, but was low in the 225-year-old, mature stand. Total ecosystem (TEC) dropped upon stand death and did not recover. Net ecosystem production (NEP) was negative just after stand death and zero thereafter.

The O2 horizon and the forest floor (O1 + O2) had greater mass, organic matter, and N capital in the mature stand than in the bare or regrowth zones. From the mature stand to the bare zone, forest-floor organic matter decreased 27% and C and N 24%. The forest-floor N decrease was offset by an equal N increase in the mineral soil at 0–15 cm depth. Mineral-soil C, as well as C and N for the sum of the forest floor + mineral soil, were constant across the death and regrowth sequence. The C/N ratio peaked for O1 material, and reached its minimum for fine roots, in the bare zone.

British Columbia Ministry of Forests. 1990. Old-growth forests: problem analysis. Research Branch, Victoria, B.C. Draft Report.

Keywords: management, general, old growth, bole wood, habitat, quantities, nutrients.

Abstract: Little is known about the ecology of British Columbia's old-growth forests yet increasingly they are a focus of public concern about the effect of forestry practices on the environment. Information on temperate coniferous old-growth ecosystems, including forest structure and composition, ecosystem functioning, the relationship of old growth to biological diversity concerns, and forest management considerations, has largely been the result of research on the coastal Douglas-fir forests of Oregon and Washington. We review major ecological characteristics of old-growth forests and show

the extent to which this information applies to British Columbia's old growth. Included are the specific sources of inventory and ecological information of our forests.

Developing working definitions to describe various old-growth forest types is an essential first step in a comprehensive research program on old-growth ecology and management. Ideally, work would begin in the forest types and geographic areas where the pressures on old growth are greatest. Definitions should be based on multiple criteria including age, disturbance patterns, forest structure and composition, and minimum areas.

The second major research area includes old-growth ecosystem processes and functioning. How old-growth ecosystems operate is poorly understood yet this basic information is important for developing and assessing sustainable forestry practices. Research in the United States suggests that baseline studies to determine the ecological roles of large woody debris and to characterize nutrient cycling, microclimate, water balance, and primary production of different old-growth ecosystems are important.

The highest priority for old-growth research relates to developing a conservation strategy to maintain biological diversity and forest productivity. Old-growth forests appear to contribute much to the provinces biological diversity. Research directed at determining the role of old growth in providing optimal habitat for forest-dwelling species is important for developing forestry management practices. Both a system of old-growth reserves and alternative management techniques to maintain old-growth values in managed stands should be investigated. An old-growth conservation strategy to address concerns relating to loss of biologic diversity and forest productivity is essential.

In addition to identifying important research areas in old-growth ecology and management we propose a research and communication strategy for meeting these needs. Both research activities and communications outputs are detailed for the research areas.

Brown, J.K. 1974. Handbook for inventorying downed woody material. U.S. Dep. Agric. For. Serv., Ogden, Utah. Gen. Tech. Rep. INT-16.

Keywords: quantities, line intersect, inventory, fuel load, methods.

Abstract: To facilitate debris management, procedures for inventorying downed woody material are presented. Instructions show how to estimate weights and volumes of downed woody material, fuel depth, and duff depth. Using the planar intersect technique, downed material is inventoried by 0- to 0.25-inch, 0.25- to 1-inch, and 1- to 3-inch diameter classes; and by 1-inch classes for sound and rotten pieces over 3 inches. The method is rapid and easy to use and can be applied to naturally fallen debris and to slash. The method involves counting downed woody pieces that intersect vertical sampling planes and measuring the diameters of pieces larger than 3 inches in diameter. The piece counts and diameters permit calculation of tons per acre.

Brown, J.K. and T.E. See. 1981. Downed dead woody fuel and biomass in the northern Rocky Mountains. U.S. Dep. Agric. For. Serv., Ogden, Utah. Gen. Tech. Rep. INT-117.

Keywords: fuel load, quantities, Rocky Mountains, site factors, management.

Abstract: Weights and volumes of downed woody material in diameter classes of one-fourth to 1, 1-3, and greater than 3 inches and forest floor duff depths were summarized from extensive inventories in northern Idaho and Montana. Biomass loadings are shown by cover types and habitat types within National Forests. Total downed woody biomass east of the Continental Divide ranged from 5 tons per acre in ponderosa pine to 23 tons per acre in spruce-fir. West of the divide, loadings range from 13 tons per acre in ponderosa pine to 33 tons per acre in cedar-hemlock. Duff depths for cover types ranged from 0.5 to 1.5 inches or approximately 10-25 tons per acre. Sixty percent of biomass greater than 3 inches diameter displayed some decay. Inasmuch as 10 tons per acre is considered desirable for on-site retention, spruce-fir and larch-grand fir cover types had the greatest excesses of biomass for utilization. Relationships proved

ineffectual for predicting loading from stand age, slope, aspect, and elevation. Loadings generally increased with increased productivity, but varied greatly with stand age. The generality that dead fuels tend to become predictably high in overmature stands, but unpredictable in young immature and mature stands, was supported. Forest fuel succession is discussed in relation to tree mortality, fuel buildup, and depletion.

Bury, RB. and P.S. Corn. 1988. Douglas-fir forests in the Oregon and Washington Cascades: relation of the herpetofauna to stand age and moisture. *In Proc. Symp. on Management of Amphibians, Reptiles, and Small Mammals in North America.* R.C. Szaro, K.E. Severson, and D.R. Patton (editors). July 19–21, 1988, Flagstaff, Ariz. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. RM-166, pp. 11–22.

Keywords: Pacific western states, site conditions, habitat environmental factors, herpetofauna.

Abstract: Pitfall traps effectively sampled amphibians but not reptiles in Douglas-fir (*Pseudotsuga menziesii*) forests. The abundance of only one amphibian species varied across an age gradient or a moisture gradient. Salamanders and frogs that breed in ponds or streams were captured in large numbers in some stands, likely due to the presence of nearby breeding habitat rather than forest conditions. Lizards occurred mostly in dry stands and clearcuts. Time-constrained searches showed different use of downed woody debris among terrestrial salamanders. The occurrence and abundance of species in naturally regenerated forests markedly differed from clearcut stands.

Carpenter, S.E., M.E. Harmon, E.R. Ingham, R.G. Kelsey, J.D. Lattin, and T.D. Schowalter. 1988. Early patterns of heterotroph activity in conifer logs. *Proc. Royal Soc. Edinburgh* 94B, pp. 33–43.

Keywords: function, decomposition, decomposers, coastal conifer forest, environmental factors.

Abstract: Findings from the first two years of a long-term study of conifer log decomposition are presented. Log decomposition is regulated by the physical and chemical states, and development of decomposer foodwebs. The functional group with the greatest initial effect on the log is the channelizers, represented in our study by ambrosia and bark beetles. They not only create multitudes of channels into the logs but vector the initial decomposer community. Ambrosia beetles exclude certain elements of the decomposer community from channels until they vacate the log, at the end of their reproductive phase. The foodweb during the early stages of decomposition includes nitrogen-fixing and other bacteria, fungi, protozoa, nematodes, and arthropods. Seasonal fluctuations of temperature and moisture are hypothesized to work in tandem to modulate the activities of the decomposer community.

Christensen, O. 1984. The states of decay of woody litter determined by relative density. *Oikos* 42:211-219.

Keywords: decomposition, decay rates, wood properties, methods.

Abstract: Relative density (RD, g cm^{-3}), based on dry weight samples, is used as an estimate of the extent of decay of woody litter. RD is critically evaluated. It is concluded that RD may be reproduced in a reasonably accurate way and the precision of RD may not show pronounced dependency of the degree of decay. Comparisons of RD may be done only in relation to the diameter of woody litter.

A significant correlation between weight loss and RD exists, being linear if weight loss includes only losses due to leaching and decomposition.

An analysis of the decay states of the various dead wood compartments shows that the mean weight loss of the attached deadwood and the soil surface dead wood compartment are 18% and 43%, respectively. A considerable weight loss prior to wood litter fall is observed and wood fall data given earlier are corrected.

It is suggested that a knowledge of the decay states by RD makes it possible to predict the presence and diversity of organisms inhabiting the deadwood habitat.

Christy, E.J. and R.N. Mack. 1984. Variation in demography of juvenile *Tsuga heterophylla* across the substratum mosaic. *J. Ecology* 72:75–91.

Keywords: Pacific northwestern states, regeneration, *Tsuga heterophylla*, mortality, habitat, seedlings.

Abstract:

- Recruitment and survival of juvenile *Tsuga heterophylla* were followed on different substrata on the west slope of the Cascade Range, central Oregon, U.S.A.
 - Whilst seeds fell mainly from October to March, some were shed in all but six of thirty-two consecutive months.
 - Almost all juveniles occurred on decaying logs even though fallen timber may cover only 10–30% of the forest floor.
 - Recruitment on all substrata varied widely from year to year, as expected in a conifer with mast years of seed production.
 - Cohorts emergent in different months during a calendar year often showed greatly different survivorship curves even on the same rooting substratum.
 - Mortality was much higher for juveniles during the first 2 years after emergence than in subsequent years. Microtine rodents probably account for most seed and seedling deaths.
 - The extent of decay of woody rooting substrata does not influence percentage emergence, although survival of juveniles was most prolonged on *Pseudotsuga menziesii* logs with rotten heartwood.
 - The age-class structures of juvenile populations were functions of the fraction of the forest floor covered by fallen wood in each decay class.

Clayton, J.L. and D.A. Kennedy. 1985. Nutrient losses from timber harvest in the Idaho batholith. *Soil Sci. Soc. Am. J.* 49:1041–1049.

Keywords: logging impacts, nutrient dynamics, inland northeastern U.S.A., *Pinus ponderosa*, *Pseudotsuga menziesii*, harvesting methods, site treatment.

Abstract: Nutrient budgets for a mature ponderosa pine/Douglas fir (*Pinus ponderosa* Dougl./*Pseudotsuga menziesii* [Mirbel] Franco var. *glauca* [Beissn.] Franco) forest in the southwestern Idaho batholith are used to evaluate the potential for accelerated nutrient losses associated with timber harvesting. Soils formed from granitic rock in the Idaho batholith are commonly shallow, coarse textured, and highly erodible following disturbance. Cycling and annual budgets for K, Ca, Mg, S, P, and N are described for an undisturbed control watershed, and accelerated losses associated with clearcutting, helicopter yarding, and broadcast burning of slash are evaluated in an adjacent treated watershed. There were small but statistically significant increases in dissolved N losses of approximately 10 times preharvest rates for a 4-year period following treatment. Dissolved transport of other elements was not increased. Small but significant increases in sediment nutrient transport of all elements occurred 3 years following harvest. The largest losses in nutrients were due to bole removal and ranged from 4% of total ecosystem N to 21% of ecosystem K. Rates of replacement from precipitation, primary mineral weathering, and N₂ fixation would restore the ecosystem to the nutrient status prior to harvest in 50 years. Based on these findings, logging systems that minimize erosion should not cause unacceptable nutrient loss over a normal timber stand rotation.

Covington, W.W. and S.S. Sackett. 1984. The effect of a prescribed burn in southwestern ponderosa pine on organic matter and nutrients in woody debris and forest floor. *Forest Science* 30(1):183–192.

Keywords: nutrients, fuel load, southwestern U.S.A., *Pinus ponderosa*, regeneration, site treatment, nutrient dynamics, organic matter dynamics.

Abstract: After 100 years of fire exclusion, controlled burning in the fall was used as a first step in the reintroduction of periodic burning in a southwestern ponderosa pine ecosystem near Flagstaff, Arizona, U.S.A. Organic matter storage in woody debris was decreased 63% from 2325 g/m² to 869 g/m², with a disproportionate (99%) decline in the large, rotten wood. Nutrient storage in the woody debris decreased by 80% for N, 62% for P, 70% for Ca, 71% for Mg, and 74% for K. Forest floor storages were less drastically affected, with organic matter content declining 37% from 3170 g/m² to 1990 g/m² immediately after burning. Nutrient content of the forest floor was not significantly affected by burning due, in part, to the transfer of nutrients from woody debris to the forest floor. By 7 months after burning, the forest floor had declined by an additional 440 g/m² of organic matter, most likely from microbial mineralization. Also during this period forest floor storages for all nutrients declined significantly, except K which was unchanged. Mg exhibited the greatest proportional decline (40%), followed by N, P, and Ca, all of which decreased by approximately 25%. Numerous potential benefits to productivity may be associated with this prescribed burn—reduced fire hazard, accelerated nutrient mobilization, and reduced forest floor interception of precipitation.

DeBell, D.S. and J.F. Franklin. 1987. Old-growth Douglas-fir and western hemlock: a 36-year record of growth and mortality. *Western J. Appl. For.* 2(4):111–114.

Keywords: input rate, mortality, old growth, *Pseudotsuga menziesii*, *Tsuga heterophylla*, *Abies amabilis*, *Thuja plicata*, *Pinus monticola*, Pacific Northwest.

Abstract: Growth and mortality were measured at 6-year intervals in a 1180 acre old-growth stand in southwestern Washington. Principal tree species were Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), Pacific silver fir (*Abies amabilis*), western redcedar (*Thuja plicata*), and western white pine (*Pinus monticola*). They composed 59, 27, 6, 6, and 1%, respectively, of the total cubic volume (13 290 ft³) in 1947. Gross volume growth averaged 94 ft³ per acre per year, and mortality averaged 86 ft³ per acre per year. Net growth was therefore minimal, and total stand volume remained nearly constant for 36 years. Douglas-fir, which accounted for only one-third of the gross growth and only 28% of the mortality is losing dominance to western hemlock, which provided nearly one-half the gross growth and 28% of the mortality. Pacific silver fir increased in importance in the lower canopy and composed 60% of the ingrowth. Thus, although net gain in timber volume was nil, substantial changes occurred in stand characteristics during the 1947–1983 period.

Delisle, G.P., P.M. Woodward, S.J. Titus, and A.F. Johnson. 1988. Sample size and variability of fuel weight estimates in natural stands of lodgepole pine. *Can. J. For. Res.* 18:649–652.

Keywords: quantities, line intersect, methods.

Abstract: This study assessed the variability of sample estimates for downed and dead woody fuel weight in natural lodgepole pine (*Pinus contorta* Dougl.) stands using line intersect sampling procedures. Equilateral triangles (30 m/side) were established at each of 40 sample sites with variable length transects on each side to estimate fuel weights by diameter class. Regardless of the number of sides measured, the standard error for fuels less than 7.0 cm was at most 20% of the mean. Even measuring only one side of the triangle using a single transect instead of the triangular sample unit still achieved standard errors less than 20% of the mean. Standard errors for classes greater

than 7.0 cm were all greater than 20% of the mean. For these classes, more samples are required to achieve the 20% standard error limit; however, depending on costs, the triangular sample unit may not be the best solution. In this study, intracluster correlations were above 0.7 for the fuel diameter classes greater than 7.0 cm, suggesting that multiple transects at a given sample location contribute little new information. This effect, although less pronounced, was also observed with the smaller diameter classes.

Edmonds R.L. 1987. Decomposition rates and nutrient dynamics in small-diameter woody litter in four forest ecosystems in Washington, U.S.A. *Can. J. For. Res.* 17:499–509.

Keywords: decomposition, Pacific Northwest, *Abies amabilis*, *Pseudotsuga menziesii*, *Tsuga heterophylla*, *Alnus rubra*, wood properties, decay rate, nutrients, twigs, branches, cones.

Abstract: Decomposition rates and nutrient dynamics in small-diameter woody litter (twigs, cones, and branches) were studied in four ecosystems in western Washington: high-elevation Pacific silver fir (*Abies amabilis* [Dougl.] Forbes) and low-elevation Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), and red alder (*Alnus rubra* Bong.). Conifer twigs decomposed faster ($k = 0.14\text{--}0.24 \text{ year}^{-1}$) than cones ($k = 0.09\text{--}0.12 \text{ year}^{-1}$) and branches ($k = 0.03\text{--}0.11 \text{ year}^{-1}$). Decomposition constants were related better to initial lignin/initial N ratios ($r = -0.64$) than initial lignin concentrations. N was generally the least mobile nutrient while K was the most mobile. Many nutrients were strongly immobilized in conifer fine woody litter, including N, Mg, Mn, and Ca. There was little immobilization of N in red alder branches. N release from decomposing woody litter appears to be controlled by a critical C/N ratio. This critical C/N ratio, however, was not constant and increased as the substrate decomposition rate increased.

Edmonds, R.L., D.J. Vogt., D.H. Sandberg, and C.H. Driver. 1986. Decomposition of Douglas-fir and red alder wood in clear-cuttings. *Can. J. For. Res.* 16:822–831.

Keywords: decomposition, *Pseudotsuga menziesii*, *Alnus rubra*, Pacific Northwest, clearcut, site factors, wood properties, decay rate.

Abstract: Decomposition rates of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) and red alder (*Alnus rubra* Bong.) wood (simulating logging residues) were determined in clearcuttings at the Charles Lathrop Pack Experimental Forest of the University of Washington, which is located approximately 120 km south of Seattle, WA. The influence of diameter (1–2, 4–6, and 8–12 cm), vertical location (buried, on the soil surface, and elevated), season of logging (summer and winter), aspect (north and south), and wood temperature, moisture, and chemistry on wood decomposition rates were determined. Red alder wood decomposed faster ($k = 0.035\text{--}0.517 \text{ year}^{-1}$) than Douglas-fir wood ($k = 0.006\text{--}0.205 \text{ year}^{-1}$). In general, buried wood decomposed faster than surface wood, which decomposed faster than elevated wood. Small-diameter wood generally decomposed faster than larger-diameter wood. Aspect and season of logging had little influence on decomposition rates. Moisture and temperature were the dominant factors related to Douglas-fir wood decomposition, with initial chemistry playing a minor role. Initial wood chemistry, particularly soda solubility, was the dominant factor related to red alder wood decomposition.

Erickson, H.E., R.L. Edmonds, and C.E. Peterson. 1985. Decomposition of logging residues in Douglas-fir, western hemlock, Pacific silver fir, and ponderosa pine ecosystems. *Can. J. For. Res.* 15:914–921.

Keywords: decomposition, logging impacts, decay rate, Pacific Northwest, *Pinus ponderosa*, *Pseudotsuga menziesii*, *Tsuga heterophylla*, *Abies amabilis*, wood properties, site factors.

Abstract: Logging residue decomposition rates were determined in four conifer forest ecosystems in the State of Washington, U.S.A. (coastal western hemlock, Puget lowland Douglas-fir, high-elevation Pacific silver fir, and eastern Cascade ponderosa pine), by examining wood density changes in a series of south-facing harvest areas with residues of different ages. Decomposition rates were determined for two diameter classes (1–2 and 8–12 cm) and two vertical locations (on and >20 cm above the soil surface). Pacific silver fir and ponderosa pine ecosystems had the lowest k values (0.005 and 0.010 year⁻¹, respectively) followed by Douglas-fir (range, 0.004–0.037 year⁻¹) and western hemlock (range, 0.010–0.030 year⁻¹). Small-diameter residues decomposed at rates significantly slower than large-diameter residues in Douglas-fir and western hemlock ecosystems; this relationship was also implied in the other ecosystems. In all four ecosystems, dry-season moisture contents were lower in smaller-diameter residues. Moisture levels associated with small-diameter residues were too low for significant decomposition to occur during the dry summer period and probably contributed to the slow annual decay rates. Residues located above the soil surface decomposed significantly slower than residues on the soil surface only in the Douglas-fir ecosystem. Dry-season residue moisture, rather than initial lignin concentration, appeared to be the dominant factor determining residue decomposition rates on exposed harvested areas.

Eubanks, S. 1989. Applied concepts of ecosystem management: developing guidelines for coarse, woody debris. *In* Maintaining the long-term productivity of Pacific Northwest forest ecosystems. D.A. Perry, R. Meurisse, B. Thomas, R. Miller, J. Boyle, J. Means, C.R. Perry, and R.F. Powers (editors). Timber Press, Portland, Oreg. pp. 230–236.

Keywords: management, Pacific Northwest, quantities, structural characteristics.

Abstract: Coarse, woody debris (harvest residues and standing dead or unmerchantable trees) is an important component of forest ecosystems. The Blue River Ranger District seeks to perpetuate this component over time in harvest areas by reducing cleanup of residues to ensure adequate supplies of soil organic matter and leaving more standing trees to ensure wildlife habitat. The District has developed guidelines that not only deal with the technical aspects (what kind, how much) to manage for, but also address how to deal with key people to ensure that the guidelines are met.

Fahey, T.J. 1983. Nutrient dynamics of aboveground detritus in lodgepole pine (*Pinus contorta* ssp. *latifolia*) ecosystems, southeastern Wyoming. *Ecol. Monog.* 53(1):51–72.

Keywords: decomposition, decay rates, nutrient dynamics, *Pinus contorta*, inland northwestern U.S.A., nutrients, accumulation, nitrogen, bark, twigs, cones, bole wood, organic matter dynamics.

Abstract: Storage and fluxes of N, P, Ca, Mg, and K in aboveground detritus were measured in six contrasting lodgepole pine (*Pinus contorta* ssp. *latifolia*) stands in southeastern Wyoming. Litterfall was predominantly leaves (67–80%) in 80- to 100-year-old stands, while woody litter was more important in an older stand (240 years old). Leaf litter nutrient concentrations were very low compared with other pine forests, particularly for N (0.40% dry mass). Dry mass loss from decomposing leaf litter was slow (15%/yr in first 2 years), and summer rates did not differ significantly from winter rates beneath the snowpack. Significant amounts of N, P, and Ca were added to decomposing leaves during the first winter, and N and Ca addition continued for 2 years. Potassium and magnesium were rapidly lost from decomposing leaves. Rates of mass and nutrient loss from decomposing bark, twigs, and cones were comparable to those observed in other studies of temperate-zone forests. Mass loss from decaying bole wood appeared to be exponential through 40 years, with an average decay coefficient (k) of 0.016, which is comparable to that in other cold temperate forests. Nitrogen content of decaying boles

doubled between 30 and 55 years following tree death, while smaller additions of P, Ca, K, and Mg also were noted.

Relatively large accumulations of organic matter and nutrients were observed in the forest floor, leading to very high steady-state residence times for dry mass (mean = 18 years), N (54 years), P (39 years), Ca (35 years), Mg (21 years), and K (18 years). Deadfall contributed by the present forest generation was a minor component of the aboveground detritus except in an old-age stand and in a dense, self-thinning forest site. In contrast, deadwood inherited from the previous forest generation (killed by fire) was a major detrital storage component, exceeding forest floor mass by several-fold in 80 to 100-year-old stands. High nutrient immobilization in the deadwood led to storage values which were similar to those of the forest floor in these stands.

Fahey, T.J., J.W. Hughes, M. Pu, and M.A. Arthur. 1988. Root decomposition and nutrient flux following whole-tree harvest of northern hardwood forest. *For. Sci.* 34(3):744–768.

Keywords: decomposition, nutrient dynamics, roots, hardwood forest, *Acer saccharum*, *Betula alleghaniensis*, *Fagus grandifolia*, *Picea rubens*, whole-tree harvest, nutrients, decay rate, northeastern U.S.A.

Abstract: Decomposition of roots of four dominant species (*Acer saccharum*, *Betula alleghaniensis*, *Fagus grandifolia*, *Picea rubens*) in a northern hardwood ecosystem was measured following whole-tree harvest of watershed 5 at Hubbard Brook Experimental Forest, New Hampshire. To quantify the importance of element release from tree root systems after forest harvest, measurements of macronutrient (N, K, P, Ca, Mg) release from roots of seven diameter classes (<0.6, 0.6–1.0, 1.0–2.5, 2.5–5.0, 5–10, 10–20, 20–100) were combined with information on root system nutrient content. Decay of fine roots (all species) was initially rapid but declined abruptly after the first summer. Ash-free weight loss from small woody roots decreased with increasing root diameter and was much slower than decay rates for corresponding aboveground tissues (twigs and branches). Weight loss rates among species generally were not significantly different; however, large woody roots (10–100 mm diameter) of sugar maple decayed much more rapidly than the other species.

Rapid release of K and Mg was observed for all roots. Initially high rates of N and P release were observed for fine roots, whereas these nutrients were effectively retained in decaying woody roots. Retention of Ca was observed for all roots, and significant accumulation of Ca was observed in the larger size classes of woody roots. Particularly for N and K, release from decaying roots was an important nutrient flux pathway supplying stream outflow and vegetation regrowth in the first two years following forest harvest.

Falinski, J.B. 1978. Uprooted trees, their distribution and influence in the primeval forest biotope. *Vegetation* 38(3): 175–183.

Keywords: uprooting, Poland, *Picea abies*, mixed forest, *Carpinus betulus*, *Pinus sylvestris*, *Betula verrucosa*, old growth, regeneration.

Abstract: The paper reports results of a long-term (1964–1974) investigation on permanent study sites in natural forest ecosystems of the *Tilio-Carpinetum* and the *Pino-Quercetum* in the Bialowieza Forest. The influence of decaying logs and root craters was investigated. It was found that the main causes of uprooting were the spring and autumn winds. Wind direction and the position of logs lying on the ground are correlated. *Picea* is most susceptible to uprooting by winds. Almost one-half of the trees of this species are alive at the moment of uprooting.

By mapping changes in the distribution of uprooted trees on a permanent area in time, a balance of the changeover in a 10-year period was determined. It appeared that

the decomposition is slower than accumulation. From this, it was concluded that the stand is in a phase of natural thinning. In the study site, compartments were distinguished with various degrees of change in the number of uprooted trees, and the consequences of differentiation and constant transformation of the biotope and biocenosis by the occurrence of uprooted trees and by their decay are described.

Franklin, J.F., K. Cromack, Jr., W. Denison, A. McKee, C. Maser, J. Sedell, F. Swanson, and G. Juday, 1981. Ecological characteristics of old-growth Douglas-fir forests. U.S. Dep. Agric. For. Serv., Portland, Oregon, Tech. Rep. PNW-118.

Keywords: *Pseudotsuga menziesii*, general, structural characteristics, Pacific Northwest, old growth, bole wood.

Abstract: Old-growth coniferous forests differ significantly from young-growth forests in species composition, function (rate and paths of energy flow and nutrient and water cycling), and structure. Most differences can be related to four key structural components of old growth: large live trees, large snags, large logs on land, and large logs in streams. Foresters wishing to maintain old-growth forest ecosystems can key management schemes to these structural components.

Franklin, J.F. and D.S. DeBell. 1988. Thirty-six years of tree population change in an old-growth *Pseudotsuga-Tsuga* forest. Can. J. For. Res. 18:633–639.

Keywords: input rate, old growth, *Pseudotsuga menziesii*, *Tsuga heterophylla*, Pacific Northwest, mortality, quantities, regeneration.

Abstract: Tree populations exhibited considerable individual plant mortality and replacement over a 36-year period in a 500-year-old *Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii* (Douglas-fir)–*Tsuga heterophylla* (Raf.) Sarg. (western hemlock) forest in the Cascade Range of southern Washington, U.S.A. Nearly 22% (113/ha) of the original stems died at an annual rate of 0.75%. This was balanced by recruitment (117/ha) of *Tsuga*, *Abies amabilis* Dougl. ex Forbes (Pacific silver fir), and *Taxus brevifolia* Nutt. (Pacific yew) saplings. Diameter distributions and relative species composition were nearly identical at the beginning and end of the 36 years. Compositional changes were slow despite the high turnover; extinction of *Pseudotsuga* is predicted in 755 years at its current mortality rate. Mortality was generally caused by wind (45.5%) or suppression and unknown causes (39.4%). Additional long-term studies of old-growth forests are needed to understand the direction and rate of successional change.

Franklin, J.F., H.H. Shugart, and M.E. Harmon. 1987. Tree death as an ecological process. BioScience 37(8) :550–556.

Keywords: mortality, environmental factors, habitat, regeneration.

Abstract: The consequences of tree death, in terms of effects on other ecosystem components and processes, depend on many variables including the species, mortality agent, position, spatial pattern (dispersed or aggregated), and numbers that have died. Tree death is an important indicator of ecosystem health and can assist recognition of stresses caused by pollutants, such as acid rain and ozone. However, the value of tree death as an indicator of anthropogenic disturbance depends on a thorough understanding of patterns of tree death under natural conditions. At the present time, adequate understanding of this is woefully lacking.

Tree death also demonstrates some principles of ecological processes: the importance of defining the spatial and temporal context of a study, the importance of stochastic processes, the fact that most ecological processes are driven by multiple mechanisms and that the relative importance of these mechanisms changes in time and space, and the importance of species' and ecosystems' natural histories. Tree death illustrates that many valid and useful perspectives on a single, presumably simple process exist. Further, it

makes clear that we need to give more consideration to the biology of organisms and ecosystems in developing, evaluating, and applying theoretical constructs.

Franklin, J.F. and T.A. Spies. 1989. Ecological definitions of old-growth Douglas-fir forests. Final draft. Unpublished.

Keywords: old growth, management, Pacific Northwest, structural characteristics, *Pseudotsuga menziesii*, quantities, bole wood.

Abstract: The potential for definitional and indexing approaches to identification of old-growth Douglas-fir stands are examined. An interim definition created by the Old-growth Definition Task Force utilizes multiple structural characteristics of forest stand—specific levels of large or old live trees, snags, down logs, and foliage canopy layers. This definition and numerous variants with different parameters and parameter values were tested for their ability to discriminate old growth from young and mature natural forests using an independently collected dataset. The criteria used in the definition vary significantly in their ability to discriminate old growth in particular geographic areas. Definitions which used density of all large (>100 cm dbh) trees rather than just Douglas-fir performed best. Further refinement of definitions should probably be directed toward site-specific efforts. Development of approaches which recognize the continuous variability in old-growth stands are recommended at the regional level. These could be simple indices based upon multiple structural characteristics or approaches using discriminant analysis; examples are provided to demonstrate the merit of both concepts. It is critical to maintain a holistic perspective on old-growth forest ecosystems in the face of these and other current efforts to characterize old growth using individual attributes.

Franklin, J.F. and R.H. Waring. 1979. Distinctive features of the northwestern coniferous forest: development, structure and function. *In* Forests: fresh perspectives from ecosystem analysis. Proc. 40th Annual Biology Colloq., Oreg. State Univ. Press, Corvallis, Oreg., pp. 59–85.

Keywords: structural characteristics, general, old growth, *Pseudotsuga menziesii*, *Tsuga heterophylla*, *Thuja plicata*, Pacific Northwest, decomposition, habitat.

Abstract: This is a general review paper describing the structural and functional characteristics of Pacific Northwest forests dominated by Douglas-fir, western hemlock, and western redcedar. It contains information on:

- biomass and productivity;
- factors responsible for evergreen dominance and massiveness;
- successional oriented studies of age structure and coarse woody debris; and
- aspects of the old-growth systems.

There is data on amount of CWD in a chronosequence of stands in the Pacific Northwest and discussion of the distinguishing characteristics of old-growth Douglas-fir forests.

Funck, J.W. and M.L. Hoag. 1985. Characteristics of logging residues from Oregon old-growth stands. *Forest Products J.* 35(6):33–40.

Keywords: old growth, quantities, Pacific Northwest, logging impacts, wood properties.

Abstract: Samples of logging residues removed at two utilization levels, 4-inch by 4-foot and 6-inch by 6-foot minimum size limits, from the Mt. Hood and Willamette National Forests in Oregon, were analyzed to determine species, moisture content, specific gravity, percentage of pieces with heavy decay, higher heating value, ash content, and proportion of wood to bark. Removal to the smaller size specification yielded an extra 15 dry tons per acre of residues and a 0.3% increase in ash content.

Douglas-fir comprised 77% of the volume of the eight species sampled; 85% of the total volume was wood. Average values were 63% moisture content (dry basis), 0.39 specific gravity, and 8500 BTU higher heating value. Ash content decreased and the percentage of pieces with heavy rot increased as piece size increased. Bark moisture contents showed large variations by season.

Gholz, H.L., G.M. Hawk, A. Campbell, K. Cromack, Jr., and A.T. Brown. 1985. Early vegetation recovery and element cycles on a clear-cut watershed in western Oregon. *Can. J. For. Res.* 15:400–409.

Keywords: nutrient dynamics, Pacific Northwest, logging impacts, clearcut, old growth, *Pseudotsuga menziesii*, nutrients.

Abstract: Aboveground biomass and leaf area, net primary production, and nutrient cycling through vegetation were studied for 3 years after clearcutting (stems only) of a 10.24-ha watershed in the Oregon Cascade Mountains. The riparian zone and four main habitats were analyzed separately. In 3 years, aboveground net primary production increased from 5 to 112 g m⁻² year⁻¹ in the ridgetop habitat; midsummer aboveground biomass increased from 8 to 196 g/m² in the riparian zone and from 198 to 327 g/m² on the ridgetop. Other values were intermediate to these. Litterfall of species with perennial aboveground parts averaged 20–27% of standing biomass. Native annuals, especially *Aralia californica* Wats., dominated the riparian zone. *Senecio sylvaticus* L., an introduced species, dominated most of the rest of the watershed, except for the ridgetop habitat, which was dominated by residual woody shrubs. Uptake of N exceeded losses in streamflow the first year and was six times greater in the second; uptake of P and K in that year was 2.5 and 3 times greater than losses. In the third year, total uptake of K (2.5 g m⁻² year⁻¹) equaled the pre-clearcutting level, and uptake of N (1.3 g m⁻² year⁻¹) and P (0.3 g m⁻² year⁻¹) was about half that level. No correlation was found between plant uptake and nutrient loss in streamflow. Uptake of all elements exceeded return through leaching and litter fall by 16%, except that of Mg, which exceeded return by 44%. Because of early dominance by species with annuals, the proportion of elements redistributed internally by vegetation was generally low. The amount of nutrients in flux through vegetation, atmosphere, and stream was small in comparison to the amount lost in the removal of tree stems.

Gore, J.A. and W.A. Patterson III. 1986. Mass of downed wood in northern hardwood forests in New Hampshire: potential effects of forest management. *Can. J. For. Res.* 16:335–339.

Keywords: quantities, logging impacts, hardwood forest, northeastern U.S.A., *Acer saccharum*, *Betula alleghaniensis*, *Fagus grandifolia*, bole wood.

Abstract: Downed (i.e., fallen, dead) wood was sampled in 1-, 15-, 50-, and 100-year-old managed stands, an uneven-aged, managed stand, and an uncut stand of northern hardwoods in New Hampshire. Mass of downed wood ranged from a mean of 32 t/ha in the 15- and 50-year-old stands to 86 t/ha in the recently cut stand. Mean estimates varied significantly among stands, although most of the variation was due to the large amount of downed wood in the recently cut stand. The range of downed-stem diameters was greatest in the 100-year-old and uncut stands. Large (>38 cm) logs were notably absent from the uneven-aged, managed stand, indicating that selective cutting utilizes mature stems efficiently. Comparison of our data with other estimates shows that the amount of downed wood in northern hardwood stands declines to about 20 t/ha within 20–30 years after logging. Quantities remain relatively stable for up to an additional 30 years and then begin to increase. They stabilize at 35–40 t/ha after approximately 100 years. Large-diameter logs become an increasingly important component of downed wood as stands mature beyond 50 years of age. Rapid decomposition of even the largest logs precludes

continued accumulation of downed wood in uncut, old-growth stands. The data suggest that less downed wood and fewer large-diameter logs are likely to accumulate under short-rotation (<50 years) harvest, whole-tree harvests, and selection cuts than under long rotations or in uncut forests.

Gower, S.T. and C.C. Grier. 1989. Aboveground organic matter and production of a montane forest on the eastern slopes of the Washington Cascade Range. *Can. J. For. Res.* 19:515–518.

Keywords: Washington, *Larix occidentalis*, *Pinus contorta*, *Pseudotsuga menziesii*, quantities.

Abstract: Aboveground biomass and production were determined for a 70-year-old mixed conifer forest of western larch (*Larix occidentalis* Nutt.), lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.), and Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) on the eastern slopes of the Cascade Range in Washington state. Live aboveground biomass, projected leaf area, and aboveground net primary production for the mixed conifer forest were 194 Mg ha⁻¹, 4.2 m² m⁻², and 6.1 Mg ha⁻¹ year⁻¹, respectively. Based on the few studies of montane forests on the eastern slope of the Cascades, aboveground biomass, leaf area index, and aboveground net primary production of these forests are more similar to those of montane coniferous forests in the Rocky Mountains than to those of similar forests located on the western slopes of the Cascades.

Graham, R.L. and K. Cromack, Jr. 1982. Mass, nutrient content, and decay rate of dead boles in rain forests of Olympic National Park. *Can. J. For. Res.* 12:511–521.

Keywords: decay rate, nutrients, Pacific Northwest, *Tsuga heterophylla*, *Picea sitchensis*, bole wood, decomposition, site factors.

Abstract: Analysis of dead boles of *Picea sitchensis* (Bong.) Carr. and *Tsuga heterophylla* (Raf.) Sarg. in open- and closed-canopy forests of the Olympic Peninsula, Washington, U.S.A., revealed that hemlock mortality in both forest types was due mainly to windthrow, whereas spruce typically died upright. The open forest contained 120 t/ha of dead bole wood; the closed forest contained 161 t/ha. Hemlock boles decayed more rapidly than the larger spruce boles, although both showed considerable variability. On a per-hectare basis, 146–223 kg of N, 147–197 kg of Ca, 39–61 kg of K, 18–29 kg of Mg, 6–14 kg of Na, and 17–29 kg of P were contained in dead boles of the open- and closed-canopy forests, respectively. Except for N and Mg, the nutrient concentrations of the wood were not significantly different after 33–68 years of bole decay. The N:P ratios increased with increasing decay for both species.

Grier, C.C. 1978. A *Tsuga heterophylla*–*Picea sitchensis* ecosystem of coastal Oregon: decomposition and nutrient balances of fallen logs. *Can. J. For. Res.* 8:198–206.

Keywords: decomposition, nutrients, Pacific Northwest, coastal conifer forest, *Tsuga heterophylla*, *Picea sitchensis*, decay rate, bole wood.

Abstract: Weight loss and changes in N, P, Ca, Mg, K, and Na content were determined for fallen *Tsuga heterophylla* (Raf.) Sarg. logs in a 121-year-old *Tsuga heterophylla*–*Picea sitchensis* (Bong.) Carr. stand on the central Oregon coast. Log ages ranged from 2 to 38 years.

Weights of fallen logs decreased in a roughly negative logarithmic pattern; after 38 years the average log had lost 34.5% of its original weight. N, Ca, and Mg contents of logs increased for about the first 20 years and declined thereafter. P and K contents decreased steadily with age. Na content increased with age. Except for Ca, nutrient input to log surfaces by litterfall and throughfall was greater than any increases in nutrient content.

Grier, C.C. and R.S. Logan. 1977. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: biomass distribution and production budgets. *Ecol. Monogr.* 47:373–400.

Keywords: quantities, old growth, Pacific Northwest, *Pseudotsuga menziesii*, organic matter dynamics, mortality.

Abstract: Living biomass, organic matter distribution, and organic matter production budgets were determined for plant communities of a small watershed dominated by 450-year-old *Pseudotsuga menziesii* (Mirb.) Franco forests. Dominant trees in the communities were large, up to 175 cm diameter and 80 m tall.

Aboveground tree biomass of the various communities ranged from 491.8–975.8 t/ha, total aboveground living biomass ranged from 500.4–982.5 t/ha, total leaf biomass ranged from 10.4–16.3 t/ha and total organic matter accumulations ranged from 1008.3 to 1513.7 t/ha.

Total tree biomass in the various communities was more related to past mortality than habitat differences. Biomass of standing dead trees and fallen logs was generally inversely related to above ground tree biomass. Amounts of woody detritus were large, ranging from 59.0 to 650.6 t/ha or 4.3–43.0% of total community organic accumulation. Aboveground tree biomass increment was negative in all communities, ranging from –2.9 to –6.2 t/ha. Positive increment by shrubs and trees <15 cm dbh produced overall aboveground biomass increment of –2.5 to –5.0 t/ha. Mortality averaged 1% of standing biomass.

Aboveground net primary production in the various communities ranged from 6.3 to 10.1 t ha⁻¹ yr⁻¹ and was roughly proportional to standing biomass. Net primary production consisted entirely of detritus. Total community autotrophic respiration ranged from 102.9 to 203.7 t ha⁻¹ yr⁻¹ of which 70% was by foliage. Gross primary production ranged from 111.2 to 216.8 t ha⁻¹ yr⁻¹ of which only 6.0%–7.9% was net primary production. Net ecosystem production ranged from 0.12 to 5.6 t ha⁻¹ yr⁻¹, entirely as an accumulation of woody detritus on the soil surface.

Available evidence indicates larger peak biomass in seral *P. menziesii* than in climax *Tsuga heterophylla* forests. These communities may be in the process of declining from seral peak to steady-state climax biomass.

Habeck, J.R. 1985. Impact of fire suppression of forest succession and fuel accumulations in long-fire-interval wilderness habitat types. *In Proc. Symp. and Workshop on Wilderness Fire.* Nov. 15–18, 1983, Missoula, Mont. U.S. Dep. Agric. For. Serv., Ogden, Utah. Gen. Tech. Rep. INT-182.

Keywords: quantities, accumulation, old growth, inland northwestern U.S.A., *Thuja plicata*, fuel loading, management, long-term impacts.

Abstract: Succession and fuel characteristics are described and discussed for a series of western redcedar (*Thuja plicata*) forests in the Selway-Bitterroot Wilderness, Idaho. Natural fire cycles in these moist forests are at 100- to 400-year intervals, and modern fire suppression may not have affected the cedar forests in this wilderness. The surrounding upland forests exhibit greater cover and fuel continuity and could threaten the long-fire-interval forest types; an operational wilderness fire plan, however, has led to the burning of thousands of upland acres during the past several years.

Hall, M. 1984. Establishment of radiata pine on a high altitude second rotation site. *Australian Forestry* 47(3): 194–198.

Keywords: *Pinus radiata*, Australia, nitrogen, logging impacts, site treatment.

Abstract: After clearfelling and removal of sawlogs and waste wood from a 33-year-old crop of radiata pine, a site on the central tablelands of New South Wales contained an estimated 222 kg ha⁻¹ of nitrogen in aboveground litter and logging slash, and 8746 kg

ha⁻¹ in the soil. Broadcast burning of the litter and slash removed 139 kg ha⁻¹ of nitrogen, but had no measurable effect on the organic matter content of the soil. Hand raking removed 212 kg ha⁻¹ of nitrogen from the litter and slash, as well as approximately 1 cm of topsoil, containing at least 124 kg ha⁻¹ nitrogen.

It was concluded that on this site the commonly used technique of windrow raking of logging slash and litter before replanting was likely to have a greater effect on site nutrient capital than broadcast burning. Neither practice had an appreciable impact on total site reserves of nitrogen, since very large quantities are contained in the mineral soil. However, since little is known of the availability of these soil reserves to the replanted crop, it would be prudent to modify existing techniques so as to minimize their impact on the aboveground nutrient capital. It is suggested that a raking operation which removed only the woody debris would probably allow sufficient access for replanting, and would leave most of the nutrient-rich fine litter and topsoil intact.

Harcombe, P.A., M.E. Harmon, and S.E. Greene. 1990. Changes in biomass and production over 53 years in a coastal *Picea sitchensis*-*Tsuga heterophylla* forest approaching maturity. Can. J. For. Res. 20: 1602–1610.

Keywords: input rate, mortality, *Picea sitchensis*, *Tsuga heterophylla*, Pacific Northwest, coastal conifer forest, mature.

Abstract: Using periodic remeasurements of tagged trees in nine 0.4-ha sample plots in a *Picea sitchensis* (Bong.) Carr.-*Tsuga heterophylla* (Raf.) Sarg. forest at Cascade Head Experimental Forest, Oregon, we calculated that biomass of bole wood increased from 570 Mg ha⁻¹ at age 85 years to 760 Mg ha⁻¹ at age 138 years. Net primary production of bole wood declined from 11 to about 6 Mg ha⁻¹ year⁻¹, and mortality loss increased from 2 to about 6 Mg ha⁻¹ year⁻¹. Values for 37-year-old plots in the same area were 210–360 Mg ha⁻¹ year⁻¹ bole biomass, 7–20 Mg ha⁻¹ year⁻¹ bole wood production, and 0–2 Mg ha⁻¹ year⁻¹ mortality loss. Indications are that bole wood production and biomass were lower in the older plots when they were 37 years old. In the older plots, biomass did not increase between ages 120 and 138. Of the photosynthate potentially available for bole wood production, some replaces biomass lost via mortality and some is allocated to maintenance (respiration plus allocation to fine roots). We estimate that one-quarter to one-half of the production is lost by mortality, and that mortality loss may thus be an important factor limiting forest biomass accumulation.

Harmon, M.E. 1987. The influence of litter and humus accumulations and canopy openness on *Picea sitchensis* (Bong.) Carr. and *Tsuga heterophylla* (Raf.) Sarg. seedlings growing on logs. Can. J. For. Res. 17:1475–1479.

Keywords: regeneration, nurse logs, habitat, accumulation, *Picea sitchensis*, *Tsuga heterophylla*, environmental factors, seedlings.

Abstract: The influence of litter and humus accumulations on the surface of logs and canopy openness upon growth and survival of *Picea sitchensis* (Bong.) Carr. and *Tsuga heterophylla* (Raf.) Sarg. seedlings was tested experimentally at Cascade Head Experimental Forest, near Otis, Oregon. This was done by adding litter and humus to the surface of freshly fallen logs. Survival rates of both species increased asymptotically as litter accumulations on logs increased. Mean maximum survival was 58% for *Picea* and 34% for *Tsuga*. *Picea* seedling survival peaked when tree canopy cover ranged from 70 to 80% with lower survival at either higher or lower values. *Tsuga* survival was highest under closed canopies. Seedling growth increased as litter-humus accumulation and canopy openness increased.

Harmon, M.E., K. Cromack, Jr., and B.G. Smith. 1987. Coarse woody debris in mixed-conifer forests, Sequoia National Park, California. Can. J. For. Res. 17:1265–1272.

Keywords: decomposition, *Abies concolor*, southwestern U.S.A., decay rate, quantities, nitrogen, bole wood.

Abstract: The decay rate of *Abies concolor* (Gord. and Glend.) Lindl. logs and cover, mass, and volume of logs and snags in six mid-elevation forest stands of Sequoia National Park, California, are reported. Based on a chronosequence, *Abies concolor* boles have a decay rate constant of 0.05 year⁻¹ and a half-life of 14 years. A decay classification system was developed for *Abies concolor*, *Calocedrus decurrens* (Torr.) Florin, *Pinus jeffreyi* Grev. and Balf., and *Pinus lambertiana* Dougl. logs. Dimensions taken from maps of six permanent plots were combined with decay-class information to estimate volume, mass, and projected cover of logs and snags. Total mass ranged from 29 Mg ha⁻¹ in a *Pinus jeffreyi* forest to 400 Mg ha⁻¹ in a *Sequoiadendron giganteum* (Lindl.) Buchh.-dominated stand. Volume, projected cover, and nitrogen storage exhibited patterns similar to mass, ranging from 84 to 1160 m³ ha⁻¹, 3.1 to 9.3%, and 41 to 449 kg ha⁻¹, respectively.

Harmon, M.E., W.K. Ferrell, and J.F. Franklin. 1990. Effects on carbon storage of conversion of old-growth forests to young forests. *Science* 247:699–702.

Keywords: carbon, logging impacts, long-term impacts, organic matter dynamics.

Abstract: Simulations of carbon storage suggest that conversion of old-growth forests to young fast-growing forests will not decrease atmospheric carbon dioxide (CO₂) in general, as has been suggested recently. During simulated timber harvest, on-site carbon storage is reduced considerably and does not approach old-growth storage capacity for at least 200 years. Even when sequestration of carbon in wooden buildings is included in the models, timber harvest results in a net flux of CO₂ to the atmosphere. To offset this effect, the production of lumber and other long-term wood products, as well as the life-span of buildings, would have to increase markedly. Mass balance calculations indicate that the conversion of 5 x 10⁶ hectares of old-growth forests to younger plantations in western Oregon and Washington in the last 100 years has added 1.5 x 10⁹ to 1.8 x 10⁹ megagrams of carbon to the atmosphere.

Harmon, M.E. and J.F. Franklin. 1989. Tree seedlings on logs in *Picea-Tsuga* forests of Oregon and Washington. *Ecology* 70(1):48–59.

Keywords: habitat, nurse log, Pacific Northwest, *Picea sitchensis*, *Tsuga heterophylla*, regeneration.

Abstract: Logs are the major seedbed for trees in coastal *Picea sitchensis*-*Tsuga heterophylla* forests. Field experiments were conducted at Cascade Head, Oregon, and Hoh River, Washington, to examine pathogens, predation, competition, and standing water as causes for this close seedling-log association.

More seedlings survived on log blocks than on soil blocks, regardless of whether the blocks were raised or placed flush with the soil surface. Standing water was therefore an unlikely cause of the seedling-log association. Comparisons of plots protected from and exposed to predation revealed that predation was minor and of equal intensity on soils and logs. Sterilizing soils did not consistently increase seedling survival above controls. Clearing ground-layer vegetation from soil plots significantly increased the survival of conifer seedlings compared with that on uncleared soils. The seed penetration rates through moss mats indicated that <1% of the seedlings germinated within moss mats.

Competition with herbs and mosses on the forest floor therefore appears to be responsible for the disproportionate number of tree seedlings found on logs. Recently fallen logs represent sites where competition is low enough for tree seedling recruitment within many *Picea-Tsuga* forests.

Harmon, M.E., J.F. Franklin, F.J. Swanson, P. Sollins, S.V. Gregory, J.D. Lattin, N.H. Anderson, S.P. Cline, N.G. Aumen, J.R. Sedell, G.W. Lienkaemper, K. Cromack,

Jr., and K.W. Cummins. 1988. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* 15:133–302.

Keywords: structural characteristics, decay rate, input rate, quantities, decomposition, decomposers, environmental factors, wood properties, habitat, general, nutrients, accumulation, bole wood, turnover time, methods, nutrient dynamics.

Abstract: Coarse woody debris (CWD) is an important component of temperate stream and forest ecosystems. We have reviewed the rates at which CWD is added and removed from ecosystems, the biomass found in streams and forests, and many functions that CWD serves.

CWD is added to ecosystems by numerous mechanisms, including wind, fire, insect attack, pathogens, competition, and geomorphic processes. Despite the many long-term studies on tree mortality, there are few published rates of CWD input on mass-area⁻¹ time⁻¹ basis. Most ecological studies have not measured CWD input over a long enough period or a large enough area to give accurate estimates. Input rates measured in temperate ecosystems range from 0.12 to 14.9 Mg ha⁻¹ year⁻¹ and vary greatly over time and space.

Once CWD enters the detrital food web, it is decomposed by a large array of organisms and physical processes. Although respiration-caused losses have been the focus of many studies, CWD is also significantly transformed physically and chemically. Movement of CWD, especially in streams, is also an important but poorly documented mechanism whereby CWD is lost from ecosystems. Many factors control the rate at which CWD decomposes, including temperature, moisture, the internal gas composition of CWD, substrate quality, the size of the CWD, and the types of organisms involved. However, the importance of many of these factors has yet to be established in field experiments.

The mass of CWD in an ecosystem ideally represents the balance between addition and loss. In reality, slow decomposition rates and erratic variations in input of CWD cause the CWD mass to deviate markedly from steady-state projections. The mass of CWD in stream and forest ecosystems varies widely, ranging between 1 and 269 Mg ha⁻¹. Many differences correspond to forest type, with deciduous-dominated systems having generally lower biomass than conifer-dominated systems. However, conifer-dominated systems with low productivity also have low CWD mass. Stream size also influences CWD mass in lotic ecosystems, while successional stage dramatically influences CWD mass in both aquatic and terrestrial settings.

CWD performs many functions in ecosystems, serving as autotrophic and heterotrophic habitat and strongly influencing geomorphic processes, especially in streams. It is also a major component of nutrient cycles in many ecosystems. We have reviewed these many functions and conclude that CWD is an important functional component of stream and forest ecosystems.

Humans have greatly affected the amount of CWD found in temperate ecosystems by removing CWD and by changing the rate of input and the rate and pattern of loss. In some cases, human influences have been so pervasive that natural conditions are difficult to define. Management practices concerning CWD often have not been based on the numerous beneficial roles this material plays in ecosystems. Better scientific understanding of these functions and the natural factors influencing CWD dynamics should lead to more enlightened management practices.

Harvey, A.E. 1982. The importance of residual organic debris in site preparation and amelioration for reforestation. *In* Site preparation and fuels management on steep terrain. D.M. Baumgartner (editor). Wash. State Univ., Pullman, Wash., pp. 75–85.

Keywords: logging impacts, organic matter dynamics, habitat, management, mycorrhizae.

Abstract: Decayed or decaying wood and other organic materials provide either the environment or the energy source for microorganisms critical to the survival and growth of conifers in the relatively infertile and frequently droughty soils of the central and northern Rocky Mountains. The microorganisms that contribute to decay processes, nitrogen conversions, and ectomycorrhizal activities are particularly important to conifers.

These microorganisms, and the above-mentioned parent materials, directly or indirectly provide forest soils with a significant fraction of their moisture and nutrient storage capacity, stability, resistance to compaction, and nitrogen supply. Ectomycorrhizal associations enable conifers to extract moisture and nutrients from substrates too dry and infertile to support non-mycorrhizal plants.

In specific instances, soil organic matter has been demonstrated to be the most important component of seedbeds and of rooting substrata supporting natural regeneration in the northern Rocky Mountains. Decayed wood was particularly important on dry sites. Thus, residual organic debris, and the soil components derived from it, can provide critical biological and physical characteristics to forest soils that directly support natural conifer regeneration. Some low organic matter soils may be difficult to regenerate without deliberate improvement of their organic reserves. This amelioration can, at least partially, be accomplished through site preparation and management of logging debris.

Harvey, A.E., M.F. Jurgensen, and M.J. Larsen. 1981a. Organic reserves: importance of ectomycorrhizae in forest soils of western Montana. *For. Sci.* 27(3):442–445.

Keywords: mycorrhizae, inland northwestern U.S.A., *Pseudotsuga menziesii*, *Larix occidentalis*, *Abies lasiocarpa*, *Picea engelmannii*, *Tsuga heterophylla*, organic matter dynamics.

Abstract: The important attributes contributed to forest soils by organic matter make it imperative to determine the quantity and type required to sustain good forest tree growth. Quantitative measurement of soil humus, decayed wood, and charcoal as related to numbers of active ectomycorrhizal root tips (in random soil cores from old-growth sites in western Montana) showed both positive and negative relationships with organic matter. Increased quantities of organic material, to 45% by volume of the top 30 cm of soil, were associated with increased number of ectomycorrhizae. At 45% organic matter or above, numbers of ectomycorrhizae decreased. Study results also showed association with soil organic matter had a relatively greater positive effect on ectomycorrhizae of the dry site than the moist sites.

Harvey, A.E., M.F. Jurgensen, M.J. Larsen, and R.T. Graham. 1987. Relationships among soil microsite, ectomycorrhizae, and natural conifer regeneration of old-growth forests in western Montana. *Can. J. For. Res.* 17:58–62.

Keywords: inland northwestern states, old growth, *Pseudotsuga menziesii*, *Larix occidentalis*, *Picea engelmannii*, *Abies lasiocarpa*, *Tsuga heterophylla*, regeneration, habitat, mycorrhizae.

Abstract: Successful establishment, root distribution, growth, and ectomycorrhizal development of conifer regeneration in three old-growth forests in western Montana showed site-specific associations with soil microsites containing organic matter. A positive association between decayed wood in the soil and establishment of seedlings occurred on the two drier sites. In general, organic soil components supported most of the root system and ectomycorrhizae on all three sites. Associations between soil organic components and occurrence (establishment) and between organic components and performance (growth) were site-specific. No observable evidence of feeder root mortality

attributable to soil-inhabiting pathogens was present in any soil component. Roots of competing understory species were notably absent in decayed soil wood.

Harvey, A.E., M.J. Larsen, and M.F. Jurgensen. 1981b. Rate of woody residue incorporation into northern Rocky Mountain forest soils. U.S. Dep. Agric. For. Serv. Res. Pap. INT-282.

Keywords: organic matter dynamics, inland northwestern U.S.A., mature, *Pseudotsuga menziesii*, *Larix occidentalis*, *Abies lasiocarpa*, *Picea engelmannii*, *Tsuga heterophylla*, turnover time.

Abstract: Research has shown organic matter, particularly decayed wood, imparts important properties to forest soils of the Northern Rocky Mountains. In order to maintain or reconstitute high-quality soils in managed forests, the production time for incorporation of soil organic materials must be considered in the long-term management process.

The research contained in this report indicates lag periods of approximately 100–300 years between the time wood is produced on a forested site and the time it becomes incorporated into the soil organic mantle. Habitat type had a major influence on time period and on the tendency of an ecosystem to equilibrate with wood biomass concentrated as undecayed soil-surface residue or as extensively decayed materials incorporated into the soil profile. The cool-moist system accumulated residue. The warm-moist system accumulated decayed wood in the soil. Douglas-fir was the most common species of wood found in the soils of these experimental sites.

In order to reconstitute adequate supplies of decayed wood in soils depleted in this resource, lag periods in the 100- to 300-year range can be expected. Also, when managing harvest residue as parent materials for soil wood, Douglas-fir is a preferred species.

Heilman, P.E. 1990. Forest management challenged in the Pacific Northwest. *J. Forestry* 88(11):16–23.

Keywords: management, long-term impacts, logging impacts.

Abstract: Conflicts in management of forest resources in the Pacific Northwest have attained unprecedented levels of intensity, complexity, and what Allen and Gould (1986) described as “wickedness” (defined as psychological, i.e., relating to emotion, tradition, and/or intuition and thus differing from the technical or scientific realm). Solutions to those conflicts will ultimately depend on how well the science and complexity of the issues were addressed in resolving conflicting political viewpoints. In a recent paper, Carroll et al. (1989), citing two successful examples, speculate that consensus-seeking will become increasingly important in resolving resource conflicts. Recent progress in the old-growth/spotted owl issue supports that prediction.

Hendrickson, O.Q. 1988. Biomass and nutrients in regenerating wood vegetation following whole-tree and conventional harvest in an northern mixed forest. *Can. J. For. Res.* 18:1427–1436.

Keywords: *Populus tremuloides*, *Pinus resinosa*, *Pinus strobus*, *Populus grandidentata*, whole-tree harvest, mixed forest, Ontario, nutrients, accumulation, logging impacts, harvesting method.

Abstract: Biomass and nutrient contents of regenerating woody plants and litterfall were measured after a northern mixed conifer-hardwood forest was harvested by conventional and whole-tree methods. Before harvest, the central Ontario study site was occupied by a 95-year-old pine (*Pinus resinosa*, *P. strobus*) and aspen (*Populus tremuloides*, *P. grandidentata*) stand growing on gently rolling, gravel-free outwash sands. Four years after harvest, aspen abundance increased 100-fold in both harvested areas, with higher densities after whole-tree harvest (WTH)(4.1 stems/m²) than after

conventional harvest (CH)(2.7 stems/m²). No self-thinning of aspen occurred between 2 and 4 years after harvest. Total aboveground woody biomass accumulated at 2.0 t ha⁻¹ year⁻¹ in the WTH area and 1.5 t ha⁻¹ year⁻¹ in the CH area; the preharvest rate was 2.0 t ha⁻¹ year⁻¹. Peak autumn litter production occurred earlier in the harvested areas than in an adjacent uncut area. Cycling of N and K in litterfall returned to preharvest rates after 4 years. Cycling of Ca in litterfall was lower after WTH than after CH. Vegetation uptake of N and K (litterfall plus woody biomass) in the harvested areas in year 4 exceeded the preharvest value.

Increased N accumulation in woody biomass (3.0 kg ha⁻¹ year⁻¹ before harvest, 10.6 kg ha⁻¹ year⁻¹ after WTH) would place a relatively greater demand on forest floor N pools in the WTH than in the CH area owing to lack of N input in logging slash. Although WTH did not reduce initial rates of biomass production, *Populus* spp. had lower concentrations of N, Ca, and Mg in the WTH area than in the CH area. There may be a danger that WTH on less fertile sites in the region will produce dense, unproductive aspen stands with low rates of self-thinning.

Hope, S.M. 1987. Classification of decayed *Abies amabilis* logs. Can. J. For. Res. 17:559–564.

Keywords: decomposition, *Abies amabilis*, Pacific Northwest, decay classes, methods, wood properties.

Abstract: Pacific silver fir (*Abies amabilis* [Dougl.] Forbes) fallen logs near Snoqualmie Pass, Washington, U.S.A., were classified according to visual, chemical, and physical characteristics. The purpose of the study was (i) to test differences in log classification according to three- and five-unit decay classes, and (ii) to determine which variables appeared to be successful descriptors of decay for Pacific silver fir.

Discriminant analysis was used to select variables to describe decay levels. According to analyses, wood density and lignin and cellulose percentages were acceptable criteria for describing decay levels using either a three- or five-unit classification system. Using a three-unit system defined by field characteristics and laboratory measures, cellulose discriminated among the classes 67% of the time. The variable wood density could be successfully classified 60% of the time. With a five-unit decay class system, individual variables placed logs within classes with less than 50% accuracy. Combinations of variables such as cellulose, wood density, and wood failure level improved class discrimination. Combined field measures were less successful in discriminating decay classes than variables measured under laboratory conditions. Results showed that (i) selection of structural characteristics can change the allocation of logs to particular classes, and (ii) three decay classes could be defined more clearly than five decay classes.

Jurgensen, M.F., A.E. Harvey, R.T. Graham, M.J. Larsen, J.R. Tonnand, and D.S.

Page-Dumroese. 1990. Soil organic matter, timber harvesting, and forest productivity in the Inland Northwest. In Sustained productivity of forest soils. Proc. 7th N.Am. Forest Soils Conf. S.P. Gessel, D.S. Lacate, G.F. Weetman, and R.F. Powers (editors). Univ. British Columbia, Fac. Forestry, Vancouver, British Columbia. pp. 392–415.

Keywords: organic matter dynamics, productivity, management, logging impacts, long-term impacts, inland northwestern U.S.A.

Abstract: Soil organic matter is an important factor for the continued productivity of Inland Northwest forests. Current harvesting practices in this region usually leave adequate logging residues to maintain soil organic matter levels. However, extensive disturbance of soil organic components from harvesting, site preparation, or wildfires can be detrimental to mycorrhizal development, nitrogen fixation, seedling establishment, and future stand productivity. The amount of management of woody residues on or in soil also have important implications for tree growth, especially on dry or shallow sites. The

maintenance of adequate soil organic matter levels is an important consideration for sustained forest productivity under the extreme moisture and temperature conditions of this region.

Jurgenson, M.F., M.J. Larsen, R.T. Graham, and A.E. Harvey. 1987. Nitrogen fixation in woody residue of northern Rocky Mountain conifer forests. *Can. J. For. Res.* 17:1288–1293.

Keywords: accumulation, nitrogen fixation, old growth, *Pseudotsuga menziesii*, *Tsuga heterophylla*, *Thuja plicata*, *Abies lasiocarpa*, *Picea engelmannii*, Rocky Mountains, methods, inland northwestern U.S.A.

Abstract: N fixation rates, as estimated by the acetylene reduction technique, were determined for large woody residues on four old-growth conifer sites in western Montana and northern Idaho. Residue loadings ranged from <50 Mg ha⁻¹ on a warm, dry Douglas-fir site in Montana to >150 Mg ha⁻¹ on a highly productive, wet, cedar-hemlock site in northern Idaho. Lignin and carbohydrate analyses indicated that wood on these sites was being decayed primarily by brown rot fungi. Ethylene production rates increased on all sites as wood decay progressed. Assuming that N-fixing bacteria were active for 180 days year⁻¹, N fixed in woody residues ranged from a high of nearly 1.5 kg ha⁻¹ year⁻¹ on a cedar-hemlock site to a low of 0.16 kg ha⁻¹ year⁻¹ on a Douglas-fir site. The application of the N fixation results from this study to the northern Rocky Mountain region indicated that the majority of stands in the Douglas-fir, subalpine fir, and cedar-hemlock cover types would have N gains <0.5 kg ha⁻¹ year⁻¹. However, in some areas where residue loadings are heavy, such as overmature stands on cool, moist sites, or following harvesting, N gains could be much greater.

Jurgenson, M.F., M.J. Larsen, S.D. Spano, A.E. Harvey, and M.R. Gale. 1984. Nitrogen fixation associated with increased wood decay in Douglas-fir residue. *For. Sci.* 30(4):1038–1044.

Keywords: accumulation, nitrogen fixation, inland northwestern U.S.A., *Pseudotsuga menziesii*, old growth.

Abstract: Nitrogen fixation rates, as estimated by the acetylene reduction technique, were determined for four decay stages of downed Douglas-fir logs on two old-growth sites in northwestern Montana. Acetylene reduction rates increased as wood decay progressed, but were not affected by site location. Wood carbohydrate, soluble sugar, total and soluble nitrogen, and moisture content also varied among decay stages. Acetylene reduction rates were positively correlated with wood moisture content and nitrogen concentration, and negatively correlated with carbohydrate level. The annual nitrogen additions to the sites from nitrogen fixation in decaying Douglas-fir logs were small, 0.72 kg/ha⁻¹/yr⁻¹ on the moister site and 0.26 on the drier site. These differences in nitrogen inputs were related to differences in residue loading between sites. Although small, such nitrogen gains may be significant over the rotation life of a stand.

Lambert, R.L., G.E. Lang, and W.A. Reiners. 1980. Loss of mass and chemical change in decaying boles of a subalpine balsam fir forest. *Ecology* 61(6):1460–1473

Keywords: decomposition, decay rates, *Abies balsamea*, nutrients, wood properties, bole wood, northeastern U.S.A., subalpine forest.

Abstract: Decay of balsam fir (*Abies balsamea*) boles was examined in an upper subalpine forest of the White Mountains, New Hampshire, U.S.A. Fifty percent of the initial mass was lost in 23 years; 90% was lost in 77 years. High decay rates were attributed to the small diameters of the boles, ample moisture, and a nitrogen-rich environment. Average dead wood mass in this forest was 4.9 kg/m², representing 25% of the sum of dead wood, live plant biomass, and forest floor organic matter.

Changes in density and moisture and in the concentrations and content of various chemical components of the boles were traced over the decay sequence. Changes in the content of cellulose, lignin, carbon, and sodium followed loss of mass during decay. Contents of calcium, magnesium, potassium, and phosphorus decreased faster than loss of mass in the early stages of decay. Much of this initial loss was ascribed to sloughing of nutrient-rich bark, which in these small boles comprised 13% of dry mass. Later in decay, the loss rates of calcium, magnesium, and potassium were about the same or slightly less than the loss rate of mass. After a steep initial drop, phosphorus content of the boles remained approximately constant between years 12 and 33. Thereafter, the loss rate paralleled loss of mass. Nitrogen content was approximately constant in the first 33 years after which it declined in parallel with loss of mass.

Lang, G.E. 1985. Forest turnover and the dynamics of bole wood litter in subalpine balsam fir forest. *Can. J. For. Res.* 15:262–268.

Keywords: input rate, mortality, quantities, bole wood, subalpine forest, *Abies balsamea*, turnover time.

Abstract: A chronosequence of three stands of balsam fir was sampled in 1974 and 1982; during these 8 years, recruitment was absent so mortality alone accounted for an 18–30% decrease in live tree density. In a mature 78-year-old stand, the mass of bole wood on the forest floor was 1.4 kg m⁻² compared with an estimated aboveground live and dead bole biomass of 17.2 kg m². During 5 years of repetitive sampling, annual bole input to the forest floor was episodic and variable in time and space, ranging from 3 to 365 g m⁻² year⁻¹. A mass balance model was used to characterize the changes in wood litter on the forest floor. If most of the live trees die within a short period of time, bole input would occur in a pulse event and cause a peak in wood litter mass, which would then decline over time (and with stand maturation) as decomposition prevails. The assumption of steady-state conditions for wood litter is not valid; rather, the mass of wood litter will wax and wane through time. Over a landscape, spatial patterns in the abundance of wood litter reflect a stand's history; old mature stands would have little wood litter while young regenerating stands would have large amounts. A maximum value for wood litter would be found in a stand located immediately behind a fir wave. Natural disturbances from wind and avalanches lead to contrasting patterns with high and low wood litter values, respectively. About 41% of forest turnover in the balsam fir zone is initiated from natural disturbance and fir waves.

Larson, F.R. 1984. Characterizing downed woody fuels by Alaska vegetation strata classes. *In* Inventorying forest and other vegetation of the high latitude and high altitude regions: Proc. of an International Symp. V.J. LaBau and C.L. Kerr (editors). Soc. Am. Foresters, Bethesda, Md., pp. 220–224.

Keywords: methods, quantities, fuel load, Alaska, line intersect, *Populus tremuloides*, *Betula papyrifera*, *Picea glauca*, *Picea mariana*.

Abstract: The Alaska Integrated Resource Inventory System has been modified to include information on dead and downed woody material. Average dry weight by size of woody material, diameter of large material, duff depth, and fuel depth are presented for 30 vegetation classes and eight fuel models as a start toward describing this important component of wild lands.

Little, S.N. and J.L. Ohmann. 1988. Estimating nitrogen lost from forest floor during prescribed fires in Douglas-fir/western hemlock clearcuts. *For. Sci.* 34(1): 152–164.

Keywords: Pacific Northwest, *Pseudotsuga menziesii*, carbon, *Tsuga heterophylla*, clearcut, nitrogen, site treatment, quantities, fuel load.

Abstract: Nitrogen loss from consumption of forest floor was studied on 33 treatment blocks burned on 11 clearcuts in western Washington and western Oregon. In

most cases, nitrogen concentration in forest floor did not change significantly following prescribed fire. Change in the amount of nitrogen in forest floor ranged from an increase of 192 kg/ha to a loss of 666 kg/ha. In most cases, nitrogen loss was directly proportional to the amount of forest floor consumed. Total nitrogen loss can therefore be estimated by multiplying expected loss of forest floor by its nitrogen concentration before the burn.

Lorimer, C.G. 1985. Methodological considerations in the analysis of forest disturbance history. *Can. J. For. Res.* 15:200–213.

Keywords: methods, input rate, mortality, structural characteristics.

Abstract: A number of nondestructive techniques for analyzing the timing, frequency, and magnitude of natural disturbance in forest stands are discussed in this paper. Intensive age determination of trees is desirable for reconstructing forest disturbance history, but age distribution alone is not always a sufficient basis for a disturbance chronology. Frequently, all-aged forests have undergone severe past disturbance which cannot be readily identified from the distribution of trees among age classes. Radial growth patterns provide more direct evidence of past canopy tree deaths. In cases where a large sample of tree ages and growth records is not feasible, structural attributes of forests can provide valuable supplementary evidence. Effects of disturbance history and age structure on diameter distributions of nonsuppressed trees potentially appear to be more reliable structural indicators of past canopy disturbance than simple size distributions. For regional studies of disturbance frequency, random dispersal of medium to large plots across large landscape units is recommended as a sample design.

Macadam, A.M. 1987. Effects of broadcast slash burning on fuels and soil chemical properties in the Sub-Boreal Spruce Zone of central British Columbia. *Can. J. For. Res.* 17:1577–1584.

Keywords: quantities, fuel load, British Columbia, sub-boreal spruce forest, clearcut, nutrients, site treatment.

Abstract: Soil samples were taken before, and 9 and 21 months after, the operational broadcast burning of logging slash in two clearcuts in the Sub-Boreal Spruce Zone of central British Columbia. Average slash consumption on the two clearcuts was estimated from line intersect samples at 20 and 24 t/ha and forest floor depth was reduced by 28 and 36%. Nine months after burning, soil N had decreased by 376 kg/ha (18% of preburn levels) while available P had increased by 37–157 kg/ha. Burning resulted in substantial increases in forest floor base saturation, pH, exchangeable Ca and Mg, and available P. Changes within the 0–15 and 15–30 cm mineral soil layers were variable and in general less pronounced. Significant positive correlations were observed between the consumption of large fuels and postburn changes in forest floor pH and exchangeable Ca and Mg. Changes in forest floor N were negatively correlated with amounts of fine slash consumed. A strongly negative correlation was observed between forest floor depth of burn and changes in forest floor exchangeable K concentrations.

McCullough, H.A. 1948. Plant succession on fallen logs in a virgin spruce-fir forest. *Ecology* 29(4):508–513.

Keywords: habitat, *Picea engelmannii*, *Abies lasiocarpa*, subalpine forest, Rocky Mountains, regeneration, old growth.

Abstract: A successional study of 153 decaying fallen logs of spruce and fir was made in the Gothic Natural Area of the Gunnison National Forest, Colorado. The logs were located in mesic, bog, and xeric habitats, and were grouped into eight decay classes.

Fallen logs are invaded first by lichens and liverworts. These are followed by mosses with *Brachythecium* the common genus in all three conditions. Succession is continued with an herbaceous stage, which varies as to species in the different habitats. In some forms, the typical *Vaccinium* or low shrub stage is the next phase before the completion

of the succession into the climax forest. The establishment of seedlings of the spruce and fir trees is not dependent upon this succession but can occur on logs showing only slight signs of decay. Separate successional studies in each area show a basic similarity to the general pattern.

McFee, W.W. and E.L. Stone. 1986. The persistence of decaying wood in the humus layers of northern forests. *Soil Sci. Soc. Amer. Proc.* 30:513–516.

Keywords: northeastern U.S.A., organic matter dynamics, turnover time, decomposition, quantities, decay rate, nutrients, mixed forest, *Betula alleghaniensis*, *Picea rubens*.

Abstract: The amount, composition, and persistence of decaying wood in humus layers was examined in yellow birch (*Betula alleghaniensis* Britton)–red spruce (*Picea rubens* Sarg.) stands in the Adirondack Region of New York. The wood is initially attacked by brown rot fungi, but thereafter decomposes very slowly and may persist in the humus layer for a century or more. Separable wood residues weighed as much as 41 800 lb/acre and composed 14–30% of the forest floor. These residues were significantly lower in N and P content than the surrounding humus.

MacMillan, P.C. 1988. Decomposition of coarse woody debris in an old-growth Indiana forest. *Can. J. For. Res.* 18:1353–1362.

Keywords: decomposition, old growth, hardwood forest, decay rate, wood properties, nutrients, bole wood, midwestern U.S.A.

Abstract: Decay rates of *Quercus* sp., *Carya* sp., *Fagus grandifolia*, and *Acer* sp. coarse woody debris in an old-growth southern Indiana forest were 0.018, 0.035, 0.019, and 0.045 per year, respectively, based on changes in density over a span of 25+ years. Their respective biomass values were 15, 2.3, 0.2, and 0.4 t ha⁻¹. The greatest differences in decay rates of cellulose were between maple (high) and oak (low), and of lignin were between beech (high) and oak (low). Carbon to nitrogen ratios approached 100 and nitrogen to phosphorus ratios approached 20 in the older age classes. On average, oak, hickory, beech, and maple logs contained 1.66, 1.10, 0.14, and 0.19 kg nitrogen and 0.056, 0.070, 0.005, and 0.016 kg phosphorus, respectively. Meentemeyer's model based on actual evapotranspiration predicted a decay rate of 0.80 per year, which is 27 times larger than the decay rates calculated on changes in density. Fragmentation loss rates for these four genera were estimated to be 0.288, 0.802, 1.171, and 0.338/year, respectively. Decay rates based on diameter of coarse woody debris ranged from 0.0027 to 0.0337/year. All these factors are important in understanding the process of decay of coarse woody debris in this forest. This role of fragmentation in the decay of coarse woody debris and of fungitoxic extractives need more study.

MacMillan, P.C., K. Cromack, Jr., and J.E. Means. 1977a. Nutrient capital and substrate quality of logs in an old-growth Douglas-fir forest. *Proc. Indiana Acad. Sci.* 87:101–102.

Keywords: nutrient dynamics, old growth, *Pseudotsuga menziesii*, bole wood, decay classes, nutrients.

Abstract: Visual criteria were used to classify Douglas-fir logs into five decay classes: 1 = recent input, to 5 = highly decayed log. These decay classes were used in our study of log nutrient capital and substrate quality in a 450 year old stand in western Oregon. Mean residence time of logs by decay class was: 7, 16, 36, 82 and 159 years. Over this time span, wood density decreased to less than one-half the original density. Percent of N, P, K, Ca, Mg, and Na all increased with residence time; changes in absolute concentrations and total kg/ha of these elements will be discussed. Percent of lignin increased and percent cellulose decreased with residence time; changes in absolute concentrations of carbon components and C/N ratios will be discussed.

MacMillan, P.C., J.E. Means, and K. Cromack, Jr. 1977b. Log input and decomposition in an old-growth Douglas-fir forest. Proc. Indiana Acad. Sci. 87:168.

Keywords: input rate, decomposition, old growth, bole wood, *Pseudotsuga menziesii*, decay classes, decay rate, wood properties.

Abstract: A five-class scheme of Douglas-fir log decomposition will be presented: 1 = most recent, to 5 = most decayed. This scheme was used in our study of log input and decomposition in a 450 year old stand in western Oregon. The numbers of Douglas-fir logs by decay class were 27, 15, 21, 39, and 128 logs/ha. Log biomass by decay class ranged from 324 to 15 mt/ha, for a total of 587 mt/ha for all classes. Estimated log input rates varied from 0.76 to 2.32 (mean = 1.33) logs/yr/ha. Mean wood density by decay class ranged from 543 to 151 mg/cm³; one-half of the original density was reached in approximately 94 years residence time. A decay rate of $k = -0.0074$ was obtained using the exponential decay model. With this and other data on Douglas-fir decomposition we found a correlation of decay rate as a function of surface to volume ratio ($r = 0.99$) using the power function model.

Maser, C., S.P. Cline, K. Cormack, Jr., J.M. Trappe, and E. Hansen. 1988a. What we know about large trees that fall to the forest floor. Chapter 2. *In* From the forest to the sea: a story of fallen trees. C. Maser, R.F. Tarrant, J.M. Trappe, and J.F. Franklin (editors). U.S. Dep. Agric. For. Serv., Portland, Oregon. Gen. Tech. Rep. PNW-229, pp. 25–45.

Keywords: structural characteristics, nutrients, decomposition, general, habitat, quantities.

Abstract: This chapter explains how living and dead trees are linked together in the living machinery of a forest. Decaying, fallen trees contribute to long-term accumulation of soil organic matter, partly because the carbon constituents of well-decayed wood are 80–90 % residual lignin and humus (Means et al. 1985). Decaying wood in the soil and establishment of conifer seedlings and mycorrhizal fungi on dry sites are positively correlated (Harvey et al. 1987). Fallen trees also create and maintain diversity in forest communities. Soil properties of pits and mounds differ from those of surrounding soil (Beatty and Stone 1985); such chemical and topographic diversity in turn affects forest regeneration processes (Lyford and MacLean 1966). All this, especially large fallen trees that reside on the forest floor for long periods, adds to spatial, chemical, and biotic diversity of forest soils, and to the processes that maintain long-term forest productivity.

Maser, C., R.F. Tarrant, J.M. Trappe, and J.F. Franklin (editors). 1988b. From the forest to the sea: a story of fallen trees. U.S. Dep. Agric. For. Serv., Portland, Oregon. Gen. Tech. Rep. PNW-GTR-229.

Keywords: general, structural characteristics, nutrients, decomposition, quantities, habitat.

Abstract: Large, fallen trees in various stages of decay contribute much-needed diversity of ecological processes to terrestrial, aquatic, estuarine, coastal beach, and open ocean habitats in the Pacific Northwest. Intensive utilization and management can deprive these habitats of large, fallen trees. This publication presents sound information for managers making resource management decisions on the impacts of this loss on habitat diversity and on ecological processes that have an impact on long-term ecosystem productivity.

Maser, C. and J.M. Trappe (editors). 1984. The seen and unseen world of the fallen tree. U.S. Dep. Agric. For. Serv., Portland, Oreg. Gen. Tech. Rep. PNW-164.

Keywords: structural characteristics, decomposition, habitat, general.

Abstract: Large, fallen trees in various stages of decay contribute much-needed diversity to terrestrial and aquatic habitats in western forests. When most biological

activity in soil is limited by low moisture availability in summer, the fallen tree-soil interface offers a relatively cool, moist habitat for animals and a substrate for microbial and root activity. Intensified utilization and management can deprive future forests of large, fallen trees. The impact of this loss on habitat diversity and on long-term forest productivity must be determined because managers need sound information on which to base resource management decisions.

Maser, C., J.M. Trappe, and D.C. Ure. 1978. Implications of small mammal mycophagy to the management of western coniferous forests. *Trans. N. Am. Wildl. Nat. Resour. Conf.* 43:78–88.

Keywords: mycorrhizae, small mammals, habitat, management.

Abstract: Management of our land and wildlife has been, and often still is, single-use oriented. However, we now have reached the stage in development of knowledge where the single-use concept is no longer valid or viable in land management. We can no longer afford a comfortably oversimplified economic view of our land and resources, “therefore land management must evolve toward total ecosystem management, not only convenient fragments thereof” (Maser and Thomas 1978:1).

Fortunately, Leopold’s (1966:251) statement—“The art of land doctoring is being practiced with vigor, but the science of land health is yet to be born” is not so true today. Although our research and management often are problem-oriented, or crisis-oriented, or both, the finely tuned, delicately balanced inner workings of coniferous forest ecosystems are slowly becoming appreciated.

The purpose of this paper is to examine some interrelationships between small mammals, hypogeous ectomycorrhiza-forming fungi, and trees, and the implications of these relationships to management of western coniferous forests. It is not our intent to present data, because relevant data are available elsewhere (Maser, Trappe, and Nussbaum 1978; Rothwell and Coleman 1978; Trappe and Maser 1976, 1978).

Mattson, K.G., W.T. Swank, and J.B. Waide. 1987. Decomposition of woody debris in a regenerating, clear-cut forest in the Southern Appalachians. *Can. J. For. Res.* 17:712–721.

Keywords: decomposition, southeastern U.S.A., clearcut, branches, bole wood, mixed hardwood, decay rates, wood properties.

Abstract: Mass losses were estimated for coarse (>5 cm) and fine (<5 cm) woody debris (CWD and FWD, respectively) during the first 7 years following clearcutting of a mixed hardwood forest at the Coweeta Hydrologic Laboratory in the Southern Appalachians of North Carolina. Estimates were based on (i) precut forest biomass, (ii) volume and density of CWD and mass of FWD at year 1, and (iii) wood density changes of CWD by year 6 and mass changes of FWD by year 7. Mass estimates of CWD at years 0, 1, and 6 were 91.2, 74.8, and 53.0 Mg/ha, respectively. Mass estimates of FWD at years 0, 1, and 7 were 30.3, 21.3, and 7.8 Mg/ha, respectively. Decay constants (k) for mass losses were relatively high compared with other studies of wood decomposition, 0.083 and 0.185 year⁻¹ for CWD and FWD, respectively, and 0.108 year⁻¹ for total (CWD+FWD) debris. Mass loss of CWD occurred largely through wood density decreases and bark fragmentation. CO₂-efflux estimates accounted for over 90% of the CWD density loss and for two-thirds (40.4 Mg/ha) of the total debris mass loss. The remaining mass loss of total debris (20.3 Mg/ha) is a source of large, organic matter inputs to the forest floor via solution fluxes and fragmentation of CWD bark and FWD. The large variation in wood-density loss among logs was examined statistically as a function of various decay factors. Density loss varied by more than 10-fold among tree species. Density loss rates were 40% higher in logs on the ground versus those off the ground, 100% higher in logs with observable fungi versus those without fungi, and 40%

higher in logs that occurred in plots with south and east aspects versus those in plots with west aspects.

Means, J.E., K. Cromack, Jr., and P.C. MacMillan. 1985. Comparison of decomposition models using wood density of Douglas-fir logs. *Can. J. For. Res.* 15:1092–1098.

Keywords: decomposition, decay rate, bole wood, *Pseudotsuga menziesii*, turnover time, wood properties, modelling.

Abstract: Logs of *Pseudotsuga menziesii* (Mirb.) Franco that had been on the ground for up to 313 years were grouped into five decay classes that ranged from 1, essentially undecayed, to 5, soft and incorporated into the forest floor but still identifiable. The mean residence times on the forest floor were 7, 17, 33, 82, and 219 years for decay classes 1 through 5, respectively. The single-exponential model of litter decomposition was fitted to the density of these logs. The summation-exponential model was constructed by summing single-exponential models fitted to lignin, cellulose, and the acid detergent soluble fraction. Both models gave virtually identical, statistically significant fits to the data. Wood density of these Douglas-fir logs decreased more slowly than that of most species other researchers have studied. The single-exponential model gave mineralization rates (k) of 0.0063 and 0.0070 year⁻¹ when residence time and decay class age (mean residence time of the decay class), respectively, were used as the independent variable. Lignin decayed more slowly than cellulose or the fraction soluble in hot acid detergent, both of which decayed at rates that were not significantly different; thus, the summation-exponential model is recommended when these constituents are of interest.

Muller, R.N. and Y. Liu. 1990. Coarse woody debris in an old-growth deciduous forest. *Bull. Ecol. Soc. Am. Supplement* to 71(2):265.

Keywords: quantities, old growth, hardwood forest, southeastern U.S.A., bole wood.

Abstract: Coarse woody debris (CWD) was surveyed in an old-growth forest in southeastern Kentucky. Volume of standing and fallen CWD >20 cm diameter averaged 66.3 m³/ha and mass averaged 20.5 Mg/ha. CWD was uniformly distributed among communities of the forest. While 23 species contributed to the accumulation of CWD, five contributed 69% of the total amount. Among these, American chestnut contributed 11% of the total. The importance of American chestnut reflects its former importance throughout the Central Hardwood Forest Region and the durability of its wood, which appears to have no contemporary equivalent. Other important species included chestnut oak (22% of total), American beech (16%), white oak (10%), and black oak (9%). The few studies of CWD in old-growth deciduous forests suggest a pattern of accumulation dominated by temperature. At lower elevations and in warmer regions, old-growth deciduous forests accumulate a mass of approximately 20–25 Mg/ha, while in cooler ecosystems at higher elevations or higher latitudes CWD may range from 30–50 Mg/ha.

Nowotny, C., T.P. Sullivan, and A.S. Harestad. 1990. Woody debris and abundance of rodents on clearcuts in sub-boreal spruce forest. Unpublished manuscript.

Keywords: habitat, mammals, British Columbia, logging impacts, clearcut, quantities, sub-boreal spruce forest, Engelmann spruce–subalpine fir forest.

Abstract: We examined the relationship between rodent densities and volumes of post-harvest debris in clearcuts in sub-boreal spruce forest of central British Columbia, Canada. Estimates of rodent densities were obtained using conventional grid systems and an index line method. Volumes of debris were calculated from diameter measurements made along transect lines. Densities of individual species and of all rodents combined were compared with debris volumes. Although a wide range of rodent densities and debris volumes were recorded, no significant correlations between the two variables were obtained.

Powers, R.F., D.H. Alban, G.A. Ruark, and A.E. Tiarks. 1990. A soils research approach to evaluating management impacts on long-term productivity. *In* Impact of intensive harvesting on forest site productivity. Proc. IEA/BE A3 Workshop, South Island, New Zealand, March 1989. W.J. Dyck and C.A. Mees (editors). IEA/BE T6/A6 Report No. 2. For. Res. Inst., Rotorua, N.Z. FRI Bull. No. 159, pp. 127–145.

Keywords: logging impacts, management, productivity, long-term impacts, harvesting methods, organic matter dynamics.

Abstract: Sustaining the inherent capacity of forest land to grow vegetation is a primary goal of modern forest management. In the United States, it is mandated by law for lands managed by the U.S. Forest Service. Soils are the basis for sustaining productivity, and the Forest Service is setting soil monitoring standards to detect significant changes in productivity potential. Such standards often are based on professional judgement, rather than hard evidence. However, research indicates that losses in soil productivity are linked with losses in site organic matter and soil porosity. A co-ordinated national research effort involving designed experiments has begun in the U.S.A. to provide a better understanding of the role of organic matter and soil porosity in the site processes controlling inherent productivity, and to generate guidelines for evaluating the probable impacts of forest management on long-term site productivity.

Prescott, C.E., J.P. Corbin, and D. Parkinson. 1989. Input, accumulation, and residence times of carbon, nitrogen, and phosphorus in four Rocky Mountain coniferous forests. *Can. J. For. Res.* 19:489–498.

Keywords: input rate, nutrient dynamics, nitrogen carbon, Rocky Mountains, *Pinus contorta*, *Picea glauca*, *Picea engelmannii*, *Abies lasiocarpa*, twigs, branches, cones, turnover time, early seral, mature, old growth.

Abstract: Annual aboveground litterfall in forests of *Pinus contorta* Loud., *Picea glauca* (Moench) Voss, *Picea engelmannii* Parry ex Engelm., and *Abies lasiocarpa* (Hook.) Nutt. in southwestern Alberta ranged from 286 to 321 g m⁻² year⁻¹. The mass of litter accumulated on the forest floors ranged from 6.3 to 11.0 kg m⁻². Residence times of organic matter in the forest floor were 11 years in a 90-year-old *P. contorta* stand, 16 years in a 120-year-old *P. glauca*–*P. contorta* stand, and 23 years in a 350-year-old *P. engelmannii* m² – *A. lasiocarpa* stand. Residence times of litter in the L layer of the forest floor were longer in a recently clearcut area than in the older forests. Residence times of individual nutrients in the forest floors were in the order N > P > C. Litter in the pine forest had lower concentrations of both N and P than did litter in the spruce-pine forest; litter in the spruce-fir forest had relatively high N and low P concentrations. Differences in nutrient concentrations of litter among sites reflected differences in the nutrient-use efficiency of the vegetation, suggesting that the species composition of vegetation is important in determining availability of nutrients in the floor of these forests.

Preston, C.M., P. Sollins, and B.G. Sayer. 1990. Changes in organic components for fallen logs in old-growth Douglas-fir forests monitored by ¹³C nuclear magnetic resonance spectroscopy. *Can. J. For. Res.* 20: 1382–1391.

Keywords: decomposition, methods, wood properties, carbon, *Pseudotsuga menziesii*, *Thuja plicata*, *Tsuga heterophylla*, decay classes.

Abstract: ¹³C cross-polarization magic-angle spinning nuclear magnetic resonance (CPMAS NMR) spectroscopy was used to characterize heartwood from decaying fallen boles of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), and western redcedar (*Thuja plicata* Donn). The sample decay classes I to V had been previously assigned based on field observations. Solid-state ¹³C CPMAS NMR spectra were analyzed to determine the proportion of C of the following chemical types: carbohydrate, lignin, aliphatic, and the sum of carboxyl plus carbonyl.

For both Douglas-fir and western hemlock, the proportion of carbohydrate C increased slightly in the early stages of decay. This was followed by a substantial increase in lignin C, while carbohydrate C declined to about 10% of total C. By contrast, the spectra for western redcedar generally showed little change with increasing decay class. One exceptional sample of western redcedar class IV was highly decomposed, indicating complete loss of carbohydrate C, and some loss of lignin side-chain C. For all three species, signals from alkyl and carbonyl C were weak, but tended to increase slightly with decomposition, most likely because of the selective preservation of waxes and resins (alkyl C), and oxidation. Accumulation of chitin was not observed, and there was little evidence for lignin decomposition or for formation of humic polymers. ¹³C CPMAS NMR offers a simple and information-rich alternative to wet chemical analyses to monitor changes in organic components during decomposition of woody litter.

Raphael, M.G. and M.L. Morrison. 1987. Decay and dynamics of snags in the Sierra Nevada, California. *For. Sci.* 33(3):774–783.

Keywords: function, decay rate, *Abies concolor*, *Pinus jeffreyi*, mortality, input rate, bole wood, southwestern U.S.A., snags.

Abstract: A study on the rates of decay, falling, and recruitment in a population of snags (standing dead trees) in the Sierra Nevada, California, during 1975–1983 showed that large-diameter (>38 cm dbh) snags fell slower than small-diameter snags. Firs (*Abies* spp.) fell at a lower rate than pines (*Pinus* spp.). Snags lost all needles and twigs within 5 years; 75% of pines and 66% of firs had lost most larger limbs within 5 years. Compared with the numbers of live trees in the parent stand, rates of new mortality were highest among Jeffrey pine (*Pinus jeffreyi* Grev. and Balf.) <15 cm dbh. Live-tree mortality exceeded the rate that snags fell during our study, causing an increase in the snag population from 1978 to 1983. A Leslie matrix model of this snag population was developed that accounted for falling rates, transitions among decay stages, and recruitment of snags. Use of the model was illustrated using field data from five unburned study plots.

Rhoades, F. 1986. Small mammal mycophagy near woody debris accumulations in the Stehekin River Valley, Washington. *Northwest Sci.* 60(3):1 50–153.

Keywords: habitat, mammals, Pacific Northwest, accumulation.

Abstract: The digestive tracts of 32 small mammals (*Sorex monticolus*, *Peromyscus maniculatus*, *Microtus longicaudus*, and *Clethrionomys gapperi*) trapped near woody debris piles were examined for presence and abundance of spores of hypogeous, epigeous and wood-inhabiting fungi. All animals contain fungal spores, usually in abundance high enough to suggest that each animal had recently consumed fungi. Spores of hypogeous fungi were the most abundant, especially those of genera *Alpova* and *Rhizopogon*.

Robison, E.G. and R.L. Beschta. 1990. Identifying trees in riparian areas that can provide coarse woody debris to streams. *For. Sci.* 36(3):790–801.

Keywords: modelling, input rate, bole wood, mortality, management.

Abstract: The natural fall of trees into mountain streams provides coarse woody debris that can improve fish habitat and influence stream morphology. Geometric and empirical equations, based on tree size and distance from the stream, were used to determine the conditional probability of a tree's adding coarse woody debris to a stream. Additional equations were developed to relate this probability to basal area factor. For conditions in the Pacific Northwest, Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) was selected to illustrate how the equations can be used for varying tree sizes and probabilities. After selecting a probability and determining basal area factor by these equations, resource managers can use prisms or wedge devices before timber harvesting

in riparian areas to identify specific trees that can potentially add woody debris to the stream.

Rosenberg, D.K., J.D. Fraser, and D.F. Stauffer. 1988. Use and characteristics of snags in young and old forest stands in southwest Virginia. *For. Sci.* 34(1):224–228.

Keywords: habitat, snags, hardwood forest, southeastern U.S.A., birds, structural characteristics.

Abstract: Snags were sampled in chestnut oak (*Quercus prinus*) and oak-hickory (*Quercus* spp.–*Carya* spp.) stands in southwest Virginia. More large (>17 cm dbh) snags were found in stands >100 years of age and more small (<10 cm dbh) snags were found in stands <80 years of age, than expected under the model of equal distribution among age classes ($\chi^2=25.3$, $df+6$, $P = 0.0003$). Log-linear models suggested that large-diameter snags are more likely to be used by foraging birds than smaller snags. Tall snags were also used more than short ones, but four-way log-linear models suggested that this was a result of a positive dbh–height relationship, rather than a reflection of bird selection of tall snags. Similarly, cavities were found more often than expected in large–dbh trees.

Sachs, D. and P. Sollins. 1986. Potential effects of management practices on nitrogen nutrition and long-term productivity of western hemlock stands. *For. Ecol. Manage.* 17:25–36.

Keywords: modelling, logging impacts, rotation length, productivity, long-term impacts, harvesting method, nitrogen, nutrient dynamics, *Tsuga heterophylla*.

Abstract: The FORCYTE-10 computer model, developed by J.P. Kimmins and K. Scoullar for Douglas-fir forests in British Columbia, was modified to simulate growth and nutrient cycling of coastal western hemlock stands. Initial calibration indicated that predicted yield was extremely sensitive to the rate of mineralization of soil organic matter (SOM), variation in SOM C:N ratio with site quality, the soil extractable NO_3^- : NH_4^+ ratio, and the decomposition rate and N mineralization pattern of large and medium-size roots and woody debris. The predictions suggested that yield and SCM remain stable under a management system consisting of six successive 90-year rotations. More intensive utilization (e.g., shorter rotations, whole-tree harvesting, and commercial thinning) causes depletion of soil and forest floor nitrogen and a small decline in site productivity in later rotations.

Schaetzl, R.J., D.L. Johnson, S.F. Burns, and T.W. Small. 1989. Tree uprooting: review of terminology, process, and environmental implications. *Can. J. For. Res.* 19:1–11.

Keywords: uprooting, management, habitat, site treatment, environmental factors.

Abstract: Floralturbation, the mixing of soil by the action of plants, is an important pedologic process in forested areas. The uprooting of trees, the most obvious form of floralturbation, is a natural process found in nearly all forested landscapes. The term uprooting is distinct from such terms as treethrow, treefall, and blowdown, which imply processes that may occur without soil disturbance, as in bole snap. Uprooting is exacerbated by shallow rooting, topographic exposure, weakened condition of the tree, certain cutting practices, and (or) low soil cohesion and shear strength. The root plate of an uprooted tree may deteriorate into a pit-mound pair, the size and shape of which depends on the characteristics of the root plate and the amount of backward displacement during uprooting. This paper (i) provides a synthesis of related terminology on the topics of treefall and uprooting, (ii) examines various lines of evidence for the widespread occurrence of uprooting, (iii) summarizes disturbance cycles for catastrophic uprooting events in different environments, (iv) discusses several examples of the economic import and scale of widespread uprooting events, and (v) reviews environmental factors and silvicultural practices that may lead to increased uprooting or can be used to minimize its likelihood.

Scott, M.L. and P.G. Murphy. 1987. Regeneration patterns of northern white cedar, and old-growth forest dominant. *Am. Mid. Nat.* 117(1):10–16.

Keywords: habitat, nurse log, regeneration, old growth, *Thuja occidentalis*, northeastern U.S.A.

Abstract: Regeneration of *Thuja occidentalis* L. was examined in an old-growth dune forest on South Manitou Island, Michigan. To estimate the current status of cedar regeneration, we determined size structure of seedlings and stems and analyzed present patterns of establishment and persistence relative to substrate type. There has been a shift in the pattern of cedar establishment from soil to log substrates. While 97% of all stems >15cm dbh are associated with a soil substrate, 81% of stems >2.5cm <15cm dbh, and 98% of all cedar seedlings are confined to log substrates. However, few cedar seedlings survive; only 1% of all seedlings on logs are >25 cm tall. There was no significant relationship between the state of log decay and the density of seedlings >25 cm in height, indicating that long-term survival is not dependent on the degree of log decomposition. However, survival on logs is associated with canopy openings. Seedlings >25 cm tall were associated with gaps, and 78% of cedar stems (>2.5 cm dbh) on logs were associated with a single windthrow gap. Thus, current cedar regeneration in this old-growth forest depends on logs and the canopy openings associated with them.

Seidl, M.T. 1985. The role of the fallen tree in an old-growth forest. *In Proc. 6th N. Am. Conf. on Mycorrhizae.* June 25–29, 1984, Bend, Oregon. *Oreg. State Univ. For. Res. Lab., Corvallis, Oreg.*, pp. 274–275.

Keywords: decomposition, mycorrhizae, habitat, mammals, nitrogen.

Abstract: Large fallen trees will have to be managed as a resource to maximize tree growth and maintain forest diversity. Complex interactions occur between fallen trees and the surrounding old-growth forest. During decomposition, fallen trees provide moisture, nutrients, and a myriad of habitats for organisms that are integral to ecological forest processes.

Silvester, W.B., P. Sollins, T. Verhoeven, and S.P. Cline. 1982. Nitrogen fixation and acetylene reduction in decaying conifer boles: effects of incubation time, aeration, and moisture content. *Can. J. For. Res.* 12: 646–652.

Keywords: nitrogen fixation, *Pseudotsuga menziesii*, nutrients, methods, nutrient dynamics.

Abstract: Free-living microaerophiles fixed $^{15}\text{N}_2$ and reduced acetylene in fallen tree boles at two old-growth *Pseudotsuga menziesii* stands in western Oregon. Acetylene reduction was most rapid under an atmosphere of 2–10% O_2 , whereas under prolonged anaerobic conditions it was at or below detection limits. Acetylene reduction rates increased up to four fold during long-term incubations in acetylene (>12 h). Ratios of acetylene reduction to N fixation frequently exceeded 6.0 during such long-term incubations but averaged 3.5 when samples were incubated <7 h; consequently, long-term incubation of low-activity indicated the N_2 fixation by free-living organisms in fallen boles was less than other potential N inputs to fallen boles and to the forest ecosystem.

Singh, T. 1987. Estimating downed-dead roundwood fuel volumes in central Alberta. *Can. For. Serv., North. For. Cent., Edmonton, Alberta. Information Report NOR-X-289.*

Keywords: quantities, fuel load, Alberta, *Picea glauca*, *Picea mariana*, *Pinus banksiana*, *Larix laricina*.

Abstract: A total of 46 pine- and spruce-dominated stands at five locations in central Alberta were sampled using the line intersect method to determine downed-dead fuel volumes. The stands were classified into five subgroups on the basis of species composition and basal area. The components of downed-dead materials were classified

into three main fuel condition classes: (1) sound, (2) partly decomposed, and (3) punky. The total downed-dead fuels (m^3/ha) in the dominant subgroups were jack pine 4.7–64.5, black spruce 1.7–63.8, white spruce 33.7–52.1, balsam fir 56.5, and tamarack 7.7. Prediction equations were derived to estimate roundwood fuel volumes from the following stand measurements: basal area, stem density, crown density, height, and age.

Smith, R.N. and L.R. Boring. 1990. *Pinus rigida* coarse woody debris inputs and decomposition in pine beetle gaps of the Southern Appalachians. *In* Bull. Ecol. Soc. Am. Supplement to 71(2):329.

Keywords: *Pinus rigida*, decay rate, decomposition, accumulation, mortality, quantities, southeastern U.S.A.

Abstract: The fate of *Pinus rigida* coarse woody debris (CWD) was examined in gaps created by southern pine beetles at Coweeta Hydrologic Laboratory, North Carolina. By killing drought-stressed trees, the beetle impact resulted in peak CWD loading of 35.6 metric tons ha occurring in gaps from 1 to 3 years old. The observed decay rate for this CWD over an 18-year period was $2.7\% \text{ yr}^{-1}$. Patterns of fungal and faunal colonization were examined. Stain fungi dominate the decomposer community in the early age classes, colonizing 31% of the available tree volume. Termites dominate later age classes, colonizing 77% of the available tree volume. Stable isotope analyses indicate that this CWD is an additional source of nitrogen input to the forest floor.

Sollins, P. 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. *Can. J. For. Res.* 12:18–28.

Keywords: input rate, decay rate, *Pseudotsuga menziesii*, *Tsuga heterophylla*, *Picea sitchensis*, *Abies amabilis*, *Abies grandis*, *Thuja plicata*, Pacific Northwest, early seral, nutrients.

Abstract: At 10 locations in Oregon and Washington, tree mortality resulted in dry-matter transfer of $1.5\text{--}4.5 \text{ Mg ha}^{-1} \text{ year}^{-1}$ of boles and branches to the forest floor and $0.3\text{--}1.3 \text{ Mg ha}^{-1} \text{ year}^{-1}$ of large-diameter roots directly to the mineral soil. The first value is about the same as that reported for leaf fall in similar stands; the second value generally is smaller than that reported for fine root turnover. Results are based on measurements by the U.S. Forest Service spanning 16–46 years and areas as large as 42 ha. Values based on intervals <10 years were highly variable and potentially misleading.

At an old-growth Douglas-fir stand in Washington, fallen boles accounted for 81 Mg/ha, standing dead for 54 Mg/ha. Density of fallen boles averaged from 0.14 to 0.27 g/cm^3 depending on decay state. Values were lower than some previously reported because (1) our sample included small-diameter fallen boles that tend to decay rapidly, and (2) we measured density with techniques that minimized compaction and shrinkage.

The decay rate at the old-growth stand, calculated indirectly by dividing bole mortality (megagrams per hectare per year) by the amount (megagrams per hectare) of fallen and standing dead woody material, was 0.028 year^{-1} . This rate, 3–5 times those previously calculated directly from change in density alone, was almost identical to values calculated elsewhere from change in both volume and density. Decay rates based on change in density alone include only respired and leached material and exclude the large amount of material lost in fragmentation. This study shows the value of permanent plots, undisturbed by salvage logging, for retrospective studies of decomposition, nutrient cycling, and productivity.

Sollins, P., S.P. Cline, T. Verhoeven, D. Sachs, and G. Spycher. 1987. Patterns of log decay in old-growth Douglas-fir forests. *Can. J. For. Res.* 17:1585–1595.

Keywords: function, decomposition, structural characteristics, wood properties, decomposers, *Pseudotsuga menziesii*, *Tsuga heterophylla*, *Thuja plicata*, Pacific Northwest, old growth.

Abstract: Fallen boles (logs) of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), and western redcedar (*Thuja plicata* Donn) in old-growth stands of the Cascade Range of western Oregon and Washington were compared with regard to their physical structure, chemistry, and levels of microbial activity. Western hemlock and western redcedar logs disappeared faster than Douglas-fir logs, although decay-rate constants based on density change alone were 0.010/year for Douglas-fir, 0.016/year for western hemlock, and 0.009/year for western redcedar. We were unable to locate hemlock or redcedar logs older than 100 years on the ground, but found Douglas-fir logs that had persisted up to nearly 200 years. Wood density decreased to about 0.15g/cm³ after 60–80 years on the ground, depending on species, then remained nearly constant. Moisture content of logs increased during the first 80 years on the ground, then remained roughly constant at about 250% (dryweight basis) in summer and at 350% in winter. After logs had lain on the ground for about 80 years, amounts of N, P, and Mg per unit volume exceeded the amount present initially. Amounts of Ca, K, and Na remained fairly constant throughout the 200-year time span that was studied (100-year time span for Na). N:P ratios converged toward 20, irrespective of tree species or wood tissue type. C:N ratios dropped to about 100 in the most decayed logs; net N was mineralized during anaerobic incubation of most samples with a C:N ratio below 250. The ratio of mineralized N to total N increased with advancing decay. Asymbiotic bacteria in fallen logs fixed about 1 kg N ha⁻¹ year⁻¹, a substantial amount relative to system N input from precipitation and dry deposition (2–3 kg ha⁻¹ year⁻¹).

Sollins, P., C.C. Grier, F.M. McCorison, K. Cromack, Jr., R. Fogel, and R.L.

Fredriksen. 1980. The internal element cycles of an old-growth Douglas-fir ecosystem in western Oregon. *Ecol. Monogr.* 50(3):261–285.

Keywords: nutrient dynamics, nutrients, old growth, Pacific Northwest, *Pseudotsuga menziesii*.

Abstract: Information on primary production, decomposition, hydrology, and element cycling was integrated in annual budgets of accumulation and flux among components of a mature Douglas-fir forest ecosystem. Annual N input in precipitation and dust was 2.0 kg/ha, and an estimated 2.8 kg/ha were fixed by cyanophycophilus lichens in the canopy. Annual N loss to groundwater was 1.5 kg/ha. N appeared to be accumulating in the ecosystem. An annual decrease of about 2.8 kg/ha in vegetation was offset by estimated increases of 5.0 kg/ha in fallen logs, and 2.8 kg/ha in soil organic matter. Microparticulate litterfall provided a large input of N to the forest floor (3.3 kg ha⁻¹ yr⁻¹).

Annual input of metallic cations in precipitation was only 545 eq/ha, whereas weathering input (net release of cations to solution from primary and secondary minerals) was estimated by difference at about 9000 eq/ha. Total annual loss to groundwater was 9400 eq/ha and, because of little cation accumulation, loss almost exactly balanced input. Net transfers of P were small. Total annual input was 0.5 kg/ha, total loss was 0.7 kg/ha, and net accumulation was -0.2 kg/ha. Input of elements in precipitation and dryfall was small compared with that in the eastern United States.

Water chemistry profiles showed that the biologically important elements N, P, and K increased in concentration as water passed through the canopy and litter layer but decreased as water passed through the rooted part of the mineral soil. In contrast, Na increased by a factor of 20 as water passed through the rooted soil.

Concentrations of all elements except Mg were lower in the stream water than in solution at 2.0 m depth in the subsoil.

At our site, unlike some eastern forests, Kjeldahl N (organic N plus NH₄⁺ accounted for most of the measured N in solution. Nitrate levels were low, averaging <20 µg/L NO₃—N at all points in the profile. Titratable alkalinity dominated anion chemistry in the

mineral soil, but in the upper parts of the water chemistry profile (precipitation, throughfall, and litter leachate) Cl and SO_4^- together accounted for 30–40% of the negative charge.

Total return to the forest floor in litterfall was greater than that reported for other Douglas-fir stands mainly because of plentiful microparticulate forms and coarse woody debris. Leaf fall accounted for less than half of the total litterfall input of N to the forest floor. Element accumulations in coarse woody debris almost cancelled the negative net annual increments in the living vegetation compartments.

Overall cycling patterns show that only the biologically limited element, N, was tightly conserved. For other elements, losses nearly equaled or even exceeded inputs. Redistribution from old to new foliage was also more important for N, P, and K than for Ca, Mg, and Na. Solution transport processes were important for all elements and dominated the cycling patterns of biologically less important elements such as Ca and Na. Vegetation absorbed metallic cations mainly from the mineral soil. However, much N and P were absorbed by roots penetrating up to or into the litter layer.

Fluxes of hydrogen ions (H^+) resulting from water flow were negligible ($<102 \text{ eq ha}^{-1} \text{ yr}^{-1}$) compared with H^+ release during carbonic acid dissociation and H^+ removal accompanying cation release in weathering (both about $10^4 \text{ eq ha}^{-1} \text{ yr}^{-1}$). Uptake of metallic cations by vegetation and release during decomposition exceeded uptake and release of sulphur and phosphorus anions, resulting in a net H^+ flux of about $3 \times 10^3 \text{ eq ha}^{-1} \text{ yr}^{-1}$. An increase in acidity of the rainfall to pH 4.0 would increase H^+ input only about $3 \times 10^2 \text{ eq ha}^{-1} \text{ yr}^{-1}$.

Spies, T.A. and S.P. Cline. 1988. Coarse woody debris in forests and plantations of coastal Oregon. Chapter 1. *In* From the forest to the sea: a story of fallen trees. C. Maser, R.F. Tarrant, J.M. Trappe, and J.F. Franklin (editors). U.S. Dep. Agric. For. Serv., Portland, Oregon. Gen. Tech. Rep. PNW-229. pp. 5–24.

Keywords: general, input rates, accumulation, old growth, second-growth, quantities, management, Pacific Northwest.

Abstract: The forest portion of the ecosystem is the sum of three diverse, mutually dependent components: physical structure, biological entities, and ecological functions. These components are dynamic, continually developing diversity.

Diversity develops in a forest as a result of changes that occur at different rates at different places. Disturbances cause relatively rapid changes in ecosystems, whereas succession slowly returns ecosystems to previous conditions or directs them to new states. Structural diversity in the current mosaic of forest age classes was created by a variety of disturbances, such as fire and wind, and this mosaic changes from succession and new disturbances. Today's forested coastal landscape bears the legacy of many landscapes in the form of remnant old-growth trees, snags, fallen trees, landslides, and patches of young and mature forests.

The forest's character changes with succession. Net primary productivity is greater in young forests than in old ones. Old forests conserve nutrients, whereas very young forests are susceptible to erosion and nutrient loss (Franklin et al. 1981). Forests of the Coast Range interior valleys produce less wood than do those on more moist sites nearer the ocean; and internally, the old unmanaged forest is more diverse than many young and mid-age forests. Old forests have deeper, multilayered canopies, larger accumulations of coarse woody debris (any dead standing or fallen tree stem at least 4 inches in diameter at breast height [dbh] on snags and at the large end on fallen trees), and more specialized plants and animals than young forests have.

A coastal Oregon forest may change slowly through growth, succession, mortality, and decay, or it may be altered rapidly by catastrophic disturbance. Whatever the agent of change, the imprints of previous forests and disturbances persist into succeeding forest

generations. Organic material in the form of dead tree stems is one of the more persistent legacies. This material exerts ecological influences on a site for hundreds and thousands of years; first, as snags and fallen trees; later, as fine organic matter in the soil. These organic remains create seed germination sites, moisture reservoirs during summer drought, sites of nutrient exchange for plant growth, habitat for forest organisms, and favourable soil structure.

Spies, T.A., J.F. Franklin, and T.B. Thomas. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. *Ecology* 69(6):1689–1702.

Keywords: structural characteristics, quantities, site factors, Pacific Northwest, accumulation, long-term impacts.

Abstract: Amounts and structural characteristics of coarse woody debris (CWD) were examined in relation to stand age and site moisture condition in 196 *Pseudotsuga menziesii* stands in western Oregon and Washington. Stands ranged from 40 to 900 years old, and most, if not all, originated after fire. In a chronosequence from the Cascade Range, the amount of CWD followed a U-shaped pattern for stands <500 years old, with moderate levels (92 Mg/ha) in stands <80 years old, lowest levels (<50 Mg/ha) in stands 80–120 years old, and highest levels (173 Mg/ha) in stands 400–500 years old. After 500 years the amounts of CWD declined to intermediate levels. In the southern Coast Range, lowest levels (32 Mg/ha) of CWD were in the youngest stands (60–80 years), primarily because they inherited little CWD from the preceding (prefire) stands. In the Cascade Range, levels of CWD inherited from preceding stands were highest in young stands and declined to near zero by 250 years. The overall decay-rate constant (k) for snags and logs in the Cascade Range, calculated indirectly from the chronosequence, was 0.029 yr^{-1} . Volume and biomass of CWD differed significantly in old-growth stands (>200 years old) among site moisture classes. Dry sites averaged 72 Mg/ha, moderate sites 137 Mg/ha, and moist sites 174 Mg/ha.

The dynamics of CWD were modeled for three fire histories, each beginning with an initial fire in an old-growth stand but differing in number and severity of subsequent fires. All three models exhibited low values of CWD between 80 and 200 years. The lowest and most prolonged minimum in CWD during succession occurred when additional fires burned early in succession, which probably happened preceding many stands in the southern Coast Range. The results of the study indicate that a steady-state condition in CWD may not be reached for >1000 years, and that the nature and timing of disturbance play a key role in the dynamics of CWD in the region.

Sprugel, D.G. 1985. Changes in biomass components through stand development in wave-regenerated balsam fir forests. *Can. J. For. Res.* 15:269–278.

Keywords: decomposition, modelling, *Abies balsamea*, accumulation, quantities input rate, organic matter dynamics, northeastern U.S.A.

Abstract: Available data on the wave-regenerated *Abies balsamea* forests of the northeastern United States are synthesized into a model (BALSAM), which predicts changes in total and component biomass through the disturbance-regeneration cycle. Measured decay rates seem to imply a higher mean forest floor mass than is actually observed, so several alterations were made in the initial model to make it predict forest floor mass correctly. With or without these changes forest floor mass decreases for about 12 years after disturbance, largely owing to low levels of litterfall in the early stages of stand development. Because changes in living biomass and dead bole mass through the disturbance cycles roughly cancel each other out, net ecosystem productivity closely parallels these litterfall-driven changes in the forest floor. Throughout the disturbance-regeneration cycle, the forest floor is derived primarily from woody tissue and its decay products, with foliage-derived material making up <25% of the total forest floor mass.

Stark, N.M. 1979. Nutrient losses from timber harvesting in a larch/Douglas-fir forest. U.S. Dep. Agric. For. Serv., Ogden, Utah. Res. Pap. INT-231.

Keywords: logging impacts, harvesting methods, nutrient dynamics, site treatment, inland northwest, *Larix occidentalis*, *Pseudotsuga menziesii*.

Abstract: Studies of the total amount of biologically essential nutrients removed in logs and water through clearcutting, shelterwood cutting, and group-selection cutting were conducted in a western larch (*Larix occidentalis*)/Douglasfir (*Pseudotsuga menziesii*) forest at the Corain Experimental Forest near Glacier Park, Montana. Nutrient removal of species was investigated under three intensities of harvest. Results show that with the most intensive logging method (clearcutting) less than 0.25% of the total content of eight biologically essential cations in the effective root zone were removed with wood and bark. This means that intensive harvest took away an equivalent of 1.4 of 1% of the nutrients stored in the soil and rock of the root zone. In theory, it would require 28 000 years of clearcutting on a 70-year rotation to exhaust the total nutrients in the present root zone. Soil development will slowly extend the root zone downward. Far more important than total nutrients are those nutrients available in the soil. Harvest of wood and bark removed an equivalent of <14% of most of the available elements in the root zone. Harvest is a one-point-in-time removal of nutrients that have been accumulated in the wood and bark of trees over 70 years' time. Removal of only 14% of what is at one moment available in the soil is a small loss. Unfortunately, we cannot yet measure the weathering rate so we cannot estimate how rapidly the removed nutrients will be returned through weathering. Harvest did remove from 14.8 to 91.7% of the available zinc in the soil (accumulated over +70 years). Although zinc is scarce in the parent material, this loss is not serious because sufficient zinc is still available for seedling growth. In most cases bulk precipitation alone will return all of the nutrients removed in harvest within 70–100 years. Nutrient losses from harvest on this relatively young, fertile soil is not a problem to management in the absence of erosion.

Nutrient levels in an intermittent stream were virtually unchanged by all logging treatments. The skyline system did not cause erosion. Because the area does not have a permanent stream or impermeable bedrock, it is unsuited to typical watershed study methods. Water samples taken below the root zone did show nutrient losses as a result of harvest, but these were at levels not significant to management. The most severe treatment studied, clearcutting by skyline and light burning, did not cause serious nutrient depletion from this forest ecosystem.

Taylor, K.L. and R.W. Fonda. 1990. Woody fuel structure and fire in subalpine fir forests. Olympic National Park, Washington. Can. J. For. Res. 20:193–199.

Keywords: fuel load, *Abies lasiocarpa*, structural characteristics, line intersect, spatial distribution, quantities, accumulation, subalpine forest.

Abstract: The fuel structure and flammability of subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) stands were studied to determine the relationship between these forests and fire. It has long been known that subalpine fir forests burn catastrophically, but the contributions of fuel structure and fuel moisture to this pattern of burning have been relatively unstudied. This investigation discovered two different relationships. First, over twice as much fuel in subalpine fir forests accumulated around the bases of the fir trees than in the forest as a whole, and the many dead branches on the lower trunks may allow fire to travel up into the canopy. Second, the fuels in subalpine fir forests were more flammable at the end of the summer than at the beginning, and maximum flammability was achieved in early August when the fuel moisture was between 16 and 22%. We also found that the fuel structure of subalpine fir was different from that of fire-stable ponderosa pine (*Pinus ponderosa* Laws.) forests. The fuel around the bases of the trees in

the ponderosa pine forests was not significantly different from that in the entire forest, and there were few branches on the lower trunks.

Taylor, R.F. 1935. Available nitrogen as a factor influencing the occurrence of Sitka spruce and western hemlock seedlings in the forests of southeastern Alaska. *Ecology* 16(4):580–602.

Keywords: habitat, nitrogen, Alaska, *Picea sitchensis*, *Tsuga heterophylla*, regeneration.

Abstract: Observations over a period of 8 years lead the writer to believe that seedlings of the two most common tree species in southeastern Alaska, Sitka spruce and western hemlock, have different seedbed requirements. The available nitrogen content of the seedbed and the percentage of the two species were thought to be related.

An investigation was carried on by sampling the seedbed on cutover land and by periodic analyses of pot cultures of certain seedbed types. The specific purpose of the investigation was to determine whether available nitrogen in the form of nitrates or ammonia is an important factor in the occurrence of Sitka spruce and western hemlock seedlings, and to examine the capacity of several of the more common seedbed types to form nitrates and ammonia. As a result of the investigation, the following conclusions have been reached:

- Nitrogen in available form is an important factor in the occurrence of Sitka spruce and western hemlock seedlings. Small quantities of nitrate nitrogen are correlated with low percentages of spruce seedlings. With increasing quantities of nitrate nitrogen comes a marked increase in the percentage of spruce. This does not continue indefinitely, however, but at approximately 50 ppm of nitrate nitrogen a saturation point is reached, and thereafter additional amounts of nitrate are not accompanied by higher percentages of spruce.
- Ammoniacal nitrogen accumulates in seedbeds containing organic material whenever oxidation to nitrates cannot occur. Spruce seedlings are not found in large numbers on such seedbeds although hemlock are abundant. Fifty ppm of nitrate nitrogen, the minimum amount necessary for a large percentage of spruce, is seldom found where ammonia forms more than 20 ppm and very rarely where it forms 60 ppm.
- The power of nitrification varies significantly with the character of the seedbed. The 10 seedbed types investigated in decreasing order of nitrifying capacity are:
 1. *Rubus spectabilis* mull;
 2. Alder mull, glacial;
 3. Sambucus mull;
 4. Alder mull;
 5. Spruce duff;
 6. *Fatsia horrida* mull;
 7. Willow-poplar mull;
 8. Hemlock-*vaccinium* duff;
 9. Hemlock duff; and
 10. Rotten wood.

- The first four types, as judged by ability to form nitrates, are capable of supporting large percentages of spruce; the other six types are not, unless measures are taken to hasten their decomposition and nitrification.

The pH values of the sample plots bear little relationship to nitrate nitrogen or ammoniacal nitrogen values which are obtained after incubation, due, it is thought, to morphological and chemical changes during storage. There is, however, a suggestion of relationship between pH and nitrate values obtained before incubation, the acidity decreasing with an increase in nitrates.

Triska, F.J. and K. Cromack, Jr. 1980. The role of wood debris in forest and streams. In *Forests: fresh perspectives from ecosystem analysis*. Proc. 40th Annual Biology Colloq., Oreg. State Univ. Press, Corvallis, Oreg. pp. 171-190.

Keywords: general, accumulation, quantities, habitat, decomposition.

Abstract: In the Pacific Northwest, old-growth forests and their associated streams contain large quantities of coarse wood debris. To date, such debris has been considered an impediment to reforestation and stream quality. Consequently, it has been virtually ignored in ecological studies, partly because man's need for wood fibre has resulted in the removal of debris from forests throughout the world but also because the extended period necessary for wood to decay makes it difficult to study nutrient recycling from such a process. In this paper, we shall attempt to correct that omission by exploring how wood debris is utilized in forest and stream ecosystems.

Such an exploration is timely in view of the diminishing amount of pristine forest.

In the Pacific Northwest, the greatest accumulation of wood debris occurs from natural mortality and blowdown in such forests. Now that forests are being cut every 80 years instead of standing 250–500 years (the interval between natural catastrophic fires), it is crucial that we determine the role of wood debris in pristine habitats and then incorporate that knowledge into existing management strategies for our forests and watersheds.

Our exploration will begin with determining the amounts of wood debris in various forest and stream ecosystems and its rates of accumulation in each. We shall then examine how debris modifies existing habitats and creates new ones. Next, we shall determine how rapidly coarse wood debris breaks down into its component elements and how its carbon and other elements are recycled. Finally, we shall discuss what implications these data have for the managers of forested watersheds in the Pacific Northwest.

Trofymow, J.A. and W.J. Beese. 1990. Quantities of coarse woody debris in old-growth forests. A brief to the Old-growth Project Research Working Group, September, 1990. Unpublished.

Keywords: British Columbia, old growth, quantities, bole wood.

Abstract: Coarse woody debris plays several important roles in temperate forests. More studies have been published on the amounts and extent of CWD in temperate forest streams than of terrestrial systems. For coastal forest types most of the published studies on CWD applicable to British Columbia have been in *Pseudotsuga menzeisii* or *Pseudotsuga-Tsuga heterophylla* forest types, although a few studies do exist for *Picea sitchensis*– and *Tsuga heterophylla*–dominated stands. Information for interior forest types comes principally from fires research studies and is available for several forest types, but the data do have limitations, as they are primarily restricted to the amounts of downed CWD.

Additional information on CWD for British Columbia forests could potentially be obtained from unpublished mensurational data from permanent sample plots, prescribed fire fuel assessments, and biogeoclimatic classification plots. If suitable plots were

available, retrospective analysis of long-term permanent sample plots combined with additional field measurements of amount and types of CWD could provide additional information on the amounts of, and the rates of formation and turnover of, CWD.

Trowbridge, R., B. Hawkes, A. Macadam, and J. Parminter. 1986. Field handbook for prescribed fire assessments in British Columbia: logging slash fuels. B.C. Min. For., Victoria, B.C. Land Manage. Handb. No. 11.

Keywords: methods, quantities, line intersect, fuel load, British Columbia.

Abstract: This is a guide for the assessment of fuel loads on sites after harvesting. It includes descriptions of the kinds of information which should be collected prior to prescribed burning, on the history and characteristics of the sites. It contains guidelines for the description of microtopography, soil moisture and nutrient regimes, and vegetation. The line intersect method is used to sample for woody fuels, along 30 m transects arranged in triangles. All pieces of woody debris >7 cm are assigned to size classes, and the percent species composition per line is estimated. Buried wood is not included in the slash assessment. Stage of decay is simply assessed as either sound and identifiable, sound but unidentifiable (designated as “U”), and decayed (designated as “D”).

Turner, D.P. and E.H. Franz. 1985. Size class structure and tree dispersion patterns in old-growth cedar-hemlock forests of the northern Rocky Mountains (U.S.A.). *Oecologia* 68:52–56.

Keywords: habitat, seedlings, nurse logs, regeneration, *Thuja plicata*, *Tsuga heterophylla*, inland northwestern states, old growth.

Abstract: Tree population size structures and dispersion patterns were studied using stem maps in three old-growth western hemlock (*Tsuga heterophylla* Sarg.) – western redcedar (*Thuja plicata* Donn.) stands in the Rocky Mountains of northern Idaho and adjacent Washington. The two species were codominant in one stand, hemlock dominated the second, and cedar the third. Shade-intolerant species such as western white pine (*Pinus monticola* Dougl.) were present only as canopy individuals. Hemlock, but not cedar, was well represented in size classes with dbh less than 20 cm. Although large individuals of both species have substantial influences on soil properties beneath them, forming distinct cedar or hemlock patches, nearest-neighbour analyses did not indicate that these patches influence tree recruitment patterns. Juvenile trees were generally found in nonspecific groups and their location was most dependent on rotting wood and other safe sites. Aggregation decreased as size class increased for both species in all cases except for cedar in the mixed stand, where the largest size class was aggregated. Aggregation of large cedars suggests that proximity to conspecifics increases survivorship among cedar in mixed stands. This may be due to the formation and maintenance of soil patches favouring a cedar nutrient cycling regime.

Van Sickle, J. and S.V. Gregory. 1990. Modeling inputs of large woody debris to streams from falling trees. *Can. J. For. Res.* 20:1593–1601.

Keywords: input rate, modelling, Pacific Northwest, old growth, *Pseudotsuga menziesii*, *Thuja plicata*, *Tsuga heterophylla*, bole wood.

Abstract: A probabilistic model predicts means and variances of the total number and volume of large woody debris pieces falling into a stream reach per unit time. The estimates of debris input are based on the density (trees/area), tree size distribution, and treefall probability of the riparian stand adjacent to the reach. Distributions of volume, length, and orientation of delivered debris pieces are also predicted. The model is applied to an old-growth coniferous stand in Oregon’s Cascade Mountains. Observed debris inputs from the riparian stand exceeded the inputs predicted from tree mortality rates typical of similar nonriparian stands. Debris pieces observed in the stream were generally

shorter, with less volume per piece, than those predicted by the model, probably because of bole breakage during treefall. As a second application, predicted debris inputs from riparian management zones of various widths are compared with the input expected from an unharvested stand.

Van Wager, C.E. 1968. The line intersect method in forest fuel sampling. *For. Sci.* 14(1):20–26.

Keywords: quantities, line intersect, fuel load, methods.

Abstract: A method for estimating wood volume on the ground is described. It requires only a diameter tally of pieces intersected by a sample line, and application of a simple formula. Theory for the formula is presented, and practical application discussed. The effect of bias in orientation of wood pieces can be largely overcome by running sample line in two or more directions. The method was demonstrated indoors with match splints scattered on a 54-inch square and tested on a 20-acre cutover area. It has potential value for measuring fuel quantities in fire research.

Wilford, D.J. 1984. The sediment-storage function of large organic debris at the base of unstable slopes. *In* Fish and wildlife relationships in old-growth forests. W.R. Meehan, T.R. Merrell, Jr., and T.A. Hanley (editors). Amer. Inst. of Fishery Research Biologists, pp. 115–119.

Keywords: British Columbia, productivity, logging impacts, structural characteristics, old growth.

Abstract: Large organic debris in old-growth forests provides important sediment-storage elements on hill slopes. As the old-growth trees fall or blow down across the slope, they form a series of cross-slope obstructions. Sediments and small organic debris from upslope mass movements are deposited behind these obstructions, forming a series of terraces, which temporarily delay the delivery of sediments to stream channels. Documentation of this storage role of large organic debris is provided from an old-growth Sitka spruce–western hemlock forest site in the Queen Charlotte Islands of British Columbia.

Yarie, J. 1986. A preliminary comparison of two ecosystem models, FORCYTE-10 and LINKAGES for interior Alaska white spruce. *In* Predicting consequences of intensive forest harvesting on long-term productivity. G.I. Agren (editor). Swed. Univ. Agric. Sci. Rep. No. 26, pp. 95–103.

Keywords: logging impacts, modelling, nitrogen, nutrient dynamics, productivity.

Abstract: The simulated development of an old-growth white spruce stand was compared between two ecosystem models, FORCYTE-10 and LINKAGES. Both models adequately depicted the development of aboveground standing crop and the biomass dynamics of the forest floor and humus layers. Only FORCYTE-10 satisfactorily portrayed stand density dynamics and nitrogen mineralization when compared to existing data. Further calibration work with LINKAGES was suggested to remedy the discrepancies.

Yoneda, T. 1982. Turnover of live and dead woody organs in forest ecosystems: An assessment based on the changes in the frequency distribution of their diameter (studies on the rate of decay of wood litter on the forest floor. IV). *Jap. J. Ecol.* 32:333–346.

Keywords: Japan, Malaysia, turnover time, input rate, accumulation, decomposition, twigs, branches, bole wood.

Abstract: The frequency $F(d)$ distribution of wood diameter (d) was determined or estimated in several forest stands of Japan and Malaysia for three different stages: 1) live woody organs in a stand [$F_1(d)$], 2) freshly fallen wood litter [$F_2(d)$], and 3) wood litter accumulating on the forest floor to decay [$F_3(d)$]. The regression of $\log F$ on $\log d$ proved to be approximately linear in all the three stages, but the gradient of regression line

differed among the stages. The ratio of $F_1(d)$ to $F_2(d)$ represented the mean turnover time of live woody organs and was proportional to $d^{0.9}$. The mean turnover time of accumulating wood litter was similarly given by $F_3(d)/F_2(d)$, which was proportional to $d^{0.2}$. A new formulation was developed for estimating the amounts of falling and accumulating wood litter from their maximum diameter to show good applicability to the data from other sources. The “breakability” of a live branch was found to be proportional to its cross-section area or d^2 .

APPENDIX 4. *Supplemental list of references*

- Note: These references are included for the general interest of readers. They were not reviewed by the author for their relevance to the material presented in this report.
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APPENDIX 5. *Decay classes: successional stages of decomposition in logs and snags*
(from Bartels et al. 1985)

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