Coarse woody debris in the old-growth forests of British Columbia[1]

M.C. Feller

Abstract: This paper synthesizes data extracted from the literature and data collected in various studies by the author on the quantity, characteristics, and functional importance of coarse woody debris (CWD) in the old-growth forests of British Columbia (B.C.). There is little agreement in the literature about the minimum diameter of CWD or the number of decay classes recognized. In western North America, five decay classes are commonly used, but recent studies suggest fewer decay classes are preferable. Comparisons among decay classes and biogeoclimatic zones and subzones in B.C. reveal that quantities and volumes are greatest (up to approximately 60 kg/m^2 and approximately 1800 m^3/ha, respectively), and CWD persists the longest (sometimes in excess of 1000 years) in the Coastal Western Hemlock (CWH) biogeoclimatic zone. The quantity and ground cover of CWD increase with forest productivity. Persistence of CWD has varied from less than 100 to over 800 years in two coastal (CWH and Mountain Hemlock (MH)) and three interior (Interior Douglas-fir (IDF), Interior Cedar–Hemlock (ICH), and Engelmann Spruce – Subalpine Fir (ESSF)) biogeoclimatic zones. Trends in CWD quantity with forest age in managed coastal B.C. forests suggest a U-shaped curve, with greater quantities occurring in recent cutovers than in old-growth forests, and lowest quantities occurring in middle-aged forests. This may be the normal trend in CWD with forest age, with departures from this trend resulting from disturbance- or environment-specific factors. Relatively large amounts of data exist on the characteristics of CWD in the CWH, IDF, ICH, ESSF, and Boreal White and Black Spruce (BWBS) biogeoclimatic zones, but such data for the Coastal Douglas-fir, Sub-Boreal Pine–Spruce, Sub-Boreal Spruce (SBS), and Spruce–Willow–Birch biogeoclimatic zones appear relatively sparse. There have been few studies of the functional role of CWD in B.C. forests, but those studies that have been completed indicate that CWD is an important habitat component for some plant and animal species. A total of 169 plant species, including $>95\%$ of all lichens and liverworts, were found to grow on CWD in old-growth forests in the CWH, MH, IDF, ICH, and ESSF biogeoclimatic zones. One third of these species were restricted to CWD. Studies in several biogeoclimatic zones have found that CWD provided preferred habitat for and was associated with higher populations of some small animal species, such as shrews, some voles, and some salamanders, in old-growth forests, but the effects varied with species and biogeoclimatic zone. The nutrient cycling role of CWD is not yet well known, but it currently appears to be relatively insignificant in B.C. old-growth forests. Although it has been considered that CWD could increase mineral soil acidification and eluviation, no

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evidence for this was found in a study of the CWH, MH, IDF, ICH, ESSF, BWBS, and SBS biogeoclimatic zones. Future studies of the functional role of CWD should consider both scale (square metre vs. hectare) and temporal (changes in CWD with forest age) issues, as studies including these are sparse and both may be important.

Key words: biogeoclimatic zones, British Columbia, coarse woody debris, old-growth forests.

Résumé : Cette communication résume les données tirées de la littérature et celles recueillies par l'auteur dans diverses études sur la quantité, les caractéristiques et l'importance fonctionnelle des débris ligneux grossiers (DLG) dans les forêts anciennes de la Colombie-Britannique (C.-B.). Dans la littérature, on ne s'entend pas sur le diamètre minimum des DLG, ou le nombre de classes de décomposition. Dans l'ouest de l'Amérique du Nord, on emploie le plus souvent cinq classes, mais des études récentes portent à croire qu'un nombre de classes inférieur serait préférable. Les comparaisons entre les classes de décomposition et les zones et sous-zones biogéoclimatiques de la C.-B. révèlent que les DLG sont plus abondants (pouvant atteindre environ 60 kg/m^2 et 1800 m^3/ha) et persistent le plus longtemps (parfois pendant plus de 1000 ans) dans la zone biogéoclimatique côtière de la pruche de l'Ouest (CWH). L'abondance des DLG et la superficie de sol qu'ils couvrent augmentent avec la productivité de la forêt. La persistance des DLG varie de moins de 100 ans à plus de 800 ans dans cinq zones biogéoclimatiques : deux zones côtières (la CWH et la zone de la pruche subalpine (MH)) et trois zones intérieures (celle du douglas taxifolié de l'intérieur (IDF), celle des cèdres et des pruches de l'intérieur (ICH) et celle de l'épinette d'Engelmann et du sapin subalpin (ESSF)). Dans les forêts côtières aménagées de la C.-B., l'abondance des DLG en fonction de l'âge de la forêt suivrait une courbe en U, les débris étant plus abondants sur les parterres de coupe récents que dans les forêts anciennes, et moins abondants dans les forêts d'âge moyen. Cette relation entre les DLG et l'âge de la forêt est peut-être la tendance normale, et les écarts par rapport à celle-ci pourraient être le résultat de facteurs propres à chaque perturbation ou milieu. Il existe beaucoup de données sur les caractéristiques des DLG dans la CWH, la IDF, la ICH, la ESSF et la zone boréale des épinettes blanche et noire (BWBS), mais il en existe relativement peu pour la zone côtière du douglas taxifolié, la zone subboréale des pins et des épinettes, la zone subboréale de l'épinette (SBS) et la zone de l'épinette, du saule et du bouleau. Peu d'études ont été consacrées au rôle fonctionnel des DLG dans les forêts de la Colombie-Britannique, mais d'après celles qui ont été réalisées, les DLG constitueraient une composante importante de l'habitat de certaines espèces végétales et animales. On a recensé 169 espèces végétales poussant sur ces débris, dont plus de 95 % de tous les lichens et hépatiques, dans les forêts anciennes de la CWH, de la MH, de la IDF, de la ICH et de la ESSF. Le tiers de ces espèces ne poussent que sur les DLG. D'après des études effectuées dans plusieurs zones biogéoclimatiques, ces débris constituent l'habitat préféré de certains petits animaux présents dans les forêts anciennes, tels que les musaraignes, certains campagnols et certaines salamandres, et sont associés à de plus fortes populations de ces animaux, mais les effets varient selon l'espèce et la zone biogéoclimatique. Le rôle des DLG dans le recyclage des éléments nutritifs n'est pas bien connu, mais il semble qu'il soit relativement négligeable dans les forêts anciennes de la C.-B. Il a été avancé que les débris ligneux grossiers pourraient accroître l'acidification et le lessivage des sols minéraux, mais de tels effets n'ont pas été mis en évidence dans une étude de la zone CWH, de la MH, de la IDF, de la ICH, de la ESSF, de la BWBS et de la SBS. À l'avenir, les études sur le rôle fonctionnel des DLG devraient tenir compte des aspects liés à l'échelle (m^2 ou ha) et temporels (modifications des DLG avec le vieillissement de la forêt) puisque les études impliquent ces paramètres potentiellement importants sont rares.

Mots clés : zones biogéoclimatiques, Colombie-Britannique, débris ligneux grossiers, forêts anciennes.

Introduction

Old-growth forests have been defined in a variety of ways in terms of stand structure (Franklin et al. 1981), stand development processes (Oliver and Larson 1996), tree age (Spies 1997; MacKinnon and Vold 1998), or a combination of factors (Spies and Franklin 1996; Wells et al. 1998). A relatively large quantity of coarse woody debris (CWD) or downed logs, particularly large logs, is considered to be an important structural feature of a wide variety of old-growth forests in North America (e.g., Franklin and Spies 1991; Caza 1993; Sturtevant et al. 1997; Spetich et al. 1999) and elsewhere (e.g., Scotts 1991; Siitonen et al. 2000). Until the last 20 years, CWD has generally been neglected as a component of a forest ecosystem. Studies of forest structure, biomass, and nutrient distribution around the world generally ignored CWD as recently as the early 1980s (e.g., IUFRO 1981; Reichle 1981; van Cleve et al. 1986).

A notable exception was in the United States (U.S.) Pacific Northwest, where, for example, Grier et al. (1974) noted the large difference in CWD and its nutrient content between old-growth forests and young plantations, and the synthesis by Edmonds (1982) assisted in developing an awareness of the ecological significance of CWD. This was given major stimulation by the definitive review of Harmon et al. (1986), who concluded that CWD was an important functional component of a temperate forest ecosystem, through its influence on plants, animals, and ecosystem chemistry. The present review shows that subsequent studies have reinforced this general conclusion, but also that there is still much to learn about CWD and some debate about its effects (e.g., on soil nutrition; Kayahara et al. 1996).

Knowledge of CWD in B.C. forests is particularly incomplete. Harmon et al. (1986) presented no data at all for B.C.; Trofymow and Beese (1990) found such data only from two unpublished theses; and Caza (1993) was still unable to find such published data several years later. Caza (1993) was also unable to find any published field studies that focused on CWD in B.C. She recommended that CWD levels in B.C. forests be inventoried and that CWD studies were needed in B.C. that focused on

(1) the functional importance of CWD to moisture retention and as plant and animal habitat

(2) CWD impacts on soil physical and chemical properties

(3) the role of CWD in soil organic matter dynamics

The present report assesses the current state of knowledge of CWD in B.C. old-growth forests compared with the very limited knowledge found by Caza in 1993.

Methods

This review synthesizes data extracted from the literature and data collected in various studies by the author.

Literature data

Although there are several definitions of old-growth forests (e.g., Wells et al. 1998), analysis of the literature was standardized using the definition of MacKinnon and Vold (1998) for their B.C. inventory: old-growth forests are those >250 years old on the coast and >140 years old for all tree species in interior B.C., except for lodgepole pine (*Pinus contorta* Dougl. ex Loud.), for which old-growth forests were considered to be >120 years old. As stated by MacKinnon and Vold, these are the ages at which structural and biological characteristics associated with old-growth forests are considered to begin to develop. This definition facilitated assessment of whether or not a forest was old growth for those reports that described forests primarily by their age. For studies reporting results for several forests, some of which were old growth and some younger, results are included here if the difference between the minimum age in these studies and those given above did not exceed 10 years. The fuel photoguides

Table 1. Nomenclature for forested biogeoclimatic zones and subzones of British Columbia (Meidinger and Pojar 1991).

Zones — Named after one or more of the dominant climax species on zonal (intermediate in moisture and nutrients) sites.	
BWBS	Boreal White and Black Spruce
CDF	Coastal Douglas-fir
CWH	Coastal Western Hemlock
ESSF	Engelmann Spruce – Subalpine Fir
IDF	Interior Douglas-fir
ICH	Interior Cedar–Hemlock
MS	Montane Spruce
MH	Mountain Hemlock
PP	Ponderosa Pine
SWB	Spruce–Willow–Birch
SBPS	Sub-Boreal Pine–Spruce
SBS	Sub-Boreal Spruce
Subzones — Zones are subdivided into subzones, each of which has a distinct climax or near-climax plant association on zonal sites. Subzones are named by modifying the zone name with two letters, according to climate characteristics.	
First letter (precipitation regime)	
x	very dry
d	dry
m	moist
w	wet
v	very wet
Second letter	
Coastal zones — continentality	
h	hypermaritime
m	maritime
s	submaritime
Interior zones — temperature regime	
h	hot
w	warm
m	mild
k	cool
c	cold
v	very cold

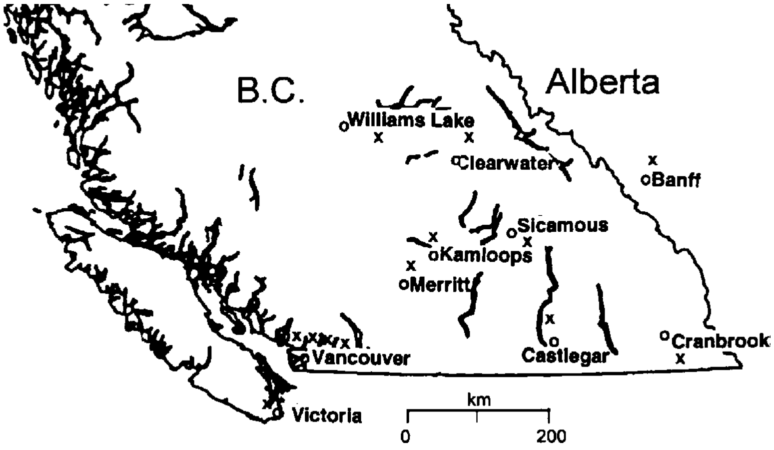
(Fischer 1981*a*, 1981*b*, 1981*c*; Anon. 1992; Ottmar and Vihnanek 1998) gave no forest age data, so old-growth status was assessed visually using the photographs contained in the guides.

Results of U.S. studies were extrapolated to B.C. by estimating the likely biogeoclimatic zone (Meidinger and Pojar 1991) in which the U.S. data were collected. (British Columbia biogeoclimatic zone nomenclature, as given by Meidinger and Pojar (1991), is described in Table 1.) This was done as described by Klinka (2003). This estimation was based on any descriptions of geographic location, climate, and vegetation given in the U.S. studies.

Studies by the author

The author has conducted several studies into nutrient cycling and fuel dynamics in forests as well as into the ecological effects of CWD. These studies have been conducted in

Fig. 1. Location of old-growth forest plots in which CWD has been measured by the author. Plot locations are indicated by crosses.



(*a*) the CWH zone in the water supply watersheds of the cities of Victoria and Vancouver and the University of British Columbia (UBC) Research Forest at Maple Ridge

(*b*) the MH zone in Cypress Provincial Park near Vancouver

(*c*) the IDF zone near the towns of Merritt, Kamloops (Opax Mountain Silvicultural Systems research area), Castlegar, and Cranbrook, as well as in the UBC Research Forest near Williams Lake, and Banff National Park

(*d*) the ICH zone near the town of Sicamous

(*d*) the ESSF zone near the towns of Clearwater and Sicamous (Sicamous Creek Silvicultural Systems research area) (Fig. 1)

In all studies by the author, CWD mass was quantified by size class and decay class (Table 2) using the line intersect method (van Wagner 1968), as well as wood density for each species from each size and decay class. The line intersects involved 3 equilateral triangles (30-m sides) per 1-ha plot, with 3–6 plots per stand (i.e., from 9 to 18 triangles per stand). The number varied depending on the objectives of the separate studies in which the CWD data were collected. Estimated wood volumes were converted to masses by multiplying volumes by wood relative densities. Relative densities were measured from the volume and dry mass of samples of each size class (1–2.9, 3–4.9, 5–6.9, 7–11.9, and >12 cm diameter) for each species and decay class. Eight to 48 samples of each species –size class – decay class combination were used to estimate relative densities. Sufficient samples were used so that there was at least an 80% chance that the 90% confidence interval of the estimated mean relative density was within 20% of the true mean. In most (60%) cases, there was at least a 90% chance that the 90% confidence interval of the estimated mean relative density lay within 10% of the true mean.

To determine the length of time that CWD remains separate from the forest floor, four samples of the most well-decayed CWD (decay class IV of Table 2) were collected from six study plots and analysed by radiocarbon (^{14}C) dating as described previously by Feller (1997).

Site index (SI) was used as an indicator of the relative productivity of a biogeoclimatic subzone in B.C. The maximum SI (breast height in metres at 50 years) for any coniferous tree species growing on a zonal site in a biogeoclimatic subzone was obtained from the Site Productivity Working Group (1997).

Table 2. Decay classes used in the work of M. Feller, and their comparison with those of Sollins (1982).

	Decay classes	
Decay class definition	Present study	Sollins (1982)
Tree has recently fallen and is essentially intact with fine twigs (0.5 cm in diameter) present. Dead foliage may be present.	I	I
Bark is intact; branches 2 cm in diameter are present; wood is original colour; and tree retains its original shape. No fine twigs or foliage are present.	II	I–II
Bark is loose or has partly fallen off; few branches, only those >5 cm in diameter, are present; wood is original colour or faded, and may be partly soft; and tree retains its original shape.	III	II–III
Bark is absent; wood is at least partly soft and generally red brown to dark brown; no branches are present; tree has at least partly lost its original shape; and is at least partly embedded in the forest floor.	IV	IV–V

Site index is the primary method of evaluating forest site productivity in North America (e.g., Fisher and Binkley 2000).

Nitrogen fixation was measured for tree foliage, stembark, *Lupinus arcticus*, *Peltigera* spp. lichens, forest floor, decay class II CWD, decay class III CWD, decay class IV CWD, and mineral soil in a chronosequence of four age classes (0–4, 5–10, 50–100, and >200-years old) *Abies lasiocarpa – Picea engelmannii* forests in central southern B.C., using the acetylene reduction method, calibrated with ^{15}N, similar to that described by Roskoski (1981). This involved acetylene reduction measurements on tree foliage, tree bark, three classes of decaying wood, *Peltigera* lichens known to fix N, lupins, forest floor, and mineral soil. Six samples of each of these components were collected as described in Cushon and Feller (1989) and placed into 1-L Mason jars equipped with rubber septa. All incubations were conducted in the field monthly during the growing season (June through September) as described by Cushon and Feller (1989). After allowing 1 h for equilibration, gas samples were taken for determination of initial C_2H_4 concentrations using the double-needle method and vacuum tubes. After 8 h, vacuum tube samples were taken for measurement of C_2H_4 production; C_2H_4 was measured in the laboratory using a gas chromatograph as described in Cushon and Feller (1989).

The acetylene reduction assay assumes a 3:1 conversion factor for C_2H_4 produced to N fixed. The true conversion factor was determined by adding a ^{15}N gaseous mixture (21% O_2, 78.9% N_2 as ^{15}N, and 0.1% CO_2) to Mason jars (four jars per plot per ecosystem component per sampling month) containing each of the components assessed for N fixation. Samples were incubated under ambient conditions in the field for 24 h, then placed into plastic bags kept cool until the samples could be dried, weighed, ground (organic materials) or sieved (2 mm mineral soil), then sent to the G.G. Hatch Isotope Laboratory at the University of Ottawa, Ontario, for analysis of their ^{15}N content by mass spectrometry.

After incubations were complete, sample dry mass was determined and fixation rates were expressed on a unit area basis using the estimated mass of each ecosystem component present per unit area. Fixation measurements were made in one stand in each of the four age classes, then averaged over three stands per age class using estimates of the masses of all the ecosystem components assessed for the three stands per age class. The masses of the ecosystem components were estimated as follows.

Tree foliage and stembark

The height (0- to 10-year-old trees) or diameter at breast height (dbh) (>50-year-old trees) of all trees present in three 20 m × 20 m plots within each study plot were measured, then tree species-specific biomass regression equations developed by the author were used to estimate tree foliage and stembark masses, based on the heights or diameters. These regression equations were determined after destructive sampling of 20 *Abies lasiocarpa* and 20 *Picea engelmannii* trees >50 years old and 20 *Abies lasiocarpa* and 26 *Picea engelmannii* trees 0–10-years old. Sampling and regression equation development were similar to that described by Feller (1992).

Lupinus and Peltigera

The percent covers of *Lupinus* and *Peltigera* lichens were determined from belt transects, then converted to masses using biomass regression equations based on cover, developed by the author. Five to thirteen randomly oriented and located transects, each 2 m wide and 30 m long, were used in each study plot. Regression equations were developed after destructive sampling of 24 *Lupinus* and 63 *Peltigera* samples.

Forest floor

Mass estimates were derived from destructive sampling of small (20 cm × 20 cm) plots.

Coarse woody debris

Mass estimates were made using the triangular line intersects described above.

Data obtained from the literature and collected in studies by the author were analysed for trends by regression analysis using SYSTAT 9 software (Anon. 1999).

Results and discussion

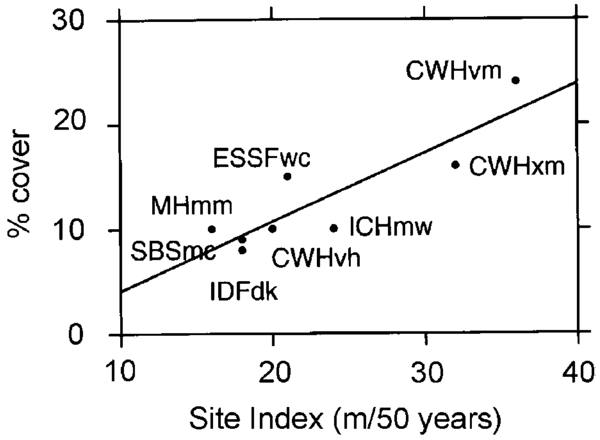
Quantity and characteristics of coarse woody debris

Results are presented by biogeoclimatic zone or subzone, the acronyms for which are defined in Table 1.

Coarse woody debris has covered an average of 1–24% of the ground surface in old-growth forests in the CWH, MH, IDF, ICH, ESSF, SBS, BWBS, and Ponderosa Pine (PP) zones (Sollins et al. 1980; Graham and Cromack 1982; Foote 1983; Franklin et al. cited in Harmon et al. 1986; Spies et al. 1988; Arthur and Fahey 1990; Harmon and Hua 1991; Means et al. 1992; Song 1997; Clark et al. 1998; Edmonds and Lebo 1998; Ohmann and Waddell 2002). This percentage generally increases as forest productivity increases (Fig. 2). The linear regression for the data in Fig. 2 suggests that ground coverage is likely to increase by an average of approximately 0.7% for each 1-m increase in SI (over a range of 15–37 m per 50 years). Owing to the lack of data for B.C. (data from only 8 out of 92 forested biogeoclimatic subzones were available), the generality of this statement is still unknown, however.

Comparison of CWD quantities among studies remains difficult due to a lack of agreement on size and decay class criteria. Harmon et al. (1986) found that minimum diameters used to define CWD varied from 2.5 to 15 cm. Such a wide variation still exists today, with minimum diameters from 15 cm (e.g., Jonsson 2000) to 1 cm (e.g., Wells and Trofymow 1997; Preston et al. 1998) being used. Similarly, there is no agreement on number of decay classes. Harmon et al. (1986) found that studies had used three to five decay classes; Sturtevant et al. (1997) used a two decay class system in Newfoundland boreal forests, and recently in Scandinavia, systems involving five to eight decay classes have been used (e.g., Jonsson 2000; Siitonen et al. 2000). In western North America, a five decay class system, similar to that described by Sollins (1982), tends to be the most popular, although work in B.C. (Daniels et al. 1997; Feller 1997; Preston et al. 1998) suggests a four-class system is more appropriate for some B.C. forests, based on age since death and chemical composition of the wood. In B.C., three (e.g., Clark et al. 1998; Stone et al. 1998), four (e.g., Feller 1997), and five (e.g., Wells and Trofymow 1997) decay class systems have all been used. Support for a four class system also comes from work in old-growth hemlock–hardwood forests in the northern U.S., where Tyrrell and Crow (1994*a*) found substantial overlap between intermediate decay classes in the time periods CWD spent in each decay class. It is

Fig. 2. The percentage cover of the ground surface by CWD in old-growth forests as a function of forest productivity (maximum SI for zonal sites) for the B.C. biogeoclimatic subzones for which CWD mass data are available. The plotted linear regression line is % COVER = $-2.43 + 0.66(\mathrm{SI})$, $R^2 = 0.78$, SE = 2.7, $P < 0.01$.



not completely clear why different workers use different decay class criteria, although it may be partly related to differing work objectives. Thus, CWD in the most advanced decay class (class five of Sollins (1982)) is mostly embedded in the forest floor, where it would be assessed as forest floor and not CWD when estimating forest fuel for forest fire research or management purposes. Wildlife biologists, in contrast, have separated the most advanced decay class CWD from the forest floor because of its special wildlife habitat attributes, such as suitability for subterranean burrows and relatively high abundance of invertebrate food sources (Maser et al. 1979). However, Bull et al. (1997) consider that three decay classes are sufficient to classify CWD for wildlife purposes and a recent wildlife habitat assessment of Washington and Oregon (Rose et al. 2001) has used only three decay classes. Although previously published studies in western North America have employed a five decay class system, recent studies suggest fewer decay classes are preferable.

The inclusion of smaller-diameter woody debris in some studies may be attributable to the purpose of these studies, which typically measure CWD to estimate forest fuel for forest fire research or management. Such inclusion will probably not substantially affect estimates of quantities in wetter forests, as the smaller-diameter woody debris usually accounts for a relatively small percentage of the total quantity present. For example, in the 44 wetter CWH, MH, ICH, and ESSF zone forests studied by the author (Table 3), the average contribution of <12-cm diameter woody debris to the total woody debris was 11% (range: 3–37% with only 4 of the 44 values exceeding 15%). For the 9 drier IDF forests, however, the <12-cm diameter woody debris made up an average 36% of the total woody debris, with only one of the nine values being less than 15%. This is generally consistent with the results of other studies, and is likely associated with the relative quantities of CWD in different forests. Drier forests tend to have smaller quantities of CWD, presumably due to one or more of the following factors: lower tree biomass production, more frequent fires, or more rapid decomposition of downed wood. The proportion of total CWD attributed to smaller-diameter material increases as the total quantity of CWD decreases (Fig. 3). The smaller-diameter classes dominate the numbers of pieces of CWD present, if not the mass (Table 3).

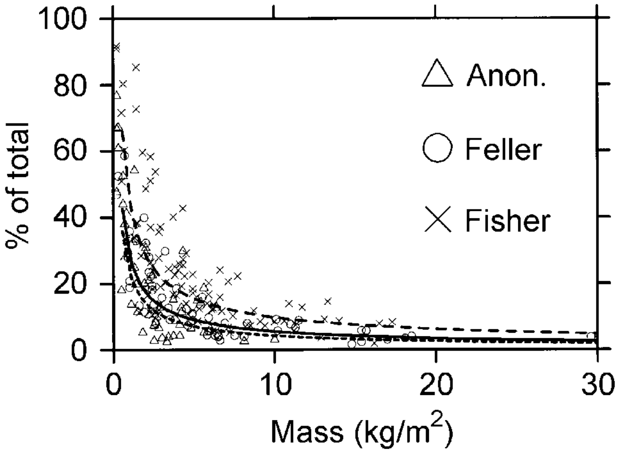
The three data sets presented in Fig. 3, despite being collected from considerably different forest areas, are similar, the two B.C. data sets being remarkably similar. The generally higher percentages in Fischer's data may be attributed to the wider diameter range used to define smaller CWD from his data. There may also be some errors associated with the absence of forest age data for both the Kamloops and Fischer data sets. The decision as to whether or not a forest was old growth was based on a subjective

Table 3. Means and ranges (in parentheses) of characteristics of coarse woody debris in B.C. old-growth forests, as found in studies by M. Feller.

		Number of pieces per 100 m of transect								Mass of >1 cm diameter CWD (kg/m^2)								
Biogeoclimatic zone/area		Diameter <12 cm				Diameter >12 cm				Diameter <12 cm				Diameter >12 cm				Total
Decay class		I	II	III	IV	I	II	III	IV	I	II	III	IV	I	II	III	IV	I–IV
Coastal forests																		
Dry CWH	($n = 3$)	51	22	42	6	4	4	9	6	0.3	0.2	0.3	0.1	1.8	1.2	2.6	1.0	7.4
		(31–70)	(15–27)	(32–48)	(2–10)	(3–6)	(1–6)	(6–12)	(4–8)	(0.1–0.4)	(0.2–0.2)	(0.2–0.4)	(0.0–0.1)	(0.9–3.0)	(0.3–2.2)	(1.4–4.3)	(0.8–1.2)	(4.7–11.4)
Moist CWH	($n = 27$)	9	12	92	8	1	1	10	7	0.1	0.1	0.7	0.1	0.5	0.7	6.4	2.1	10.5
		(0–53)	(0–27)	(14–410)	(1–20)	(0–7)	(0–7)	(2–22)	(1–14)	(0.0–0.5)	(0.0–0.2)	(0.1–3.0)	(0.0–0.2)	(0.0–3.4)	(0.0–7.8)	(0.4–15.0)	(0.0–4.3)	(2.2–29.6)
MH	($n = 4$)	5	17	41	4	1	2	6	7	0.0	0.1	0.3	0.0	0.1	0.2	1.9	1.1	3.8
		(0–11)	(10–21)	(22–49)	(2–7)	(1–1)	(1–2)	(4–12)	(4–8)	(0.0–0.1)	(0.1–0.1)	(0.1–0.4)	(0.0–0.1)	(0.1–0.1)	(0.1–0.4)	(1.6–2.4)	(0.8–1.4)	(3.2–4.5)
Interior B.C. Forests																		
IDF	($n = 9$)	14	11	28	2	1	0	2	2	0.1	0.1	0.3	0.0	0.3	0.1	0.3	0.6	1.7
		(0–55)	(1–24)	(6–64)	(0–6)	(0–3)	(0–0)	(0–3)	(0–3)	(0.0–0.7)	(0.0–0.4)	(0.1–0.5)	(0.0–0.2)	(0.0–1.4)	(0.0–0.3)	(0.0–0.8)	(0.0–1.1)	(0.2–3.7)
ICH	($n = 3$)	0	26	47	2	1	2	5	9	0.0	0.1	0.3	0.0	0.6	0.8	1.3	1.7	4.8
		(0–1)	(20–33)	(46–49)	(1–3)	(0–1)	(1–3)	(2–9)	(7–11)	(0.0–0.0)	(0.1–0.2)	(0.2–0.4)	(0.0–0.0)	(0.0–1.0)	(0.6–1.0)	(0.4–1.9)	(1.2–2.3)	(4.0–5.9)
ESSF	($n = 8$)	8	23	39	3	4	4	15	15	0.1	0.2	0.2	0.1	0.5	1.3	2.6	1.9	6.8
		(1–22)	(7–42)	(12–64)	(1–4)	(0–24)	(1–7)	(7–24)	(11–23)	(0.0–0.2)	(0.1–0.3)	(0.1–0.3)	(0.0–0.1)	(0.0–2.6)	(0.4–2.2)	(1.1–4.1)	(1.5–2.8)	(4.1–9.6)

Note: Decay classes are defined in Table 2, *n* = number of forest stands sampled. All data are for B.C. forests, except one plot in the IDF which was in Banff National Park, Alberta. Discrepancies between total masses and the sum of the individual decay and diameter class masses are due to rounding errors.

Fig. 3. The percentage of the total CWD mass in old-growth forests attributed to smaller diameter CWD in three different data sets. Data were calculated from the results of Anon. (1992) for the Kamloops Forest Region in B.C. (Anon.), Fischer (1981*a*, 1981*b*, 1981*c*) for Montana forests (Fischer) and data collected by the author in southern B.C. (Feller). Smaller diameter CWD was considered to range from 1.0 to 7.0 cm in the B.C. data sets, and 0.6 to 7.5 cm in the Montana dataset. Regression equations for the data sets (all significant at $P < 0.01$) are: Feller (——), % of total = 27.04 $(\text{MASS})^{-0.59}$, $R^2 = 0.87$, SE = 7.2; Anon. (- - -), % of total = 26.77 $(\text{MASS})^{-0.59}$, $R^2 = 0.88$, SE = 10.1; and Fischer (– –), % of total = 43.94 $(\text{MASS})^{-0.51}$, $R^2 = 0.86$, SE = 12.1.



determination from the photo given for each sampled forest, so Fig. 3 may include data from younger forests.

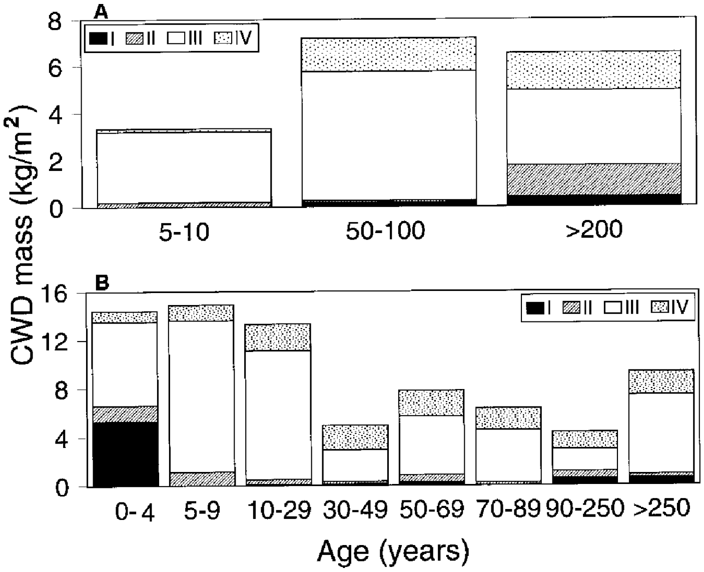
The decay class distribution of the CWD in old-growth forests assessed by the author (Table 3, Fig. 4) generally indicated greatest quantities in decay class III, followed by decay class IV, with the smallest quantities in either decay class I (MH, moist CWH, ICH) or II (some moist CWH, IDF). The dominance of decay class III is consistent with other studies that have found greatest quantities in the intermediate decay classes (e.g., Harmon et al. 1986; Spies et al. 1988; Wells and Trofymow 1997; Jonsson 2000; Siitonen et al. 2000). The quantities of CWD in each decay class are a function of the state of decay of logs when they hit the ground and the residence time of woody debris in each decay class. Residence times have not been well studied. However, for the four decay classes of *Thuja plicata*, Daniels et al. (1997) found that residence times increased from <10 years for decay class I, by an order of magnitude for each successive decay class, exceeding 1000 years for decay class IV. Although Jonsson (2000) reported similar residence times for all decay classes, an increase in residence time with each class is consistent with the results of other studies (Harmon et al. 1986; Tyrell and Crow 1994*a*) and results in greatest amounts of CWD in an intermediate decay class (Harmon et al. 1986).

There is some evidence that the decay class distribution in old-growth forests differs from that in younger forests. Several studies have found a more even distribution of different decay classes in old growth, with younger forests having one or two decay classes of CWD absent, or almost so (Crites and Dale 1998; Siitonen et al. 2000; Spies et al. 1988; Tyrrell and Crow 1994*b*). However, this is not always the case (Wells and Trofymow 1997).

After an initial input of fresh CWD following a disturbance such as forest harvesting (Fig. 4*b*, age 0–4 years), there is a period of reduced CWD inputs resulting in a relative reduction in decay class I and (or) II CWD. This was found in B.C. for *Abies lasiocarpa – Picea engelmannii* forests of ages 5–10 and 50–100 years (Fig. 4*a*) and for *Tsuga heterophylla – Thuja plicata* forests of ages 5–29 and 70–89 years (Fig. 4*b*).

Total CWD mass found in studies by the author ranged from 0.2 to 29.6 kg/m^2 (Table 3) and quantities found in different biogeoclimatic zones were similar to those found by others working in

Fig. 4. Mass of CWD in different decay classes (I–IV) in two chronosequences of forests in B.C. (*a*) *Abies lasiocarpa – Picea engelmannii* forests in the ESSF zone (n = 3–6 per age class); (*b*) *Tsuga heterophylla – Thuja plicata* forests in the CWH zone (n = 11–31 per age class).



the same biogeoclimatic zones in B.C. and elsewhere (Table 4). Substantial quantities of CWD data have been obtained for some biogeoclimatic zones, such as the CWH, ICH, IDF, ESSF, and BWBS zones, but no mass data appear to be currently available for old-growth forests in the CDF, SBPS, and SWB zones (Table 4). Mass data are sparse for the BWBS, MH, PP, and SBS zones. Volume data appear to be absent for the CDF, PP, and SWB zones, and sparse for the MH, MS, and SBPS zones (Table 4). Considerably fewer CWD volume than mass data appear currently available (Table 4). Only 5 of the 56 studies reviewed in Table 4 contained both volume and mass data. Seven of these studies contained only volume data, and the remaining 44 studies contained mass data only. Interestingly, given the preponderance of forest fuel studies, the original data were mostly collected using the line intersect method (van Wagner 1968) and measured as volumes, which were then used to estimate CWD mass. A recent comprehensive survey of CWD in Oregon and Washington forests (Ohmann and Waddell 2002) gives both volume and mass data, based on over 16 000 field plots. The vegetation types used in this study, however, do not allow extrapolation to B.C. biogeoclimatic units.

Coarse woody debris masses reported in the literature have varied from 0 to 58 kg/m^2 with the greatest masses being found in CWH zone forests and the least in the PP and BWBS zone forests (Table 4). This can be partly explained by forest productivity. The mass of CWD in western Montana and northern Idaho forests has been shown to increase with forest productivity (Fig. 5), as also occurs in hardwood forests in northern central U.S.A. (Spetich et al. 1999). A similar relationship can be demonstrated for the 14 B.C. biogeoclimatic subzones for which data were available (Fig. 6*a*). The plotted linear regression line suggests that CWD mass will increase by an average of approximately 0.5 kg/m^2 for each 1-m increase in maximum SI. Again, because of the lack of data for B.C. (data are available for only 14 out of 92 forested biogeoclimatic subzones), the generality of this statement is still unknown. Although it might appear intuitively obvious that CWD mass should increase with forest tree productivity, the relationship is complicated by (1) differences in fire history, as CWD mass would be reduced by more frequent forest fires; (2) tree fall-down dynamics, as CWD mass would be reduced in forests whose dead trees decompose mostly as snags, rather than as CWD on the ground; and (3) rates

Table 4. Means and ranges (in parentheses) of mass and volume of CWD in some old-growth B.C. forest ecosystems, and similar ecosystems in the U.S., and Alberta.

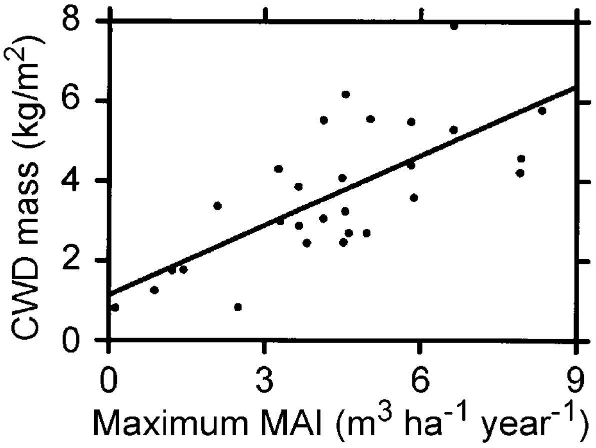
Biogeoclimatic zone/subzone	Number of studies	Number of plots studied	CWD volume (m^3/ha)	CWD mass (kg/m^2)
BWBS				
BWBSdk	1	11	54 (1–122)	—
BWBSmw	1	50	59 (0–151)	—
BWBSwk	1	4	59 (43–83)	—
BWBS?	4	135	—	1 (0–11)
BWBS	1	3	31 (2–52)	—
CDF	0	—	—	—
CWH				
CWHdm	1	30	179 (41–440)	—
CWHvh	1	15	750 (407–1487)	—
CWHvh	4	123	—	16 (8–21)
CWHvm	3	190	554 (13–1788)	—
CWHvm	3	31	—	19 (2–40)
CWHxm	1	4	119 (??)	—
CWHxm	2	7	—	5 (3–11)
CWH?	3	430	555 (527–603)	—
CWH?	10	439+	—	21 (2–58)
ESSF				
ESSFdc	1	6	—	3 (1–4)
ESSFdk	1	2	209 (135–282)	—
ESSFmv	1	15	74 (5–201)	—
ESSFwc	1	7	—	6 (4–7)
ESSFwk	1	35	145 (4–373)	—
ESSF?	3	16+	243 (30–430)	—
ESSF?	12	1278+	—	5 (0–25)
ICH				
ICHdw	1	2	165 (162–167)	—
ICHmc	1	151	115 (9–583)	—
ICHmw	1	42	348 (33–679)	—
ICHmw	2	8	—	5 (2–6)
ICHwc	1	3	399 (277–546)	—
ICHwk	1	3	327 (158–557)	—
ICH?	2	1+	407 (254–559)	—
ICH?	9	297+	—	8 (0–25)
IDF				
IDFdm	1	17	109 (32–428)	—
IDFdk	2	4	—	2 (1–3)
IDFdw	1	2	165 (162–167)	—
IDFmw	1	9	—	4 (1–6)
IDFxh	1	19	51 (23–110)	—
IDFxh	2	14	—	2 (0–5)
IDFxm	1	1	—	1 (–)
IDF?	2	2+	332 (155–478)	—
MH				
MHmm	1	34	140 (10–434)	—
MHmm	1	4	—	4 (3–5)
MH?	5	58+	—	3 (1–5)

Table 4. (*concluded*).

Biogeoclimatic zone/subzone	Number of studies	Number of plots studied	CWD volume (m^3/ha)	CWD mass (kg/m^2)
MS				
MSdk	1	30	102 (23–219)	—
MSdm	1	4	—	7 (3–10)
MSxk	1	10	—	2 (0–6)
MS?	1	1+	351 (??)	—
MS?	5	26	—	4 (0–8)
PP				
PPxh	1	6	—	1 (0–2)
PP?	6	21+	—	2 (0–4)
SBPS				
SBPSxc	1	16	105 (20–326)	—
SBS				
SBSdk	1	152	55 (2–473)	—
SBSdw	1	122	116 (0–468)	—
SBSmc	2	916	151 (2–661)	—
SBSmk	1	5	26 (7–36)	—
SBSvk	1	4	—	11 (8–16)
SBSwk	1	8	51 (21–101)	—
SWB	0	—	—	—

Note: ? indicates subzone is unknown; ?? indicates that only mean values were given; + indicates that number of plots was not always given. The above data were extracted from 56 studies.

Fig. 5. Mass of CWD as a function of maximum tree mean annual increment (MAI) for western Montana and northern Idaho forests in the equivalent of Interior Douglas-fir, Montane Spruce, Interior Cedar–Hemlock, and Engelmann Spruce–Subalpine Fir biogeoclimatic zones. Adapted from Fischer and Bradley (1987). The plotted linear regression line is MASS = 1.13 + 0.58 MAI, $R^2 = 0.51$, SE = 1.2, $P < 0.001$.



of decay that vary with species and environment, as CWD mass would be relatively lower in forests with greater rates of wood decomposition.

Coarse woody debris volume shows the same trend with SI as does CWD mass (Fig. 6*b*), with the regression line indicating that CWD volume will increase by an average of approximately 15 m^3/ha for

Fig. 6. Mass (*a*) and volume (*b*) of CWD as a function of maximum site index (SI) for zonal sites (index of forest productivity) for the B.C. biogeoclimatic subzones in Table 4, for which CWD mass and volume data are available. The plotted linear regression lines are: MASS = $-5.41 + 0.53(\mathrm{SI})$, $R^2 = 0.41$, SE = 4.3, $P = 0.01$; and VOLUME = $-150.7 + 14.7(\mathrm{SI})$, $R^2 = 0.49$, SE = 99.2, $P = 0.00$.

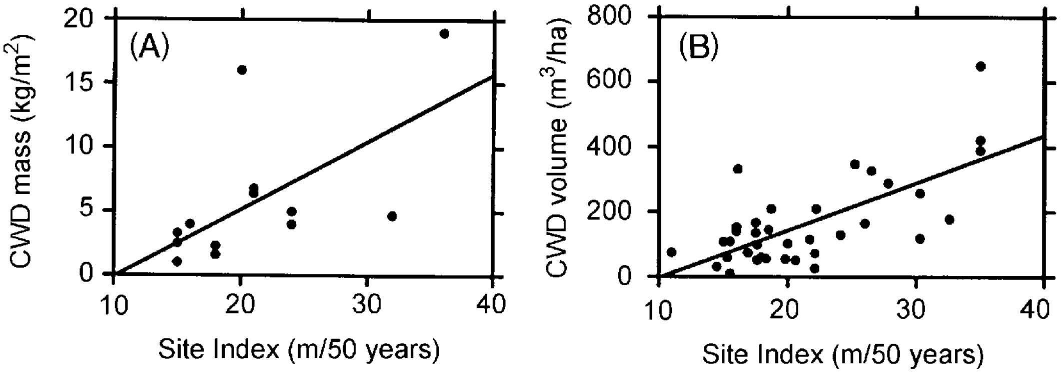
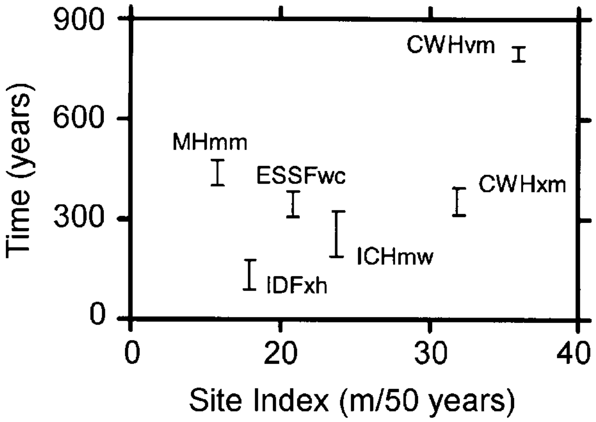


Fig. 7. The average time since death (n = 3–4) of decay class IV CWD in six forest ecosystems in B.C., plotted as a function of maximum SI (index of forest productivity) for the sites in which the CWD samples were collected.Vertical bars represent the range of uncertainty from the radiocarbon dating method used. Data are from Feller (1997).



each 1-m increase in maximum SI. The presence of data for 36 of the 92 B.C. forested biogeoclimatic subzones allows some confidence in the generality of this statement.

Coarse woody debris may persist on the ground for extended periods, which vary with ecosystem, microclimate, log size, and methods of measurement (cf. Stone et al. 1998). Radiocarbon dating of the date of death of trees contributing to decay class IV CWD (CWD in the most advanced state of decay), indicated ages of 70–1200 years for old-growth forests in six biogeoclimatic subzones in B.C. (Feller 1997). The length of time CWD remains on the ground does not appear to be as well related to forest productivity (SI) as are CWD mass and volume (Fig. 7). Climate, species, and fire history would all interact to determine CWD longevity, with decay-resistant species such as *Thuja plicata* and *Chamaecyparis nootkatensis* in moist environments with few fires (CWHvm and MHmm biogeoclimatic subzones, acronyms defined in Table 1) producing the longest surviving CWD.

Although many studies have quantified CWD decomposition rates (e.g., Caza 1993), very few studies have quantified CWD persistence, which may not always be related to decay rate. Studies elsewhere have found persistences varying from 35 to 45 years for *Pinus contorta*, *Abies lasiocarpa*, *Picea glauca*, and *Picea engelmannii* in south-western Alberta (Laiho and Prescott 1999) to >130 years for *Pseudotsuga menziesii* (Harmon et al. 1986), to 100–300 years for *Picea sitchensis* – *Tsuga heterophylla* in western Washington (Graham and Cromack 1982). It is unclear why the Albertan persistence times differ so much from the 300 to 400 years found by Feller (1997) for similar Engelmann spruce – Subalpine fir zone forests in B.C. However, the difference may be associated with differences in climate or in log size; e.g., Laiho and Prescott (1999) used only small logs of 15-cm diameter.

Coarse woody debris quantities may not always reach their maximum values in old-growth forests, and several trends in CWD quantity with forest age have been reported. Brown and See (1981) described different trends in CWD mass with forest age for each of three studies of *Pinus contorta* forests. One trend was a general increase with increasing age, peaking in old growth. Another was an inverse U-shaped curve, with maximum CWD mass occurring in mature (110–160 years old) forests. The third trend was a U-shaped curve with maximum values occurring in the youngest as well as the oldest forests. These same three trends were also found by Brown and See (1981) within four studies of *Abies lasiocarpa* forests, and similar variation occurs within other published studies. Of these trends, U-shaped curves, similar to those described by van Wagner (1983), have been found to be the most common in B.C. (e.g., Muraro 1971; Wells and Trofymow 1997; Clark et al. 1998), similar to results in the adjacent U.S. Pacific Northwest (e.g., Fahnestock 1976; Agee and Huff 1987; Spies et al. 1988). Support for the existence of U-shaped curves comes from other Canadian forests, including boreal conifer forests in Newfoundland (Sturtevant et al. 1997), aspen forests in Alberta (Lee et al. 1995), and from U.S. hardwood forests (Spetich et al. 1999). However, a boreal forest in Quebec exhibited a continuous increase in CWD with age (Hely et al. 2000). In timber-harvesting areas, CWD quantities, enhanced by logging slash, can be greater in young plantations than in old-growth forests (e.g., Wells and Trofymow 1997). The same result was found in a study of CWD in 126 forests within the Coastal Western Hemlock biogeoclimatic zone of B.C. (Fig. 4*b*) — the same zone in which Wells and Trofymow's study occurred.

A U-shaped curve results from an initial large input of CWD that follows a disturbance, such as forest harvesting or fire. Over time, this CWD decreases as decomposition occurs. Following the stem exclusion phase of tree growth, CWD inputs begin again, increasing as larger trees collapse in the old-growth phase. If the initial post-disturbance inputs are relatively low, as a result of a severe fire, slow collapse of snags, or low pre-disturbance tree biomass, CWD may not display a U-shaped curve with forest age. If tree mortality is particularly high during the mid-life period of a forest, as a result of high tree densities, insects, disease, or blowdown, then an inverse U-shaped curve may occur. Thus, the normal trend in CWD with forest age may be a U-shaped curve, with departures from this trend resulting from disturbance- or environment-specific factors.

Coarse woody debris may also change with time within old-growth forests, as they age. This has been poorly studied, but Spies et al. (1988) reported that CWD mass in *Pseudotsuga menziesii* forests in Washington and Oregon increased, then decreased from age 200 to 900 years. Spies et al. (1988) considered that a steady-state CWD mass might not be reached for >1000 years in their study forests.

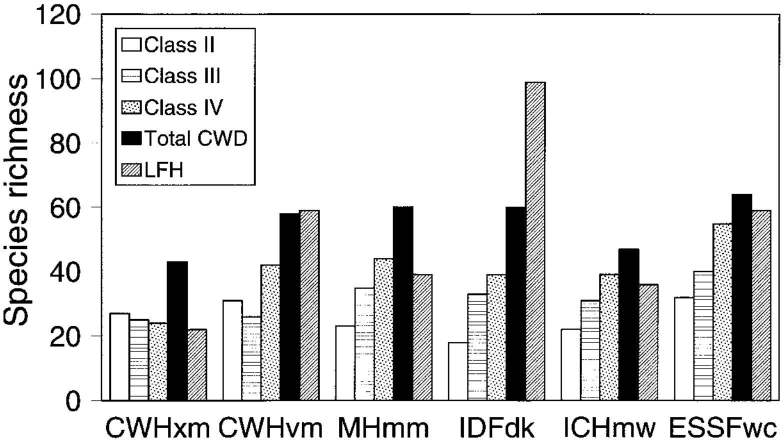
Functional importance of coarse woody debris

Within B.C. old-growth forests, studies have assessed the role of CWD as habitat for vegetation and small mammals and in N cycling and soil development. There appear to be no published quantitative data for B.C. on other functions of CWD, such as habitat for invertebrates and microorganisms (e.g., Harmon et al. 1986; Amaranthus et al. 1994; Berg et al. 1994; Torgersen and Bull 1995; Edmonds and Lebo 1998), or slope stabilization – soil erosion prevention (e.g., Harmon et al. 1986).

Habitat for vegetation

Coarse woody debris provides a substrate for a wide variety of plant species (e.g., Harmon et al. 1986; Caza 1993). Tree seedling establishment, particularly for species such as *Tsuga heterophylla*,

Fig. 8. Species richness of plants growing on the forest floor (LFH) and on different decay classes of CWD within old-growth forests in six biogeoclimatic subzones in B.C. Data are from Song (1997).



Thuja plicata, *Abies lasiocarpa*, and *Picea engelmannii*, has often been better on CWD than on the adjacent ground surface, for reasons such as reduced competition, higher moisture levels, or longer snow-free periods (e.g., Harmon et al. 1986; Harmon and Franklin 1989; Caza 1993). Coarse woody debris has been shown to be particularly important as a substrate for lichens and bryophytes outside B.C. (e.g., Harmon et al. 1986; Söderström 1988; Berg et al. 1994; Ohlson et al. 1997; Crites and Dale 1998; Kruys and Jonsson 1999), as well as within B.C. (e.g., Song 1997; Hong et al. 1999).

Song (1997) studied the influence of CWD on vegetation in old-growth forests in six B.C. biogeoclimatic subzones. The following was found:

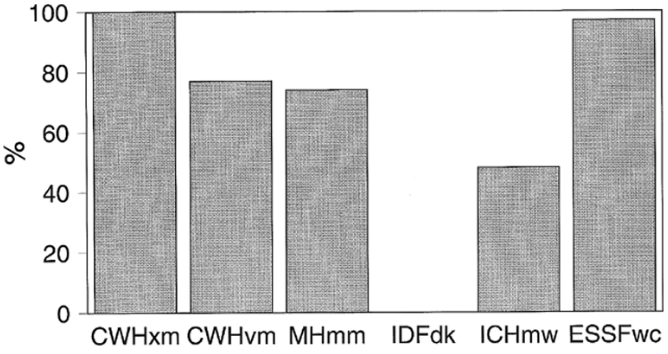
(1) species richness generally increased with increase in decay (Fig. 8), as found by other workers (e.g., Harmon et al. 1986; Crites and Dale 1998

(2) for four of the six biogeoclimatic subzones studied, >70% of all tree seedlings were growing on CWD (Fig. 9), the absence of seedlings on CWD in the Interior Douglas-fir (IDF) subzone being attributed to dessication of CWD in the open forests present during the hot dry summers characteristic of this subzone

(3) for all subzones combined, 70% of the 243 plant species recorded grew on CWD, with 23% of all species being restricted to CWD. For lichens, 95% of the 59 species recorded occurred on CWD, and 71% of all lichen species were restricted to CWD. For liverworts, 96% of the 28 species recorded occurred on CWD, and 25% of all liverwort species were restricted to CWD

Crites and Dale (1998) found that diversity and relative abundances of bryophytes and lichens on CWD in aspen–mixedwood forests in Alberta were greater in old growth than in younger forests. They found that 74% of the 96 nonvascular species present occurred in old forests, compared with only 56 and 51% in young and mature forests, respectively. Ten, 11, and 28 species were restricted to young, mature, and old forests, respectively. This was attributed to the greater diversity of CWD decay classes in the old-growth forests. In situations where younger forests, unlike old-growth forests, are missing one or more decay classes of CWD, the old-growth forests may then be very important in maintaining nonvascular plant diversity.

Fig. 9. The percentage of all tree seedlings present which were growing on CWD in old-growth forests in six biogeoclimatic subzones in B.C. Data are from Song (1997).



Habitat for animals

The importance of CWD as animal habitat has been noted for some time (e.g., Harmon et al. 1986). Thomas (1979), for example, reported that 57% of the vertebrate species breeding in the Blue Mountains of Eastern Washington and Oregon, used CWD. Recently, Keisker (2000) considered that 78 species of vertebrates in the SBS, ICH, and ESSF biogeoclimatic zones of North-Central B.C. used CWD. The abundance, size, state of decay, and spatial distribution of CWD are all factors affecting its use by wildlife (e.g., Harmon et al. 1986; Keisker 2000). Although much has been hypothesized about the value of CWD to animals (Maser et al. 1979; van Horne 1981), relatively few studies have quantified CWD and its influence on animals. Some of the studies that have quantified this influence have suggested that small mammal abundance, for example, is not always related to the quantity of CWD (Corn et al. 1988; Aubry et al. 1991). Work does suggest, however, that terrestrial vertebrates use CWD for cover, feeding, reproduction, resting, preening, bedding, lookout, drumming, sunning, roosting, hibernating, and travel corridors both in summer (on top) and in winter (gaps beneath the snowpack) (Harmon et al. 1986; Ruggiero et al. 1991; Sturtevant et al. 1996; Bull et al. 1997).

The importance of some of the CWD–wildlife relationships in B.C. has been recognized for some time (e.g., Sadoway 1986) but quantitative studies in B.C. have only been published since 1995. Bunnell and Kremsater (1990) provided a B.C. perspective on the importance of CWD to wildlife, considering that the nature of CWD in old-growth forests (heterogeneity, large size, state of decay) is a prime determinant of suitable habitat for a number of wildlife species that prefer old-growth forests. Dupuis et al. (1995) found three to six times more *Plethodon vehiculum* salamanders in old growth, than in younger forests in coastal B.C. This was attributed partly to CWD availability. Davis (1998) found two salamander species in coastal B.C. each used different decay classes of CWD. Old-growth forests, providing a range of decay classes, are more likely to provide suitable habitat for both species, than are single-aged managed forests. Keisker (2000) described the different attributes of CWD making it valuable to different wildlife species. Although considerable detail is given in Keisker's report, many of the relationships appear to be based on anecdotal observations and not on scientific studies. Apparently recognizing this, Keisker considered that research was required on the characteristics of CWD in different forests of different ages and on the effects of forest management on these characteristics. He considered research was also needed on the relationships between CWD characteristics and on the relationships between CWD characteristics and many different types of vertebrate users of CWD.

Craig (1995, 2002) has studied the influence of CWD on small mammal populations in several old-growth forest ecosystems. She concluded that CWD is an important habitat component that enhances populations of some, but not all, small mammal species in old-growth forests in the CWH, IDF, and ESSF biogeoclimatic zones. The influence of CWD on small mammals varied with mammal species, vegetative cover, and biogeoclimatic zone. For example, deer mice (*Peromyscus maniculatus*) populations displayed no trends with CWD volumes in an IDF forest or in an ESSF forest (Craig 2002). Red backed vole (*Clethrionomys gapperi*) populations, however, increased with CWD volumes at the IDF site, but displayed no trends at the ESSF site. This was attributed to the more abundant shrubs at the ESSF site, shrubs being considered to serve a similar role as CWD, with respect to cover (Craig 2002). The ability to detect the influence of CWD on small mammals, however, was scale dependent. Studies at fine spatial scales (i.e., movements of individuals) could sometimes indicate an influence when studies at larger scales did not. For example, in old-growth CWH zone forests, shrews tended to travel close to CWD pieces, but no relationship could be found between shrew density and CWD quantity on a per hectare basis (Craig 1995). In this case, CWD may be a preferred, but not necessarily critical, habitat component, or there may be some critical minimum level of CWD, not reached in Craig's work, below which shrew density declines.

Influence of coarse woody debris on nutrient cycling

Coarse woody debris has been considered to have beneficial effects on soil nutrients and forest productivity by providing a stable long-term source of nutrients (e.g., Caza 1993; Hagan and Grove 1999) and by enhancing soil N status, often as a result of N fixation occurring within the wood (e.g., Harmon et al. 1986; Harvey et al. 1989; Caza 1993). Jurgensen and coworkers have emphasized the importance of this fixation to the nutrient status of poor dry soils in the U.S. Intermountain region (e.g., Larsen et al. 1978, 1982; Jurgensen et al. 1984, 1987).

There is, however, some debate about the influence of CWD on soil nutrients and forest productivity. Thus, Heilman (1990) considered that CWD was generally not critical for sustained productivity of forests and Busse (1994) and Laiho and Prescott (1999) have found that CWD did not contribute significantly to nutrient cycling in *Pinus contorta* and *Abies lasiocarpa – Picea engelmannii* forests. Caza (1993) and Harmon et al. (1986) determined that the nutrients stored in CWD make up only a small percentage of the total ecosystem nutrients. The studies they reviewed, together with others in old-growth forests in the north-western U.S. (e.g., Grier et al. 1974; Turner and Singer 1976; Arthur and Fahey 1990) all suggest CWD contains <5% of the total ecosystem nutrient content for each nutrient, although it may contain up to 20% of the total biomass nutrient content. This is generally similar to the findings of Feller (1997) for two old-growth *Abies lasiocarpa – Picea engelmannii* ecosystems in B.C., although CWD contained 6–10% of the total biologically active S, Mg, and Ca in one of those ecosystems. The relevance of such measures must be tempered by uncertainties in accurately measuring biologically active quantities of nutrients.

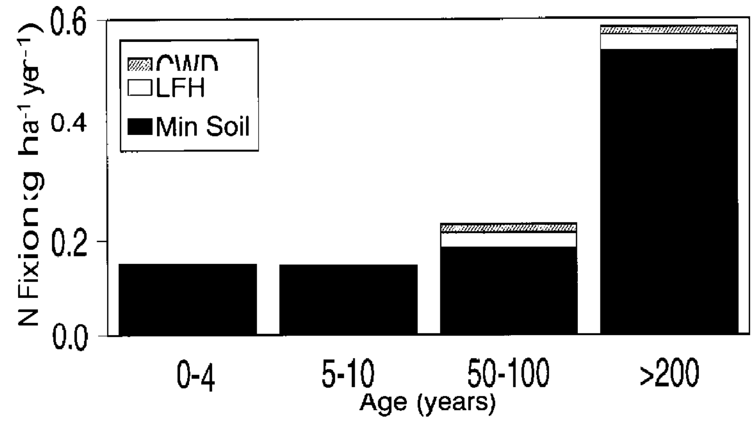
The significance of N fixation in CWD is also in question, as the quantities fixed have generally been low (e.g., Silvester et al. 1982; Jurgensen et al. 1984, 1987; Harmon et al. 1986; Hart 1999): <1 kg ha^{-1} year^{-1}. However, even low levels of N fixation can be important if fixation occurs for thousands of years (Jurgensen et al. 1984; Crawford et al. 1997), or if the N fixed becomes a source of readily available N for the decomposer organisms present (Griffiths et al. 1993), or if there are no other net inputs of N into the ecosystem (Feller 1997). Elevated levels of N fixation in CWD (>1 kg ha^{-1} year^{-1} for N) have also been found (e.g., Jurgensen et al. 1987).

There appear to be no published data for N fixation in B.C. old-growth forests. One of the author's studies indicates that N fixation is approximately three times greater in old-growth *Abies lasiocarpa – Picea engelmannii* forests than in younger age classes of forest, but only 2% of this fixation occurred in CWD (Fig. 10).

Influence of coarse woody debris on soil development

The value of CWD in supplying organic matter and associated microorganisms and nutrients to forest soils has been stressed by many workers (e.g., Harmon et al. 1986; Harvey et al. 1989; Caza 1993). However, it has been hypothesized that accumulations of CWD could lead to increased eluviation,

Fig. 10. Nitrogen fixation found by the author in different age classes of *Abies lasiocarpa – Picea engelmannii* forest in the ESSFwc biogeoclimatic subzone in B.C. CWD, coarse woody debris; LFH, forest floor; Min soil, mineral soil.



podzolization, acidification, and loss of soil nutrients (Klinka et al. 1995; Kayahara et al. 1996). Such concerns have only been expressed for B.C., and the U.S. Pacific Northwest (Caza 1993; Kayahara et al. 1996), possibly because more attention has been given to CWD in these forests, than in other forests. Recent studies on the influence of CWD on such soil development processes in old-growth forests in the CWH, MH, IDF, ICH, ESSF, BWBS, and SBS biogeoclimatic zones in B.C. (Kayahara et al. 1996; Kayahara 2000) suggest that CWD does not appear to enhance eluviation, acidification, or podzolization. Only slight, and not pedologically significant, differences between forest floor and CWD leachates were found. Some uncertainty still remains, however, as a several-year study cannot represent thousands of years of soil development.

Conclusions

(1) Recent studies continue to confirm the significance of CWD in old-growth forests: many plant and animal species depend on old-growth forests, at least partly because of the full array of CWD present in these forests.

(2) The characteristics of CWD in many B.C. old-growth forests can be moderately well described, particularly for forests in the CWH, IDF, ICH, ESSF, and BWBS biogeoclimatic zones, although this is partly due to extrapolation from U.S. studies.

(3) Very few studies provide both mass and volume data for CWD. Most studies describe mass, but not volume, of CWD. Published mass data appear to be lacking for CWD in old-growth forests in the CDF, SBPS, and SWB zones, and such data are sparse for the BWBS, MH, MS, PP, and SBS zones. Published CWD volume data appear to be lacking for the CDF, PP, and SWB zones and are sparse for the MH, MS, and SBPS zones.

(4) Quantification of the functional role of CWD in most B.C. old-growth forests is still in its infancy. There do not appear to be any published studies on the influence of CWD on invertebrates or soil–slope stabilization in these forests, and studies on the influences of CWD on other ecosystem components, such as vegetation, animals, nutrients, and soils, have only just begun.

(5) There is a need for future studies of the functional role of CWD to consider both scale and temporal issues. Studies at fine spatial scales (square metre) may better indicate CWD ecological functions,

than studies at larger (hectare) scales. Coarse woody debris function may change with time as a forest ages, with changes in the distribution of different CWD decay classes, for example. Very few CWD studies have addressed scale or temporal considerations.

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