Coarse Woody Debris in Douglas-Fir Forests of Western Oregon and Washington

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COARSE WOODY DEBRIS IN DOUGLAS-FIR FORESTS OF WESTERN OREGON AND WASHINGTON[1]

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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 yr 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 yr old, with moderate levels (92 Mg/ha) in stands <80 yr old, lowest levels (<50 Mg/ha) in stands 80–120 yr old, and highest levels (173 Mg/ha) in stands 400–500 yr old. After 500 yr 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 yr), 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 yr. 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 yr 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 yr. 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 yr, and that the nature and timing of disturbance play a key role in the dynamics of CWD in the region.

Key words: coarse woody debris; decay rate; fire; old-growth stands; Pacific Northwest; Pseudotsuga menziesii; *succession.*

INTRODUCTION

Coarse woody debris (CWD), a consequence of forest disturbance, is important in many ecological and physical processes in forest and stream ecosystems (Harmon et al. 1986). The amount, structure, and dynamics of CWD in forests can influence species composition, nutrient cycling, productivity, and geomorphology for centuries and millennia. Coarse woody debris can also affect the timing, spread, and severity of disturbances such as fire and insect outbreaks (Furniss and Carolin 1977, Agee and Huff 1987). Detailed descriptions of CWD structure and dynamics in a variety of forest and stream ecosystems are necessary to understand the role of CWD in ecosystem function, especially ecosystem response to disturbance, and to provide forest land managers with information useful in maintaining biological diversity and ecosystem productivity.

Unfortunately, studies of variation in the amount, structure, and dynamics of CWD as a function of forest type, succession, disturbance history, and decomposition are uncommon. The dynamics of CWD during succession have been investigated in a limited number of stands of wave-regenerated *Abies balsamea* (L. Mill) <80 yr old (Lambert et al. 1980, Lang 1985), northern hardwoods <150 yr old (Tritton 1980), and *Pinus contorta* Dougl. <550 yr old (Romme 1982, Fahey 1983). These studies indicate that amounts of CWD can be very high early in succession, low in mature forests, and somewhat greater in older forests. The generality of this pattern within and among forest landscapes has not been clearly demonstrated because of small sample sizes and a lack of studies of long forest seres. Simu-

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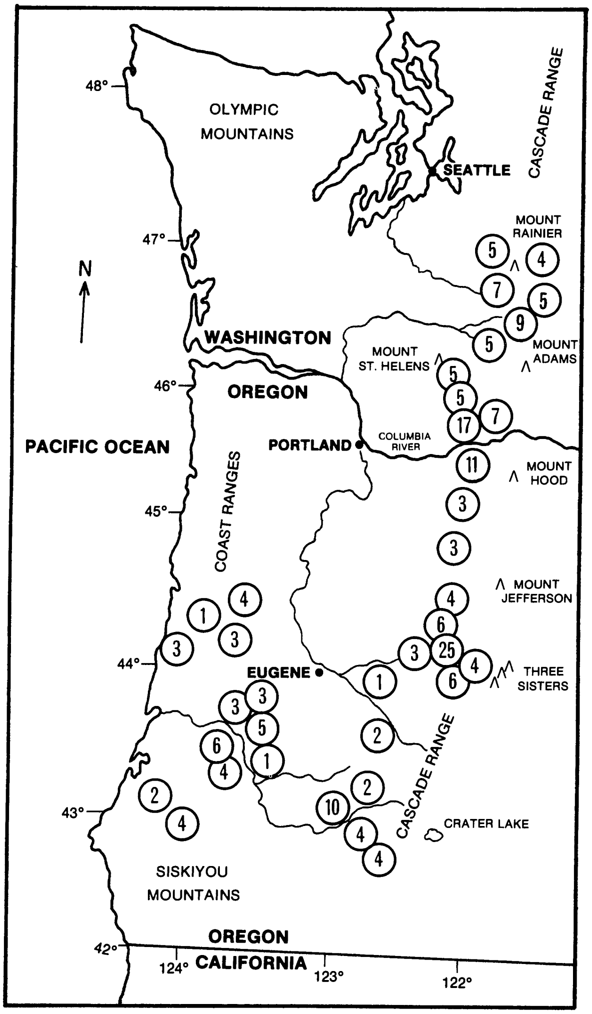

FIG. 1. Location of stands in western Oregon and Washington. Numbers indicate total number of stands at a location.

lation models (Lang 1985, Harmon et al. 1986) indicate that differences in disturbance history and stand development could lead to considerable variability across a region in the structure and accumulation of CWD.

Natural Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) forests of western Oregon and Washington provide an opportunity to study the effects of succession and disturbance on CWD over long chronosequences and a variety of sites. Stands 400–500 yr old are common, and stands up to 1000 yr old have been located. Amounts of CWD in old-growth forests can reach more than 200 Mg/ha (Franklin and Waring 1980), which is among the highest reported for temperate forest ecosystems (Harmon et al. 1986). The large sizes of tree boles and slow decay rates of CWD in these forests (Franklin and Waring 1980, Sollins 1982) suggest that CWD mass may remain high throughout succession, not showing the low accumulations that have been observed in the middle stages of succession in forests with smaller, more rapidly decaying wood. The very long seres of these forests also suggest that CWD accumulations may continue to increase for 800–1000 yr and persist at high levels for one or two more centuries. Despite the importance of CWD in the structure of Douglas-fir forests, few systematic studies have been done to determine the characteristics and accumulations of CWD across successional stages and site conditions. Data exist for old-growth stands in relatively few locations in the Cascade Range and Olympic Mountains (Grier and Logan 1977, Franklin and Waring 1980, Graham and Cromack 1982, Sollins 1982, Agee and Huff 1987).

Our study was part of a larger old-growth and wildlife-habitat research project (Ruggiero and Carey 1984), to characterize forest succession and wildlife habitat. We report here on the deadwood structure of Douglas-fir forests from youth to old age. Our specific objectives were (1) to characterize the amount and distribution of CWD in relation to stand age and site moisture conditions across three physiographic provinces in western Oregon and Washington, and (2) to characterize the dynamics of CWD using models based on data from a chronosequence of Douglas-fir stands.

STUDY AREA

The study was conducted in Douglas-fir-dominated forests in Washington and Oregon in three physiographic provinces: the southern Washington Cascade Range, the west Cascade Range in Oregon, and the southern half of the Coast Range of Oregon (Franklin and Dyrness 1973). These provinces are all characterized by steep, deeply dissected terrain with well-developed soil. Parent materials are Tertiary basalts and andesites in the Cascade Range and early Tertiary sedimentary rocks in the Coast Range. The climate is mild and wet in winter and cool and dry in summer. Annual precipitation is heavy, ranging from 800 to >3000 mm. Highest amounts of precipitation occur near the upper western slopes of the Coast Range and in the Cascade Range in Washington and northern Oregon (Franklin and Dyrness 1973). Lowest precipitation occurs on the eastern slopes of the Coast Range and in the southern Oregon Cascades.

The study area encompasses two major vegetation zones: the Western Hemlock (*Tsuga heterophylla* [Raf.] Sarg.) Zone and the lower elevational portion of the Pacific Silver Fir (*Abies amabilis* Dougl. ex Forbes) Zone (Franklin and Dyrness 1973). Western hemlock and Pacific silver fir are the climax species on most sites within these zones; on dry sites, Douglas-fir may be climax. In southern Oregon, the northern margin of the Mixed Conifer Zone was sampled. In the Coast Range, the eastern margin of the Sitka Spruce (*Picea sitchensis* [Bong.] Carr.) Zone was sampled.

Most Douglas-fir stands in the region originated after catastrophic wildfire (Franklin and Hemstrom 1981); see Franklin and Dyrness (1973) for a generalized, natural successional sequence. Young stands originating

TABLE 1. Descriptive statistics for site characteristics and ages of young (Y), mature (M), and old-growth (OG) stands for all stands and by province.

				Province								
	All stands			Washington Cascades			Oregon Cascades			Coast Range		
Characteristic	Y	M	OG	Y	M	OG	Y	M	OG	Y	M	OG
Number of stands	30	51	85	13	15	24	12	27	43	5	9	18
Elevation (m)												
$\bar{X}$	732	715	749	709	719	796	940	788	847	289	487	449
SE	56	36	28	51	51	45	73	47	32	62	88	43
Slope (%)												
$\bar{X}$	40	47	38	40	46	34	40	46	37	39	53	47
SE	3	3	2	4	4	4	5	4	3	11	5	4
Aspect*												
$\bar{X}$	1.1	0.8	0.9	1.2	0.9	1	1	0.6	1	0.8	1.1	0.8
SE	0.1	0.1	0.1	0.2	0.2	0.1	0.1	0.1	0.2	0.2	0.2	0.1
Topographic position†												
$\bar{X}$	2.9	2.9	2.6	2.9	3	2.3	2.7	2.7	2.6	3.1	3.3	3.1
SE	0.1	0.1	0.1	0.1	0.2	0.1	0.2	0.2	0.1	0.2	0.2	0.1
Age (yr)												
$\bar{X}$	65	121	404	65	131	434	68	123	417	60	100	331
SE	2	4	14	2	8	32	3	7	19	6	5	21
Min	40	80	200	42	80	250	43	84	200	40	80	200
Max	79	195	900	75	190	900	79	195	750	70	120	525

* Cosine transformation: northeast = 2.0, southwest = 0.

† 1 = valley bottom, 2 = lower ⅓ of slope, 3 = middle ⅓ of slope, 4 = upper ⅓ of slope.

from wildfires are typically densely stocked and dominated by Douglas-fir, although western hemlock or red alder (*Alnus rubra* Bong.) may dominate in some areas. By 200 yr many stands exhibit old-growth characteristics (Franklin et al. 1981, Franklin and Spies 1984), such as co-dominance of western hemlock in the overstory, diverse vertical foliage distribution, and large accumulations of woody debris. True climax forests are rare because pioneer Douglas-fir can persist in stands for >1000 yr, and wildfires occurred more frequently than this on most sites.

METHODS

General design

A total of 196 Douglas-fir stands in Washington and Oregon representing different ages (40–900 yr) and site conditions were sampled during 1983 and 1984 (Fig. 1). All stands originated after wildfires, which killed all or nearly all the overstory trees. The design was to sample along two gradients: (1) a chronosequence of Douglas-fir stands on sites with moderate moisture, and (2) a full range of site moisture conditions for old-growth Douglas-fir stands (≥200 yr old). Extremes of site moisture were not sampled for stands <200 yr of age to restrict and concentrate the sampling effort. Consequently, the results of the chronosequence analyses are based only on moderate sites (Table 1) (from young through old growth), and the results of the site moisture analyses were based only on old-growth stands. To maintain a similar geographic distribution among ages of sampled stands, sampling was typically centered in areas within each province that contained all three of the following broad age classes: young (<80 yr), mature (80–199 yr), and old growth (≥200 yr).

Site moisture classification

Stands older than 200 yr were classified in the field into three broad moisture classes—dry, moderate, and moist—based on observations of vegetation composition (Zobel et al. 1976, Franklin 1979), physiography, and soils. Dry sites occurred on steep upper slopes of southerly aspects, commonly with skeletal soils. Moderate sites were on deeper soils of mid to low topographic position, and moist sites occurred on lower northerly slopes, wet benches, and river terraces.

Stand selection and plot measurements

Stand size ranged from ≈4 to 20 ha. Within each stand, five nested circular plots were established systematically. In a few very small stands, only three or four plots were established. Plots were spaced either 100 or 150 m apart, depending on stand size, with the wider spacing used in large stands. The locations of the plots were determined before the field sampling by the size and shape of the stand as seen on aerial photographs.

Each set of nested plots consisted of a 0.05-ha plot for logs, a 0.1-ha plot for all snags (standing dead trees), and a 0.2-ha plot for snags >50 cm diameter at breast height (dbh) and >15 m tall. The plot for large snags was added in 1984 to obtain a better sample of large snags. Data on slope, aspect, topographic position, and shape of topographic cross section were collected from the 0.1-ha plot. Ages were determined for young and mature stands by increment coring at least one dominant Douglas-fir per plot at breast height, adding 5–7 yr for growth to breast height (depending upon site), and averaging the plot estimates to obtain an age estimate for the stand. For old-growth stands, age estimates were made from stumps in nearby clearcuts, along trails or roads, or sometimes, from increment cores on dominant trees. Data collected by Hemstrom (1979) were used to estimate ages of the stands in Mount Rainier National Park.

All logs >10 cm diameter (large end) that projected into the plot were measured. Data recorded included length (within the plot), horizontal diameter at both ends, species, and decay class using a five-class scheme developed for Douglas-fir logs (Fogel et al. 1973, modified by Sollins 1982). Class I logs are intact, not decayed, whereas class V logs appear as linear, moss-covered mounds on the forest floor and are flattened in cross section. The decay classification was used for all species, although it was developed for Douglas-fir, because no classification was available for the other species. Decayed logs of the major species, Douglas-fir, western hemlock, western redcedar (*Thuja plicata* Donn), and Pacific silver fir, could typically be distinguished by a combination of log size, ring width, wood structure, and structure of bark fragments.

All snags >0.1 m tall with upper diameters ≥10 cm (10 cm dbh for snags ≥1.4 m) were measured in the 0.1-ha plot and recorded by species, dbh, height, and decay class using the five-class system of Cline et al. (1980). In this system decay class I (least decayed) through class V (most decayed) are distinguished by characteristics of limbs, branches, height, bark remaining, and sapwood and heartwood condition. Snag heights were estimated visually after the heights of a few snags or trees on each plot were measured with a clinometer and tape.

Logs and snags were classified by origin in the preceding (prefire) or current stand. Classification of logs by origin was not done until the second field season, when it became apparent that it was possible to collect this information. Consequently, 79 stands of all ages in the Oregon and Washington Cascade Range lack this data. Stand origin was determined by considering the size, decay state, and species of the log or snag in comparison with live stems of the current stand. This was relatively easy for stands <200 yr but not possible in stands >250 yr. It was assumed that most logs or snags originating in the preceding stand were gone or had reached class V by 300–400 yr (Means et al. 1985), the age of most of the old growth. Consequently, we underestimated the CWD contributions from the preceding stand in our old-growth samples. The underestimation was probably negligible, however, because the biomass of decay class V material is relatively low, and the CWD from the preceding stand represents only a small portion of it.

Volume and biomass calculations

The volume and number of logs and snags and the projected area of logs (projected horizontal area calculated from log length and diameter) were computed by species and decay class for each plot in a stand. Volume was computed using the formula for a cone. Stand values were then calculated from the means of the plot values. Logs in decay classes I to IV were considered round in cross section. For decay class V logs, which are flattened in cross section, vertical diameters were estimated by multiplying the horizontal diameter by 0.439, a ratio determined from a sample of 20 logs (J. Means, *personal communication*). We estimated the upper diameters of snags using a taper value of 0.12 cm/dm, determined from diameters and lengths of class I–III logs.

Biomass of logs and snags was determined from density estimates for decay classes of Douglas-fir and western hemlock logs (P. Sollins, *personal communication*). The values used for Douglas-fir logs and snags were (density in grams of dry mass per cubic centimetre of green volume) I = 0.390, II = 0.369, III = 0.221, IV = 0.166, and V = 0.127. The values used for western hemlock logs and snags were I = 0.383, II = 0.319, III = 0.230, IV = 0.172, and V = 0.127 (estimated from Douglas-fir because decay class V is rarely encountered in western hemlock [Graham 1982]). The densities of the decay classes for all other species were estimated by multiplying the estimates of density of sound wood of the species (United States Department of Agriculture Forest Products Laboratory 1976) by the ratio of the density of sound wood for Douglas-fir to the density of the decay class for Douglas-fir.

Statistical analyses

The effects of age class, site moisture class, and province on amounts of CWD were evaluated by performing analysis of variance in an unbalanced design (Freund and Littell 1986) in SAS. Most CWD variables were transformed logarithmically to attain normality. *F* tests were performed in a split-plot design with province as the main "plot" factor and either age class or moisture class as the "subplot" factor. Where the overall *F* tests were significant, multiple comparisons of age class × province means were obtained with Tukey's Studentized range test in a completely randomized design. Because stands were not randomly selected and sample sizes were relatively small, statistical tests were conducted more to aid in interpreting the data than to perform strict hypothesis testing about larger populations of stands.

Additional analyses of the effects of site conditions were conducted by regressing CWD biomass on site characteristics and age. Stepwise regression analysis was used to select variables to include in the model ($\alpha \leq 15\%$). In this analysis all stands from the two Cascade provinces were combined to simplify the analysis and because the relationships of CWD mass to age and

TABLE 2. Volume (m³/ha) and biomass (Mg/ha) of logs and snags (standing dead) in young (Y), mature (M), and old-growth (OG) stands for all stands and by province. Sample sizes are as in Table 1.

Characteristic	All stands*			Province‖								
				Washington Cascades			Oregon Cascades			Coast Range		
	Y	M	OG	Y	M	OG	Y	M	OG	Y	M	OG
Volume (m³/ha)												
Logs												
$\bar{X}$	248†	148‡	313†	292^{ab}	146^{bcd}	319^{a}	272^{ab}	159^{bcd}	346^{ab}	77^{d}	121^{cd}	228^{abc}
SE	29	13	22	42	17	23	46	20	38	18	34	31
Snags												
$\bar{X}$	175†	101‡	221†	211^{ab}	102^{ab}	227^{a}	172^{ab}	100^{ab}	248^{ab}	86^{ab}	104^{b}	148^{ab}
SE	24	10	18	39	16	25	40	14	30	19	30	31
Total												
$\bar{X}$	423†	250‡	534†	502^{ab}	248^{bc}	544^{a}	445^{ab}	259^{c}	594^{a}	163^{c}	225^{c}	379^{abc}
SE	51	21	33	74	29	36	85	30	55	25	64	53
Biomass (Mg/ha)												
Logs												
$\bar{X}$	43†	20‡	66§	52^{abc}	28^{cde}	63^{a}	47^{abcd}	32^{bcde}	73^{ab}	14^{e}	25^{de}	54^{abc}
SE	5	3	5	8	3	4	8	4	8	3	8	9
Snags												
$\bar{X}$	35†	23†	57‡	40^{ab}	24^{ab}	58^{a}	36^{ab}	23^{ab}	63^{ab}	19^{b}	21^{b}	41^{ab}
SE	5	2	5	8	3	8	8	3	8	3	4	10
Total												
$\bar{X}$	78†	52‡	123§	92^{ab}	52^{bcd}	121^{a}	83^{abc}	54^{bcd}	136^{a}	32^{d}	46^{c}	95^{ab}
SE	9	4	8	14	6	10	15	6	13	4	12	15

* Means of age classes with the same symbol are not significantly different at $P = .05$ (Tukey's Studentized Range Test).

‖ Means of the province × age class combinations with the same letter are not significantly different at $P = .05$ (Tukey's Studentized Range Test).

site characteristics were similar in the two provinces. Stands were divided into those 50–150 yr old and those 151–549 yr old. These divisions were made for two reasons. First, 150 yr represented a low point and break in the scatter of CWD biomass vs. stand age; and second, the age ranges gave approximately linear scatters of the ln (CWD) vs. age. In addition, stands <150 yr old developed after settlement of the region by Europeans, and therefore may have had a different fire history than older stands. The entire data set (including all old-growth stands) was used in the regression analysis except for three stands <50 yr old that had snag felling and perhaps some salvaging.

The decay rate (k) of snags and logs was estimated by fitting a line to the mass of CWD originating in the previous stand and assuming a simple exponential decay model (Olson 1963), which appears to fit decomposition of Douglas-fir boles as well as more complicated exponential models (Means et al. 1985).

RESULTS

Structure of coarse woody debris

Volume and biomass by age class and province.— For all provinces combined, the volume and biomass of CWD were highest in old growth, intermediate in young growth, and lowest in mature age classes (Table 2). This pattern also occurred for logs and snags separately. The proportions of the total volume and biomass in snags was ≈41 and 44%, respectively, for all three age classes.

The Washington and Oregon Cascade Range had similar amounts of CWD for all three age classes (Table 2). Some of the lowest amounts of CWD biomass in old growth ($\bar{X}$ = 74 Mg/ha) occurred in six stands on moderate sites from the southernmost part of the study area in the Cascade Range in Oregon.

Coast Range stands had less CWD in all three age classes than did stands in the two Cascade Provinces, although the differences were significant only for young stands (Table 2). Mass and volume in young stands in the Coast Range were <40% of the values in young stands in the other two provinces. Amounts of woody debris in mature stands were only slightly lower in the Coast Range, however. Total biomass in old-growth stands in the Coast Range was 70 and 78% of the biomass in old-growth stands in the Cascade Range of Oregon and Washington, respectively.

Size and number of logs by age class and province.— The number and diameter of logs in a given forest age class depended on the size of logs considered. The number of logs of all sizes was greatest in young stands and similar between old-growth and mature stands (Table 3). The number of small logs (<30 cm in diameter) in young and mature stands was >1.5 times as high as in old-growth stands; however, old-growth stands had twice as many large logs (>60 cm in diameter) as mature stands and slightly more large logs than the young stands.

The total number of logs per hectare in the three age classes was similar in the two Cascade provinces. Stands

TABLE 3. Number of logs per hectare by size class and projected area (m^2/ha) of logs in young (Y), mature (M), and old growth (OG) for all stands and by province. Sample sizes are the same as Table 1.

Characteristic	All stands*			Province‖								
				Washington Cascades			Oregon Cascades			Coast Range		
	Y	M	OG	Y	M	OG	Y	M	OG	Y	M	OG
Number of logs												
<30 cm diameter												
$\bar{X}$	370†	308†	193‡	456^{a}	353^{abc}	213^{bcd}	358^{ab}	279^{abcd}	191^{bcd}	174^{cd}	321^{abcd}	170^{d}
SE	36	26	13	54	53	26	53	32	18	34	75	23
30–60 cm diameter												
$\bar{X}$	177†	112†	164‡	194^{ab}	133^{abc}	208^{a}	192^{ab}	103^{bc}	161^{abc}	96^{bc}	102^{c}	112^{bc}
SE	19	10	11	36	20	13	25	13	16	18	29	21
>60 cm diameter												
$\bar{X}$	53†‡	28†	59‡	64^{abc}	23^{bc}	66^{c}	55^{abc}	31^{abc}	64^{ab}	18^{abc}	25^{c}	36^{abc}
SE	8	3	4	14	5	8	14	4	7	4	12	5
All sizes												
$\bar{X}$	600‡	447†	415†	714^{a}	509^{abc}	487^{abc}	605^{ab}	413^{bc}	417^{bc}	289^{c}	449^{bc}	317^{c}
SE	50	34	21	72	65	35	74	45	30	37	92	37
Projected cover area (m^2/ha)												
$\bar{X}$	979†	649‡	933†	1136^{a}	715^{abc}	1060^{ab}	1056^{ab}	655^{bc}	996^{ab}	387^{c}	521^{c}	615^{bc}
SE	89	50	48	122	79	57	134	75	79	57	119	63

* Means of age classes with the same symbol are not significant at $P = .05$ (Tukey's Studentized Range Test).

‖ Means of the province × age class combinations with the same letter are not significant at $P = .05$ (Tukey's Studentized Range Test).

in Washington had the highest absolute number of logs in all age classes, although those stands were significantly different only from young stands in the Coast Range (Table 3). The number of logs per hectare in young stands in the Coast Range averaged only ≈40 and 48% of the numbers in young stands in the Cascade Range of Washington and Oregon, respectively. Old-growth stands in the Coast Range had ≈65 and 76% of the number of logs found in old growth in Washington and Oregon.

Projected cover of logs by age class and province.—The projected area covered by logs was relatively high in young and old-growth stands (9.8 and 9.3% of the area) and low in mature stands (6.5%) (Table 3). Stands in southern Washington had slightly higher coverage of logs in all three age classes than did stands in the Oregon Cascades. The stands in the Coast Range had lower coverage of logs than did either of the other two provinces.

Size and number of snags by age class and province.—The mean diameter of snags in old-growth stands was 55 cm, whereas the mean diameter in young and mature stands was only 33 and 32 cm, respectively (Table 4). The mean snag diameter by age class also varied by province.

The density of snags of all sizes was much higher in young stands than in mature or old-growth stands. This pattern was also evident for snags >5 m tall and for snags <50 cm dbh. This was not true, however, for large snags (>50 cm dbh and >5 m tall, and >50 cm dbh and >15 m tall), which were most numerous in old-growth stands, intermediate in young stands, and lowest in mature stands (Table 4). Stands in southern Washington had the highest densities of snags for most age and size classes, although the differences were not significant. Snags in the largest size class (>50 cm dbh and >15 m tall), which are the most important snags for cavity-nesting birds (Mannan et al. 1980), were twice as common in the Washington Cascades (8 snags/ha) as in the Coast Range stands (4 snags/ha), and were intermediate in the Oregon Cascades (6 snags/ha). Old-growth stands in all three provinces had at least twice as many snags in the largest size class as were found in young and mature stands.

Distribution of CWD among decay classes by age class and province.—The distribution of total biomass of woody debris by decay class differed among age classes but was similar across provinces (Fig. 2). In general, the proportion of total biomass in highly decayed material (decay classes IV and V) was highest in young stands and lowest in old growth. The percentage of the total biomass in decay class IV and V was significantly different among the age classes ($P < .0001$), with young stands averaging 59%, mature stands averaging 37%, and old-growth stands averaging 27%. The distribution of woody debris in young stands was concentrated in decay classes III, IV, and V. In mature stands, woody debris was more evenly distributed among decay classes II through V, with a higher proportion of total CWD biomass attributed to decay class II. In old-growth stands, woody debris was concentrated in decay classes II and III.

The relatively high proportion of total CWD biomass attributed to snags in decay classes I and II reflected the fact that trees in the region typically die standing (J. F. Franklin, *personal observation*) and de-

TABLE 4. Number of snags (standing dead) per hectare by size class and mean dbh (cm) of snags in young (Y), mature (M), and old growth (OG) for all stands and by province. Sample sizes are the same as Table 1.

Charac-				Province‖								
	All stands*			Washington Cascades			Oregon Cascades			Coast Range		
teristic	Y	M	OG	Y	M	OG	Y	M	OG	Y	M	OG
Number of snags												
<50 cm dbh												
$\bar{X}$	145†	105†	32‡	133^{a}	118^{a}	37^{bc}	175^{a}	94^{ab}	34^{c}	102^{a}	115^{a}	23^{c}
SE	19	12	3	19	17	5	40	15	4	22	45	3
≥50 cm dbh												
$\bar{X}$	27†	16‡	27†	30^{ab}	17^{ab}	36^{a}	26^{ab}	15^{b}	26^{ab}	18^{ab}	17^{b}	17^{ab}
SE	3	2	2	4	2	3	4	2	3	4	6	3
>5 m tall												
$\bar{X}$	108†	73‡	30§	103^{a}	77^{ab}	34^{bcd}	127^{a}	68^{abc}	32^{cd}	72^{ab}	80^{abc}	22^{d}
SE	15	9	2	15	11	3	34	12	3	17	30	2
>50 cm dbh and >5 m tall												
$\bar{X}$	10†	8†	14‡	14^{ab}	8^{ab}	18^{a}	7^{bc}	7^{abc}	14^{ab}	4^{c}	7^{bc}	10^{ab}
SE	2	1	1	2	1	2	2	1	2	2	3	2
>50 cm dbh and >15 m tall												
$\bar{X}$	2.8†	2.5†	6.4‡	4^{abc}	3.5^{bcd}	8.3^{a}	2.5^{cd}	2.4^{bcd}	6.3^{ab}	0.6^{d}	1.1^{cd}	4.2^{abc}
SE	0.6	0.5	0.5	1	1.1	0.9	1.1	0.5	0.5	0.4	0.6	1
All sizes												
$\bar{X}$	171†	121‡	60§	164^{a}	135^{ab}	73^{bcd}	201^{a}	109^{abc}	60^{cd}	120^{ab}	132^{abc}	41^{d}
SE	19	13	3	19	19	6	40	17	5	24	43	4
Diameter at breast height												
$\bar{X}$	33†	32†	55‡	33^{c}	30^{c}	57^{a}	34^{c}	32^{c}	56^{a}	30^{c}	37^{bc}	51^{ab}
SE	2	2	2	3	1	3	5	2	3	3	6	3

* Means of age classes with the same symbol are not significant at $P = .05$ (Tukey's Studentized Range Test).

‖ Means of the province × age class combinations with the same letter are not significant at $P = .05$ (Tukey's Studentized Range Test).

cay before falling to the forest floor. The proportion of total CWD biomass attributed to logs was higher in decay classes IV and V. In decay classes I and II, logs constituted only 38% of the CWD for all age classes combined, but in decay classes IV and V, 74% of the CWD was composed of logs.

Biomass of CWD in old-growth stands by moisture class and province.—Total CWD in old-growth stands, grouped by province, exhibited a wide range in biomass (21–369 Mg/ha), and differed significantly among site moisture classes ($P < .001$). Dry sites had the lowest CWD biomass, while moist sites had the highest (Fig. 3). Moderate sites were not significantly different from moist sites ($P > .001$), although the lack of statistical significance may be due to the high variability in stands on moist sites and relatively low sample sizes. The highest average biomass of CWD (218 Mg/ha) was in stands on moist sites in Washington (Fig. 3), primarily because of four stands on terraces of the Carbon and Nisqually Rivers that had amounts ranging from 263 to 339 Mg/ha. The relative differences in CWD biomass among the site classes were the same in all three provinces (Fig. 3).

The differences in mass of CWD among the site moisture classes was apparently not a result of differences in age among the moisture classes. In the two Cascade provinces combined, ages of stands on dry sites averaged 314 yr, on moderate sites 442 yr, and on moist sites averaged 480 yr. When similar-aged stands were compared, differences in CWD still existed among the moisture classes. For stands 300–400 yr old in the two Cascade provinces, CWD averaged 92 Mg/ha (SE = 18, $n = 5$) on dry sites, 115 Mg/ha (SE = 12, $n = 11$) on moderate sites, and 166 Mg/ha (SE = 45, $n = 3$) on moist sites. The results were similar in the Coast Range stands.

Little difference in the relative proportions of mass of snags and logs was found among the moisture classes for old-growth stands. The proportion of total CWD mass in logs averaged 54-58% across the moisture gradient. The highest proportion of biomass in logs, 63%, occurred in stands on moist sites in the Washington Cascades which were some of the wettest in the study.

Dynamics of CWD

Age and site relations.—The relation of total CWD biomass to stand age was more evident when biomass was plotted against a finer division of age classes (Fig. 4). Total CWD in the Cascades (Washington and Oregon combined) was moderately high in stands 60–80 yr old, dropped to a minimum in stands 80–120 yr old, gradually rose to a maximum in stands 400–600 yr old, and declined thereafter (Fig. 4A). In the Coast Range, stands 60–80 yr old had much less CWD biomass (32 Mg/ha) than in similar age stands in the Cascades, but the pattern of accumulation in older stands

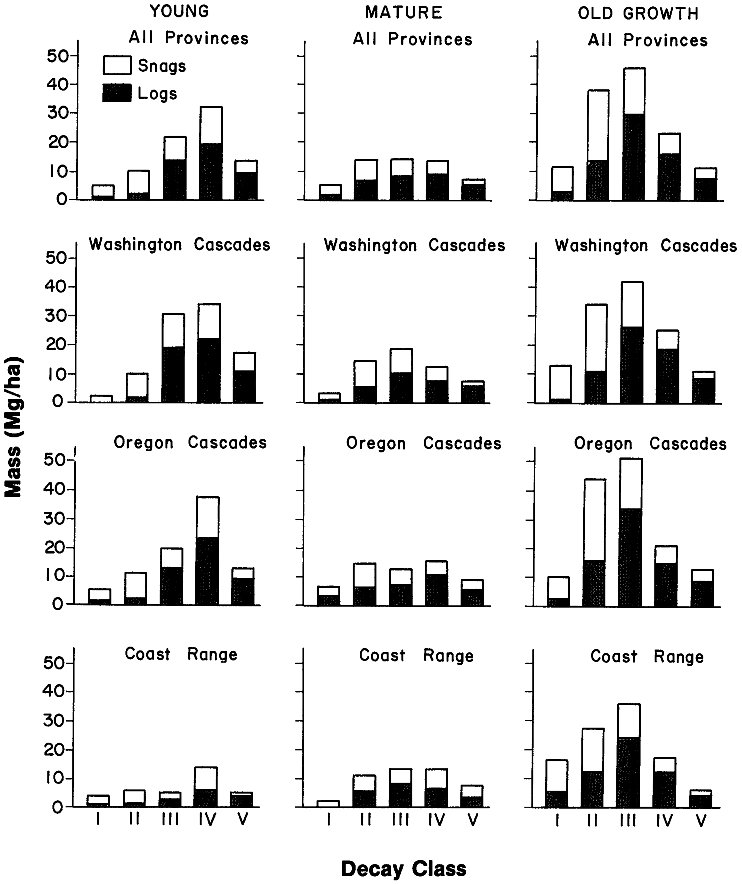

FIG. 2. Distribution of total mass of CWD among wood decay classes by age class and location. Decay classes represent a gradient from slightly decayed (class I) through well decayed (class V).

was the same as in the Cascades. Similar relations of biomass to stand age occurred for both snags and logs (Figs. 4B, C).

Although the mean trend of CWD biomass in relation to stand age was distinct, the high variability among stands weakened any predictive models based on age alone. Including site variables in the regression models improved the ability of the models to account for variation in amount of CWD (Table 5). Age was generally a poor predictor of CWD biomass for stands younger than 150 yr in both the Cascades and Coast Range (Table 5). For Coast Range stands, aspect and topographic position alone accounted for 63% of the variance in CWD biomass. In the Cascade Range, age and site variables accounted for only 23% of the variation in CWD biomass in stands <150 yr old.

Age explained a greater proportion of the variation in amount of CWD for stands 150–550 yr of age than for younger stands (Table 5). As with the younger stands, age was less correlated with CWD biomass in the Coast Range than in the Cascade Range, and aspect was a more important variable in the Coast Range models than in the Cascade Range models.

Coarse woody debris from previous stand.—Coarse woody debris originates from two sources, the previous (predisturbance) stand and the current stand. The relative contributions of these two components to the total CWD pool differed with stand age. The amounts of CWD originating in the previous stand were highest in young stands and declined to very low values by age 250 (Fig. 5A). In stands 60–80 yr old in the Cascades, CWD from the previous stand averaged ≈76% of the total CWD. For stands 120–160 yr of age, CWD from the previous stand was only 39% of the total. The pattern in the Coast Range was not the same (Fig. 5A); coarse woody debris from the previous stand constituted only 58% of the total for stands 60–80 yr old.

The decay rate (k) of snags and logs in the Cascades was estimated, based on the amount of CWD originating in the preceding stand for stands ≤ 200 yr of age on moderate sites ($n = 34$). The least squares solution for a single exponential model was $k = 0.029$ ($P < .001$, $R^2 = 0.64$). Examination of the residual plots indicated a reasonable fit for this model. In contrast, the residual plots of a linear model ($R^2 = 0.43$, $P < .001$) indicated a poorer fit and underestimate of CWD for stands >140 yr.

The intercept of the decay model was 432 Mg/ha (SE

= 1.5 Mg/ha), which was an estimate of the amount of CWD present on sites in the Cascade Range when the current stand began. This was somewhat lower than expected for the amount of CWD immediately following a catastrophic wildfire in an old-growth stand in which very little of the tree stem biomass would be consumed by the fire (Huff 1984, Harmon et al. 1986). The live biomass estimates of Grier and Logan (1977) indicate that CWD accumulations of 600–1000 Mg/ha would be found shortly after a catastrophic wildfire, including 100 Mg/ha of prefire CWD. The lower value in our analysis may have been a result of the difference between estimated stand age and the time since the destruction of the old-growth stand. Evidence shows that delays of >100 yr can occur between an initial fire and the time of complete establishment of the postfire stand (Hemstrom 1979, Franklin and Hemstrom 1981, Huff 1984). If we assume that our estimate of stand age approximated the most frequent tree age in a stand, then the fire and first establishment of trees could have occurred at least 20 yr before. If we assume a 20-yr lag in tree establishment, then the decay model yields an intercept of 772 Mg/ha, which is more in line with predictions based on estimates of live-stem biomass in old-growth stands.

CWD from current stand.—The accumulation of CWD from the current stand was similar for both the Cascade and Coast Ranges (Fig. 5B). In the Cascades, the accumulation was <25 Mg/ha for stands younger than 100 yr of age but rose steeply to >170 Mg/ha for stands 400–500 yr of age. This represents an average annual accumulation rate of 0.41 Mg/ha. The average annual accumulation rate for the Coast Range stands was 0.32 Mg/ha for stands 50–500 yr old. The difference between the two areas was not significant ($P >$ .05). After 500 yr, CWD derived from the current stand in the Cascades declined to about 120 Mg/ha for stands 600–800 yr old and may decline even further by age 900, although this last value is based on only one stand.

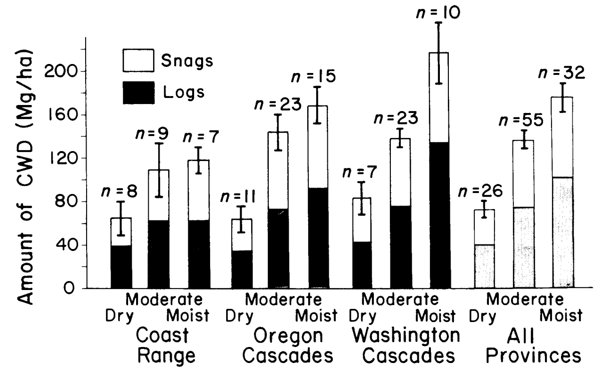

FIG. 3. Distribution of mass of total CWD among site moisture classes, by province. Narrow vertical bars represent standard errors of mean total CWD.

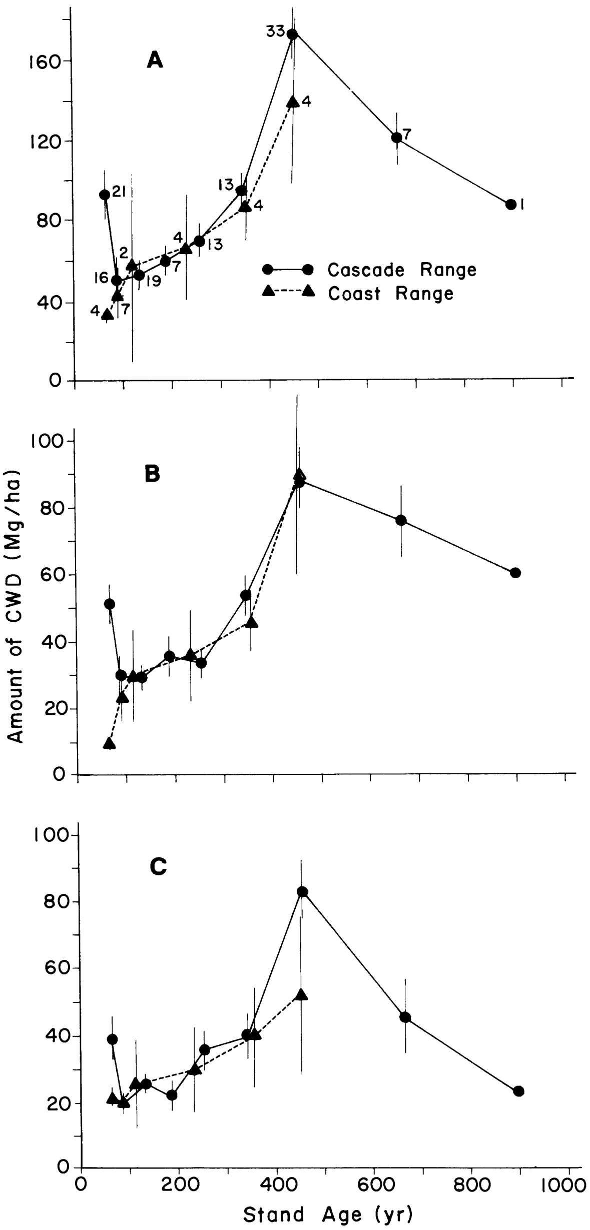

FIG. 4. Mass of total CWD (A), logs (B), and snags (standing dead, C) in a chronosequence of *Pseudotsuga* stands in the western Cascade Range and in the southern Coast Range. Data points are plotted at age class means. Numbers in A indicate sample size, and vertical bars represent standard errors.

DISCUSSION

Structure of CWD in Douglas-fir stands

Accumulations of CWD in old-growth Douglas-fir forests of the Pacific Northwest are among the highest reported for forest ecosystems (Harmon et al. 1986). Even mature stands, in which CWD accumulations typically are lowest, had higher amounts of CWD than have been reported for many deciduous forests. The

TABLE 5. Best variables and coefficients of determination from stepwise multiple regression of total coarse woody debris mass (ln transformed) on stand age and site variables by location and age class. Values in parentheses are signs of the regression coefficients and partial R^2s. All regressions significant at $P < .005$.

Location and age class	R^2 (adjusted)	Independent variables*
Cascades		
50–150 yr	0.23	Age (−) (0.09), slope (−) (0.08), aspect (+) (0.07), vertical shape (+) (0.04)
151–549 yr	0.54	Age (+) (0.48), slope (−) (0.06)
Coast Range		
50–150 yr	0.63	Aspect (+) (0.53), topographic position (+) (0.15)
151–549 yr	0.47	Age (+) (0.21), aspect (+) (0.15), latitude (−) (0.12), slope (−) (0.07)

* Only those variables that increased the overall R^2 by ≥0.04 are shown.

volume and mass estimates of CWD in old-growth and mature stands were within the ranges reported in other studies of Douglas-fir stands in the Cascades and Coast Ranges, in which different methods were used (Grier and Logan 1977, Franklin and Waring 1980, Sollins 1982, Harmon et al. 1986).

The projected cover of logs (6–10%) was less than the 12–20% that has been reported for mature and old-growth Douglas-fir forests in the Cascade Range (Harmon et al. 1986). Our lower values may result in part from sampling a wider range of sites and stand ages in our mature and old-growth classes than was done previously, or from not sampling some class V logs that were buried in the forest floor. Our values were still much higher than the projected areas of 1–2% reported for pine and temperate deciduous forests (Harmon et al. 1986).

The snag sizes and numbers agreed well with other studies in the region. For old-growth stands in the Cascade Range, Franklin et al. (1981) reported a mean dbh of 57 cm for snags >4.4 m tall and a mean density of 32 snags/ha, which are values nearly identical to our estimates. For old-growth stands in the Coast Range, Cline et al. (1980) reported a mean snag density of 18 snags/ha for snags >4.4 m tall, which is close to our estimate of 22 snags/ha for snags >5 m tall.

The biomass distributions among decay classes generally fit a model in which the residence times in each decay class increase geometrically. Under steady-state conditions with respect to decay classes, this model results in the intermediate-aged classes having the most biomass (Harmon et al. 1986). Deviations from this steady-state distribution were apparent in young stands where a high proportion of total CWD biomass was in decay classes IV and V. This distribution is evidence of catastrophes that killed the previous stands and converted live trees into large quantities of CWD that is now well decayed. Lambert et al. (1980) observed a similar high proportion of well-decayed CWD in *Abies balsamea* stands >30 yr of age that originated after a wave of mortality.

Differences in biomass of CWD along the site moisture gradient probably resulted from a complex of factors. Moist sites had highest amounts of CWD, probably because these sites produce more live biomass and larger tree boles; have wetter, more slowly decaying wood; have higher mortality rates (J. F. Franklin, *personal observation*); are less subject to surface fires that can consume CWD; and collect CWD from upper slopes because of their typically concave topography and low topographic position. There may also be feedback from accumulations of CWD to production of CWD because moist, well-decayed logs can serve as a primary site of mycorrhizal activity during dry periods (Harvey et al. 1976, 1979), thereby increasing wood production. Productive sites with large amounts of CWD may owe some of their productivity to the large biomass of CWD in the forest floor and soil, while unproductive sites with high moisture stress may be below their potential productivity because of low amounts of CWD.

Decay rate

Several models of decomposition in CWD have been proposed, including linear, single-exponential, multiple-exponential, and lag-time (Harmon et al. 1986). Using the chronosequence data of CWD from the preceding stand, we could compare the fit of the first two models but not the last two, because the data could not be divided into components and stands <40 yr old were not sampled. The reasonable fit of the single exponential model follows similar findings by Means et al. (1985), whose models concerned loss of mass from respiration and leaching. Our data, however, also include loss from fragmentation. This would explain why their decay rate constants (k) were lower, about 0.007 yr^{-1}, in contrast to our estimate of $k = 0.029\ \mathrm{yr}^{-1}$. Sollins (1982) estimated a nearly identical decay rate constant of $k = 0.028\ \mathrm{yr}^{-1}$, including both respiration and fragmentation, from a 30-yr record of mortality in an old-growth Douglas-fir forest in the Cascades of southern Washington.

Influence of disturbance on accumulation of CWD

The poor relationship between stand age and CWD biomass for stands <150 yr old illustrates the importance of disturbance history in the dynamics of CWD during forest succession. Because most CWD in young stands is carry over from the previous stand, time since last disturbance and amount of input at the time of the disturbance are more closely related to total CWD biomass than stand age. The importance of site characteristics in the Coast Range in explaining variation in CWD in relatively young stands suggests that fire history, as affected by topography, controlled the amounts of CWD in stands <150 yr old. Fire has been extensive and frequent in the last 150 yr in the Coast Range (Juday 1976). It is probable that stands on north-facing slopes and moist sites experienced less severe and frequent fire than drier sites. Consequently young stands on more protected sites probably inherited more CWD than fire-prone sites because they were preceded by older, more massive stands rather than young stands or mixed-age stands. The effect of site characteristics on site productivity and rate of stand establishment and development probably also played a role. The low proportion of variance in CWD explained by age and site variables in the regression model for young stands in the Cascade range is difficult to explain. It may be that topographic influence on fire regime, productivity, and stand development are less in the Cascade stands, most of which occur in wetter, cooler climates than that of stands in the southern and eastern half of the Coast Ranges where slopes are steeper and topography more deeply dissected. Fires may have been less frequent, but larger and more intense, in the Cascade Range, especially to the north, and may have been less constrained by topography.

The influence of previous disturbance history appeared to wane after 150 yr and stand age became a better predictor of CWD biomass accumulation. The similarity in the CWD accumulation curves between the Cascade and the Coast Ranges indicated that the two areas are not fundamentally different in their potential standing crops of CWD. This suggests that the balance between within-stand, small-scale (not stand-replacing) mortality and the decay rate of CWD is similar in the two regions. The differences between the two areas result largely from differences in fire history and perhaps rate of stand reestablishment. The potential standing crops of CWD in the three provinces may, therefore, be the same. In fact, personal observations indicated that amounts of CWD in many young stands in the northern half of the Coast Range were higher and more similar to amounts found in young stands in the Cascades than to amounts found in the southern part of the Coast Range, where fire has probably been more frequent.

Although our data suggest the general pattern of CWD accumulation following disturbance and during succession, the variation we observed indicates that many variations of CWD dynamics have occurred in these landscapes. Harmon et al. (1986) propose that the dynamics of CWD can be predicted from the amount of CWD removed by the disturbance, the timing of the inputs, and the decay patterns. We used our data and the model by Harmon et al. (1986) to examine the effects of three different fire histories on accumulation patterns of CWD (Fig. 6). These particular histories represent three of the more common fire-history patterns in the region, but many combinations of initial fire intensity, subsequent disturbance, and recolonization rates are possible for a given site.

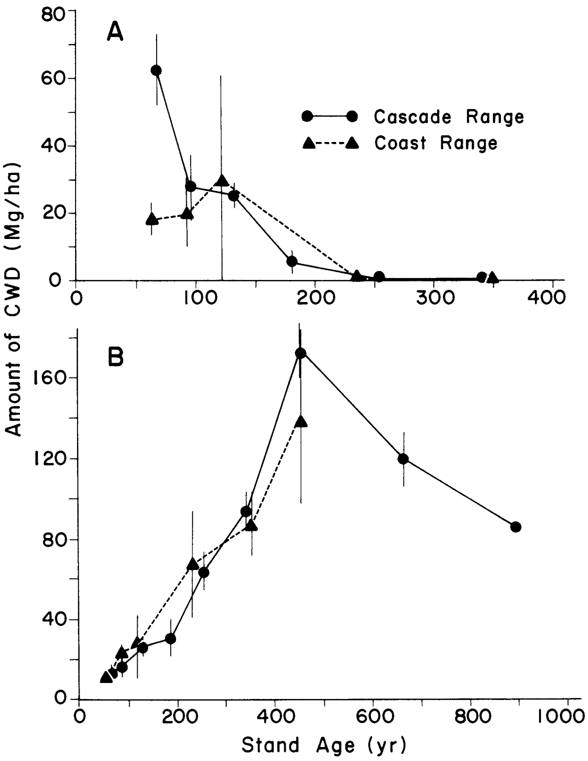

FIG. 5. Mass of total CWD originating in: (A) the preceding stand and (B) the current stand, in a chronosequence of *Pseudotsuga* stands in the western Cascade Range and in the southern Coast Range. Data points are plotted at age class means. Vertical bars represent standard errors.

In the first and most simple case, a single catastrophic fire occurred in a 450-yr-old stand of Douglas-fir and killed all the canopy trees (Fig. 6A). The prefire stem and bark biomass of the stand was assumed to be ≈645 Mg/ha (Grier and Logan 1977), and the mass of CWD was 180 Mg/ha. We assume consumption of only ≈25% of existing CWD, primarily decay class IV and V material, and none of the stem biomass (Harmon et al. 1986); this converted 645 Mg/ha to CWD. The total accumulation was 780 Mg/ha of CWD immediately after the fire. Assuming a decay rate constant of $k = 0.03\ \mathrm{yr}^{-1}$ (from this study) and no lag in the onset of decay, 95% of the CWD was gone 100 yr after the fire. The young stand that developed after the fire (assuming no delay) did not begin to produce significant CWD (>10 cm diameter) until ≈50 yr of age. The decay of the previous stand material and the long period before inputs of CWD from the new stand created a low point of 40 Mg/ha in the total accumulation

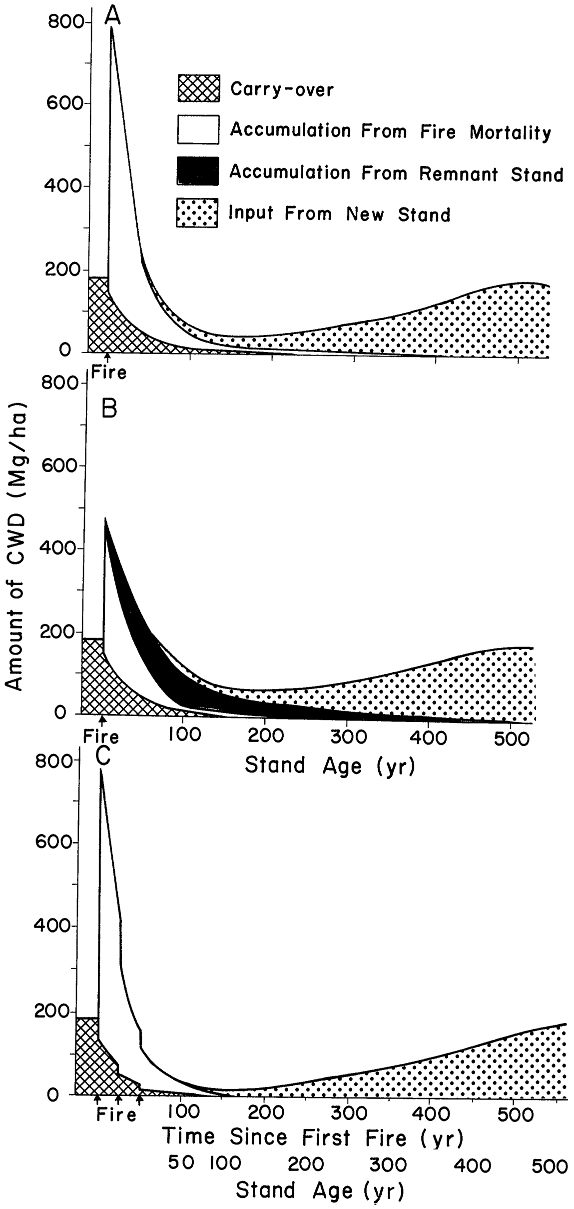

FIG. 6. Predicted changes in CWD mass following fire in a 450-yr-old *Pseudotsuga–Tsuga* forest: (A) catastrophic fire, (B) partial burn, (C) catastrophic fire and two subsequent fires 25 and 50 yr later. CWD is divided into: present before the fire, created by the fire, produced by the remnant stand, and produced by the stand growing after the fire.

of CWD at about age 150. After 300 yr, essentially all the CWD was from the current stand.

In the second case, a partial burn killed about one-half of the old-growth overstory trees, so that the input of dead wood after the fire was about one-half of that in the previous cases (Fig. 6B). The remaining Douglas-fir trees (about 15 trees/ha) died over 400–500 yr, based on an annual mortality rate of 1.0% for the first 50 yr and then 0.5% for the remaining period. Inputs of CWD from the remnant stand during the first 200 yr after the fire helped to maintain relatively high accumulations of CWD during the time when the pre-fire CWD had lost much of its mass and accumulations from the new stand were still relatively low. As a consequence, the low point in the accumulation of CWD was relatively high, perhaps 75 Mg/ha or higher. This type of fire and pattern of CWD accumulation probably occurred in many patches within or adjacent to major fires throughout the region (Morrison and Swanson 1988) and was probably more common in the southern Cascade Range and portions of the Coast Range than in other areas.

In the third case, additional fires occurred 25 and 50 yr after the initial catastrophic fire (Fig. 6). This scenario was common in many major fires in the Cascade and Coast Ranges (Martin et al. 1974, Lucia 1983). The reburns directly reduced the mass of CWD and delayed additions from the new stand until at least 100 yr after the initial burn. The low point (20 Mg/ha) in this case occurred at a stand age of ≈100 yr. This scenario may have been responsible for the low accumulations seen in many young stands in the Coast Range and in some young stands in the Cascades.

These models of CWD accumulation after fires are simple in that constant decay rates, no lag in the onset of decay, and no lag in the postfire colonization of the sites are assumed. They illustrate, however, the influence of the initial disturbance on the timing of establishment of the postfire stand and on the initial large input of CWD, and the low point in CWD at 100–200 yr. Repeated fires, delays in recolonization caused by those fires, inadequate seed sources, and unsuitable regeneration conditions will depress the low point in the biomass curve, while partial burns and rapid recolonization will raise it.

Fire is, of course, not the only disturbance that affects biomass accumulations in these forests. Wind, insect, and disease outbreaks and mass movements of soil kill overstory trees. These natural disturbances, with the exception of rapid mass soil movements, all cause increases in CWD on the site and result in biomass accumulation curves shaped like those for fire, except that no predisturbance CWD will be lost and decay rates may be lower because most of the CWD exists as logs, which decay less rapidly than snags (Graham 1982). In addition, a post-blowdown stand may have a higher proportion of western hemlock because advance regeneration is released and conditions are not favorable for the establishment of Douglas-fir. Stands dominated by western hemlock should have lower peak CWD biomass levels in the old-growth stage than will stands dominated by Douglas-fir in an old-growth stage.

CWD accumulation late in succession

The data indicated an "overshoot" in the mass of CWD at 400–500 yr with a decline to a lower amount and perhaps a steady state. This pattern has been identified for live biomass increases (Peet 1981, Shugart 1984), and it is reasonable to expect in values for CWD in old-growth Douglas-fir forests, although the timing will probably differ greatly among stands depending on initial composition, stocking, and productivity.

Douglas-fir is the major component of the mass of CWD in these stands, so CWD loadings will tend to follow the pattern of the live stem volume of this species. Douglas-fir averaged 80% of the mass of CWD in stands up to 600 yr old, but only 63% in stands >600 yr old. The density of live Douglas-firs declined from >150 trees/ha in 200-yr-old stands to <50 trees/ha in stands 400–500 yr of age and the relative dominance (based on basal area) of Douglas-fir declined from >75% at age 200 to <50% by age 500. This indicates that as succession proceeds, an increasing proportion of the inputs of CWD are composed of other species, such as western hemlock and Pacific silver fir. This change will eventually result in less CWD, because the boles of these species decay more rapidly than those of Douglas-fir (Graham 1982) and would lead to steady state in CWD biomass. This would probably not occur until 1200–1500 yr after stand establishment because of the longevity of Douglas-fir and the decay resistance of large Douglas-fir logs. Before this happens, however, succession will likely be disrupted by fire or a major windstorm. A similar lack of a steady state in CWD has been observed in *Abies balsamea* forests (Lang 1985, Sprugel 1985).

Effects of forest management

Amounts of CWD have been quite high in Douglas-fir forests under natural disturbance regimes over long periods, despite periods of low CWD. The simple models presented above indicated that amounts of CWD on a site stay above 100 Mg/ha for 150–300 yr of a 500-yr successional sequence, depending on the fire intensity, number of repeat fires, and number of years for trees to recolonize the site.

Forest-management activities greatly reduce the amount of CWD below minimums typically encountered under natural ecosystem dynamics. Clearcutting removes ≈90% of the live stem volume, and the remaining 10% is input as relatively small, broken pieces that decay rapidly. Removing existing CWD such as snags or large, relatively undecayed logs directly reduces CWD. Thinning operations in young stands reduce the inputs of CWD from suppression mortality in the stand, and short rotations of 100 yr or less keep accumulations low. One or two rotations after the harvest of old growth, most of the preharvest CWD is lost and accumulations of CWD remain very low, with a maximum of <50 Mg/ha for short periods, <30 Mg/ha for most of the rotation, and little or no large pieces (<50 cm diameter) (Spies and Cline 1988). Our research suggests that if managers plan to maintain even moderate amounts of CWD in managed forests, substantial changes are required in current harvesting and silvicultural practices, and management guidelines will need to take into account successional, site, and geographic variation.

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