MODELING HISTORICAL PATTERNS OF TREE UTILIZATION IN THE PACIFIC NORTHWEST: CARBON SEQUESTRATION IMPLICATIONS[1]

MARK E. HARMON, STEVEN L. GARMAN, AND WILLIAM K. FERRELL

Department of Forest Science, Oregon State University, Corvallis, Oregon 97331-7501 USA

Abstract. We have developed a model, HARVEST, that predicts the mass of woody detritus left after timber harvest in Pacific Northwest forests from 1910 to the present. Inputs to the model include the species, diameter at breast height, and age distribution of trees; the minimum tree size to be harvested; the minimum top diameter; and stump height and slope steepness. Model output includes the absolute amount and the proportion of bole biomass removed as well as that left as stumps, tops, breakage, and decay. The model also predicts the biomass of nonmerchantable parts such as branches, coarse roots, and fine roots left after harvest. Model predictions were significantly correlated to residue levels reported in the literature over this period. Both model output and historical data indicate that the total amount of aboveground woody residue left after logging has decreased at least 25% over the last century. This means that release of carbon to the atmosphere from woody residue has decreased by a similar amount.

Key words: carbon sequestration; coarse woody debris; disturbance; fine woody debris; fire fuels; logging residue; modeling; Pacific Northwest; woody detritus.

INTRODUCTION

When forests are harvested, a large amount of woody detritus remains in the ecosystem in the form of tops, stumps, broken and decayed boles, branches, and roots (Cramer 1974). This detritus strongly influences the pattern of succession that follows (Gosz et al. 1973, Gore and Patterson 1986). Although woody detritus has a low nutrient content, the quantity of material left after timber harvest can produce a substantial pool of nutrients that are slowly and steadily released over many years (Boyle and Ek 1972, Fahey et al. 1988, Harmon and Hua 1991). The ecosystem can also be a net source of carbon to the atmosphere for years to several decades as the detritus decomposes (Houghton et al. 1983, Harmon et al. 1990), even though vegetation is regrowing. Woody detritus left on the harvested site also may serve as an important habitat for invertebrates (Ausmus 1977, Harmon et al. 1986) and vertebrates (Corn and Bury 1991, Welsh and Lind 1991).

Despite its ecological importance, ecologists have made few attempts to measure the quantity of detritus left in harvested areas (Mattson et al. 1987, Mattson and Swank 1989). One approach used in forest-resource-related studies has been to correlate the amount of aboveground logging residue to variables such as slope, aspect, elevation, ownership, stand age, volume, basal area, and species (Howard 1973, Koss et al. 1977, Snell and Brown 1980, Howard and Fiedler 1984, Howard and Bulgrin 1986). Unfortunately, these estimates apply only to the harvesting system used at the time

of field sampling, which can change markedly over time and space. Moreover, it is difficult to know how to adjust the estimates when variables such as the minimum diameter harvested, stump height, and top diameter are altered from the original standards or when certain portions of trees such as stumps or roots are excluded. Without empirical data or models, expert opinion is often used to "guestimate" the mass of woody detritus following harvest (e.g., Houghton et al. 1983, Detwiler and Hall 1988, Harmon et al. 1990).

As an alternative, we have developed a model that can be used to predict the mass of woody detritus left after timber harvest for forests of the Pacific Northwest. Unlike previous stand-level methods (Koss et al. 1977), our model uses the extensive forestry literature on the merchantable volume, decay, and breakage of tree boles to estimate the detritus left behind for individual trees. We tested the sensitivity of the model to variations in input parameters, assumptions, and forest stand structures. We then used the model to examine how the utilization standards of trees have changed in the last century in the Pacific Northwest and the consequences of those changes on carbon sequestration.

METHODS

Model description

The HARVEST model estimates the amount of woody biomass left on a site after timber harvest. Inputs to the model include the species, diameter at breast height, and age distribution of trees; the minimum tree size to be harvested; the minimum top diameter of logs removed by harvest; stump height; and slope steepness. Woody material left on the site is divided into parts that are potentially merchantable and those that are

641

TABLE 1. Regression coefficients used to calculate bole bark and wood biomass for species used in HARVEST.

Species	Bark			Wood		
	B_0*	B_1*	r^2	B_0*	B_1*	r^2
Abies amabilis	2.965718	2.317900	0.86	4.124354	2.497000	0.95
Abies concolor	2.106921	2.727100	0.94	2.551192	2.785600	0.97
Abies grandis	2.106921	2.727100	0.94	2.551192	2.785600	0.97
Abies lasiocarpa	2.253295	2.314900	0.88	4.018261	2.389100	0.97
Acer macrophyllum	2.333800	2.574000	0.98	3.414800	2.723000	0.99
Alnus rubra	2.265355	2.461700	0.98	4.238755	2.461800	0.98
Betula papyrifera	2.265355	2.461700	0.98	4.238755	2.461800	0.98
Chamaecyparis nootkatensis	2.902625	2.481800	0.83	4.841987	2.332300	0.97
Larix occidentalis	2.902625	2.481800	0.83	4.841987	2.332300	0.97
Libocedrus decurrens	0.500948	2.859400	0.95	1.992026	2.733400	0.96
Picea engelmannii	3.022829	2.224500	0.90	3.424138	2.620400	0.97
Picea sitchensis	4.731108	1.705900	0.82	4.664733	2.363300	0.95
Pinus contorta	1.012802	2.067600	0.38	4.572091	2.343800	0.96
Pinus monticola	2.183174	2.661000	0.93	2.455550	2.777000	0.97
Pinus ponderosa	3.884462	2.167700	0.97	1.991941	2.926000	0.98
Populus tremuloides	2.265355	2.461700	0.98	4.238755	2.461800	0.98
Populus trichocarpa	2.265355	2.461700	0.98	4.238755	2.461800	0.98
Pseudotsuga menziesii	2.902625	2.481800	0.91	4.841987	2.332300	0.97
Thuja plicata	2.385440	2.198700	0.81	3.862652	2.445400	0.98
Tsuga heterophylla	2.766209	2.347400	0.84	4.176308	2.535300	0.95

  * The regression equation was of the form: $\ln(M_{bole}) = B_0 + B_1\cdot\ln(dbh)$ where M_{bole} is the bole bark or wood mass (g), dbh is the diameter at breast height (cm), and B_0 and B_1 are the regression coefficients.

rarely removed except in the most intensive harvest system (entire tree harvest). Potentially merchantable wood is divided into logs, stumps, tops, breakage, and decay. Aside from logs, which are the portions of the boles that are harvested, the other parts are left on the site. Tops are the upper portions of boles too small to be merchantable, breakage are portions too short or shattered to have value, and decayed sections have too much material missing or are too degraded to be of value. Nonmerchantable parts include small trees (whips), foliage, branches, and coarse roots.

Total bole.—The total bole mass of trees was estimated from allometric regression equations of the form:

$$\ln(M_{bole}) = B_0 + B_1\ln(dbh), \qquad (1)$$

where M_{bole} is the bole bark or wood mass (in grams), dbh is the diameter at breast height (in centimetres), and B_0 and B_1 are regression coefficients. These regressions for bark and wood mass were developed from published (Harcombe et al. 1990) and unpublished tree volume data, which were measured for individual trees with an optical dendrometer (Table 1). Bole mass was calculated with the mean densities of bark and wood weighted by their respective volumes in mature trees (Harcombe et al. 1990).

Stumps.—The fraction of the bole left on the site as a stump was calculated as a function of tree diameter, stump height, and site steepness. The stump volume was derived from the top and base diameters and height of the stump, with the appropriate form for each species:

$$SV = SH[BA_{top} + BA_{base} + (BA_{top}\cdot BA_{base})0.5]/F, \quad (2)$$

where SH is the stump height (in metres), BA_{top} and

BA_{base} are the basal areas of the stump top and base (in square metres), respectively, and F is the form of the stump. For Sitka spruce (*Picea sitchensis*), Engelmann spruce (*Picea engelmannii*), western redcedar (*Thuja plicata*), incense cedar (*Libocedrus decurrens*), and Alaska yellow cedar (*Chamaecyparis nootkatensis*), we assumed that stumps were frustrums of a neiloid ($F = 4$); for all other species stumps were assumed to be frustrums of a cone ($F = 3$). Stump mass was calculated by multiplying species-specific bole density by the stump volume of each species.

Regressions that related stump top and base diameter to dbh and stump height were estimated from butt-taper tables (Breadon 1957, British Columbia Forest Service 1966a). These equations were of the form:

$$SD = dbh + B_2\cdot dbh\cdot(1.38 - SH), \qquad (3)$$

where SD is the stump diameter (in centimetres), dbh is the diameter at breast height (in centimetres), SH is the stump height (in metres), and B_2 is the regression coefficient (Table 2). Eq. 3 was also used to estimate stump basal diameter by setting stump height equal to zero.

On steep slopes, the stump height on the uphill side can be much less than on the downhill side of the stump. We assumed that the uphill height was equal to the stump height on level ground, but that the downhill height increased with both slope steepness and stump diameter:

$$HI = 0.5\cdot SD_{top}\cdot\tan(A). \qquad (4)$$

HI is the height increase of stumps (in metres) caused by sloping ground, SD_{top} is the stump top diameter, and A is the slope angle in degrees. On sloping ground the

TABLE 2. Regression statistics for the relationship between diameter at breast height, stump height, and stump diameter.

Species	B_2*	r^2	N	Diameter range (cm)†
Abies amabilis	0.204	0.926	62	25–102
Abies lasiocarpa	0.201	0.800	64	25–63
Acer macrophyllum	0.167	0.959	34	25–63
Alnus rubra	0.168	0.854	27	25–51
Betula papyrifera	0.155	0.945	64	25–63
Chamaecyparis nootkatensis	0.200	0.948	65	25–127
Larix occidentalis	0.240	0.936	79	25–140
Picea engelmannii	0.311	0.932	56	25–100
Picea sitchensis	0.323	0.968	81	25–140
Pinus contorta	0.136	0.924	56	25–56
Pinus monticola	0.217	0.935	45	25–76
Pinus ponderosa	0.177	0.943	72	25–127
Pseudotsuga menziesii	0.181	0.976	161	25–140
Thuja plicata	0.282	0.956	149	25–140
Tsuga heterophylla	0.200	0.944	156	25–140

* The regression equation was of the form: $D = B_2 \cdot \text{dbh} \cdot \text{SB}$ where D is the difference between diameter at breast height and stump diameter (cm), dbh is the diameter at breast height (cm), and SB is the difference between stump height and breast height (cm).

† Diameter of stumps was determined for each 0.12 m at seven stump heights of 0.15, 0.30, 0.46, 0.61, 0.76, 0.91, 1.06, 1.21, and 1.37 m.

stump height was increased by HI before calculating stump volume (Eq. 2).

Tops.—The volume (in cubic metres) left in tops (Tv) was approximated with an integrated form of Kozak's taper equation (Avery and Burkhart 1983):

$$\text{Tv} = 0.0000785(\text{dbh})^2$$
$$\times \left[B_3 \cdot h + (B_4/2)(h^2/H) + (B_5/3)(h^3/H^2) \right]\Big|_h^H, \quad (5)$$

where h is height (in metres) to the specified minimum harvestable top diameter and H is total height (in metres) of the bole. Parameters B_3, B_4, and B_5 are species-specific taper coefficients derived from the following nonlinear regression of the top diameter of bole segments on dbh:

$$d = \text{dbh}\sqrt{B_3 + B_4(h/H) + B_5(h^2/H^2)}, \quad (6)$$

where d is the outside bark diameter (in centimetres), h is the cumulative length of bole segments (in metres), and H is the total length (in metres) of the bole. Parameters were constrained to sum to zero such that d equals zero when h and H are equal.

Total height of a tree used in Eq. 5 is estimated from the Chapman–Richards equation:

$$H = 1.37 + B_6[1 - e(B_7 \cdot \text{dbh})]^{B_8}, \quad (7)$$

where parameters are species specific and were estimated with nonlinear regression (Garman et al. 1995). Height-to-top diameter in Eq. 5 was derived with:

$$h = \{-B_4 \cdot H$$
$$-\sqrt{B_4 \cdot H^2 - 4B_5[B_3 \cdot H^2 - (d_{\text{top}}^2 \cdot H^2)/(\text{dbh})^2]}\}/2B_5, \quad (8)$$

where d_{top} is the minimum harvestable top diameter (in centimetres).

Top mass was obtained by multiplying the top volume (calculated as a cone) by the bole density for each species.

Decay.—The amount of decay in stems is a function of species, location (Boyce 1932), tree age, and size (Boyce 1932, Englerth 1942). As trees become older and larger, the proportion of the stem with decay increases. We chose to model this relationship with age as the sole predictive variable. Age-specific decay data indicate that the proportion of decay increases asymptotically with age. We therefore used nonlinear regression analysis to parameterize a logistic function for those species with age-specific data:

$$D_f = D_{\text{max}}/(1 + B_9 e^{-B_{10}\text{age}}), \quad (9)$$

where D_f is the percent of the bole on a cubic volume basis with decay, D_{max} is the maximum extent of stem decay, age is the age at breast height (years), B_9 is the regression coefficient that influences the diameters where D_f is 0, and B_{10} is the regression coefficient that determines the inflection point of the curve (Table 3).

For species without age-specific decay information, we used the average decay volumes for mature trees reported by the British Columbia Forest Service (1966b) to estimate the maximum extent of decay:

$$D_{\text{max}i} = D_{\text{max}h} D_i/D_h, \quad (10)$$

where $D_{\text{max}i}$ is the maximum decay for species i, $D_{\text{max}h}$ is the maximum decay for western hemlock (percent), D_i is the average decay of a mature tree of species i for trees that are >28 cm dbh, and D_h is the average decay of western hemlock as reported by the British Columbia Forest Service (1966b).

To estimate the regression coefficients B_9 and B_{10} for species without age-specific data, we used the ratio of maximum age of the species lacking age-specific data to that of the known species to rescale the regression. Western larch (*Larix occidentalis*), lodgepole pine (*Pinus contorta*), and ponderosa pine (*Pinus ponderosa*) were assumed similar to western white pine (*Pinus monticola*); Alaska yellow cedar was assumed similar to western redcedar; and all other species lacking age-specific data were assumed similar to western hemlock (*Tsuga heterophylla*).

Breakage.—Breakage of boles during felling also can convert merchantable bole volume into pieces too small to be harvested. Breakage differs widely among species (British Columbia Forest Service 1966b), and increases with tree size and with roughness of topography (Boyce 1932).

As Douglas-fir (*Pseudotsuga menziesii*) was the only species with size-specific breakage data (Boyce 1932),

TABLE 3. Mean quantity of wood (%) that is decayed and nonmerchantable for mature trees, maximum species age, maximum decay (%), and regression coefficients for selected Pacific Northwest tree species.

Species	Mean decay (%)*	Age_{max} (yr)†	D_{max} (%)‡,§	B_9‡,§	B_{10}‡,§	r^2	N	Data sources‖
Abies amabilis	12	600	46.0	23	0.0101	0.67	44	1
Abies concolor		600	21.6	14979	0.0922	0.88	12	2
Abies grandis		600	28.1	33	0.0181	0.40	22	3
Abies lasiocarpa	11	300	10.0	26	0.0175			4
Acer macrophyllum	10	300	48.0	26	0.0175			
Alnus rubra	3	100	14.4	26	0.0522			
Betula papyrifera	33	200	100.0	26	0.0261			
Chamaecyparis nootkatensis	22	1000	75.3	34	0.0111			
Larix occidentalis	9	900	11.4	5636	0.0365			
Libocedrus decurrens		550	36.7	11293	0.0396	0.98	10	5
Picea engelmannii	9	600	9.9	92	0.0238	0.97	24	6
Picea sitchensis	5	750	28.0	59	0.0078	0.84	28	7
Pinus contorta	12	500	15.1	5636	0.0651			
Pinus monticola	8	600	10.1	5636	0.0543	0.90	11	8
Pinus ponderosa	4	700	5.1	5636	0.0465			
Populus tremuloides	59	200	100.0	26	0.0261			
Populus trichocarpa	73	250	100.0	26	0.0208			
Pseudotsuga menziesii	6	1000	12.9	6080	0.0362	0.38	38	9
Thuja plicata	28	1000	95.9	34	0.0111	0.94	11	10
Tsuga heterophylla	12	500	57.6	32	0.0083	0.83	75	11

* Decay volume (%) in mature trees, based upon forest zone 1 values in British Columbia Forest Service (1966b).
† Fowells (1965).
‡ Those values with r^2 and N were computed from nonlinear regression (see Eq. 9).
§ Those species without age specific data were scaled relative to the decay of similar species (see Eq. 10).
‖ Data sources: (1) Bier et al. 1948, Buckland et al. 1949, Foster et al. 1958, (2) Meinecke 1916, (3) Aho 1977, (4) Hinds et al. 1960, (5) Boyce 1920, (6) Etheridge 1958, (7) Bier et al. 1946, Kimmey 1956, (8) Weir and Hubert 1919, (9) Boyce 1932, Boyce and Wagg 1953, (10) Kimmey 1956, (11) Englerth 1942, Buckland et al. 1949, Foster and Foster 1951, Foster et al. 1954, 1958, Kimmey 1956.

we used a nonlinear regression for that species to fit a logistic function:

$$Br_f = Br_{max}/(1 + B_{11}e^{-B_{12}dbh}), \quad (11)$$

where Br_f is the fraction of the bole subject to breakage loss, Br_{max} is the maximum extent of breakage loss on level ground, dbh is the diameter at breast height, and B_{11} is the regression coefficient that influences the diameters where Br_f is 0, and B_{12} is the regression coefficient that determines the inflection point of the curve (Table 4).

For species without size-specific breakage information, we used the average breakage for mature trees >28 cm dbh reported by the British Columbia Forest Service (1966b) to estimate the maximum extent of breakage:

$$Br_{max_i} = Br_{maxdf} Br_i/Br_{df}, \quad (12)$$

where Br_{max_i} is the maximum breakage for species i on level ground, Br_{maxdf} is the maximum breakage estimated for Douglas-fir, Br_i is the average breakage of species i for trees that are >28 cm dbh, and Br_{df} is the average breakage of Douglas-fir as reported by the British Columbia Forest Service (1966b).

To estimate the parameters B_{11} and B_{12} for species without size-specific breakage data, we recomputed the regression for Eq. 11 after rescaling dbh relative to that of Douglas-fir:

$$dbh_i = dbh_{max_i} (dbh_{df}/dbh_{maxdf}), \quad (13)$$

where dbh_i is the diameter at breast height for species i, dbh_{max_i} is the maximum dbh of species i, dbh_{df} is the original diameter of the Douglas-fir data, and dbh_{maxdf} is the maximum diameter at breast height of Douglas-fir.

Although increases in the roughness of topography are known to increase breakage, none of the reported data is presented as a continuous function of slope steepness (Boyce 1932). We therefore assumed that breakage would increase linearly as a function of slope steepness so that the maximum breakage (Br_{max}) at 100% slope would be twice that on level ground.

Nonmerchantable portions.—Nonmerchantable woody portions of trees left after harvest were estimated from published and unpublished biomass equations for foliage, branches, and roots (Table 5). Species-specific allometric regression equations were used to predict leaf, live branch, and dead branch mass:

$$\ln(M_{part}) = B_{13} + B_{14}\ln(dbh), \quad (14)$$

where M_{part} is the mass (in grams) of a given part, dbh is the diameter at breast height (in centimetres), and B_0 and B_1 are regression coefficients. For coarse roots, there are few published or unpublished regression equations for the tree species of the Pacific Northwest. We therefore used the following equation to predict the coarse root mass of all species:

$$\ln(M_{root}) = 2.2117 + 2.6929 \cdot \ln(dbh), \quad (15)$$

TABLE 4. Mean quantity of wood (%) undergoing breakage into nonmerchantable pieces of mature trees, the maximum species dbh, maximum breakage (%), and regression coefficients for selected Pacific Northwest tree species.

Species	Mean breakage (%)*	dbh$_{max}$ (cm)†	Br$_{max}$ (%)‡	B_{11}‡	B_{12}‡
Abies amabilis	13.6	200	12.3	7.53	0.0613
Abies concolor	13.6	225	12.3	7.53	0.0522
Abies grandis	13.6	225	12.3	7.53	0.0522
Abies lasiocarpa	13.6	80	12.3	7.53	0.0930
Acer macrophyllum	17.8	250	16.1	7.53	0.0490
Alnus rubra	8.2	150	7.4	7.53	0.0816
Betula papyrifera	41.8	75	37.9	7.53	0.0980
Chamaecyparis nootkatensis	16.7	300	15.1	7.53	0.0409
Larix occidentalis	9.9	240	9.0	7.53	0.0535
Libocedrus decurrens	26.0	250	23.5	7.53	0.0480
Picea engelmannii	7.7	200	7.0	7.53	0.0613
Picea sitchensis	7.4	400	6.7	7.53	0.0306
Pinus contorta	11.4	200	10.3	7.53	0.0613
Pinus monticola	8.0	200	7.2	7.53	0.0613
Pinus ponderosa	6.3	275	5.7	7.53	0.0471
Populus tremuloides	49.2	95	44.6	7.53	0.0907
Populus trichocarpa	73.2	200	66.3	7.53	0.0613
Pseudotsuga menziesii	10.6	425	9.6§	7.53§	0.0288§
Thuja plicata	26.0	350	23.5	7.53	0.0351
Tsuga heterophylla	12.5	225	11.3	7.53	0.0544

* Breakage volume (%) in mature trees, based upon forest zone 1 values in British Columbia Forest Service (1966b).
† Fowells (1965).
‡ Scaled relative to the breakage of Pseudotsuga menziesii (see Eqs. 12 and 13).
§ Computed from nonlinear regression (see Eq. 11; $r^2 = 0.94$, $N = 10$).

where M_{root} is the mass of coarse roots (in grams) and dbh is the diameter at breast height (in centimetres). The coefficients used in these regression equations were from compiled published sources (Means et al. 1994).

All branches were added to the woody detrital pool, whereas roots were only added if the species was not able to sprout.

Sensitivity analysis

In many potential applications of the model, there could be considerable uncertainty for input parameters such as utilization standards, size structure, and species composition. We therefore tested the sensitivity of the model to variations in these input parameters, and tested whether the estimates changed linearly as parameters were varied.

TABLE 5. Regression coefficients used to estimate biomass of the nonmerchantable portions of trees.*

Species	Leaf			Live branch			Dead branch		
	B_{13}	B_{14}	r^2	B_{13}	B_{14}	r^2	B_{13}	B_{14}	r^2
Abies amabilis	2.359100	2.192600	0.97	1.670800	2.626100	0.96	−0.177240	2.850000	0.93
Abies concolor	2.359100	2.192600	0.97	1.670800	2.626100	0.96	−0.177240	2.805000	0.93
Abies grandis	2.359100	2.192600	0.97	1.670800	2.626100	0.96	−0.177240	2.805000	0.93
Abies lasiocarpa	2.359100	2.192600	0.97	1.670800	2.626100	0.96	−0.177240	2.805000	0.93
Acer macrophyllum	0.415955	2.503300	0.78	2.671760	2.430000	0.88	4.791800	1.092000	0.15
Alnus rubra	−2.447300	3.243400	0.96	−0.911945	3.488600	0.92	−0.707845	2.624300	0.63
Betula papyrifera	−2.447300	3.243400	0.96	−0.911945	3.488600	0.92	−0.707845	2.624300	0.63
Chamaecyparis nootkatensis	4.061600	1.700900	0.86	3.213700	2.138200	0.92	3.378800	1.750300	0.84
Larix occidentalis	4.061600	1.700900	0.86	3.213700	2.138200	0.92	3.378800	1.750300	0.84
Libocedrus decurrens	4.061600	1.700900	0.86	3.213700	2.138200	0.92	3.378800	1.750300	0.84
Picea engelmannii	1.085755	2.780000	0.81	1.718655	2.518000	0.80	3.378800	1.750300	0.84
Picea sitchensis	1.085755	2.780000	0.81	1.718655	2.518000	0.80	3.378800	1.750300	0.84
Pinus contorta	3.289100	1.836200	0.84	2.307360	2.353300	0.89	3.378800	1.750300	0.84
Pinus monticola	2.884800	2.032700	0.52	−0.729250	3.364800	0.81	3.110900	1.742600	0.53
Pinus ponderosa	2.646560	2.096700	0.84	2.333000	2.464500	0.94	4.331200	1.444000	0.64
Populus tremuloides	−2.447300	3.243400	0.96	−0.911945	3.488600	0.92	−0.707845	2.624300	0.63
Populus trichocarpa	−2.447300	3.243400	0.96	−0.911945	3.488600	0.92	−0.707845	2.624300	0.63
Pseudotsuga menziesii	4.061600	1.700900	0.86	3.213700	2.138200	0.92	3.378800	1.750300	0.84
Thuja plicata	4.290800	1.782400	0.91	3.641700	2.087700	0.94	3.378800	1.750300	0.84
Tsuga heterophylla	2.777800	2.128000	0.96	1.758800	2.778000	0.97	−0.177240	2.805000	0.93

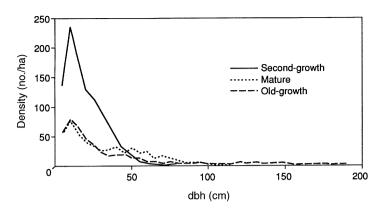* See Eq. 14 for the form of the regression equation used.

FIG. 1.   Mean size class distributions for second-growth, mature, and old-growth forests used in sensitivity analysis.

For these evaluations of model behavior, we used old-growth, mature, and second-growth stands dominated by Douglas-fir as our test cases. The species composition, size-class structure, and age of representative stands of each successional stage were obtained from field data in the Oregon State University Forest Science Data Bank. These data were from stands that were <1000 m in elevation, represented a range of site productivities, and were primarily from the western side of the Cascade Range in Oregon and Washington. Size class distributions used for each successional stage were averages of that stage (Fig. 1). The mean (± standard deviations) diameters for the second-growth, mature, and old-growth stands used in the analysis were 19.9 ± 12.3, 32.1 ± 23.6, and 34.7 ± 36.6 cm, respectively.

Utilization standards.—To evaluate model sensitivity to changing utilization standards, we varied stump height, top diameter, and minimum dbh values over the ranges reported from the turn of the century (maximum case) to the present time (minimum case). Because size class structure affects model response to changes in utilization parameters, we compared old-growth and mature successional stages. Given that our main purpose was to examine the effect of utilization parameters, all species were changed to Douglas-fir in these tests.

Parameter values for each of the three components (stump height, minimum top diameter, and minimum tree dbh) were varied independently. When values of one parameter were being varied, the other two were held at their minimum value. Because slope affects stump mass, two slope classes (0 and 100%) were employed when stump height was varied.

Size class structure.—To evaluate the sensitivity of the model to the size class distributions, we predicted residue levels from a bell-shaped or normal, positive exponential, and uniform size class distributions that had the same stocking density and quadratic mean dbh as the observed stands. We did not examine a negative exponential distribution, as this was quite similar to the observed size class distributions. The quadratic mean DBH for the second-growth, mature, and old-

growth stands were 23.4, 39.8, and 50.7 cm, respectively. The mean stocking densities for these same stands were 1062, 501, and 462 trees/ha. These distributions were used in addition to the observed reverse "J," because they represented the types of size class distributions generally observed for trees.

In some cases, size class distribution data may not be available; we therefore tested the ability of the model to predict residue biomass from the quadratic mean dbh and stocking density. These predictions were compared to the observed distributions with the same quadratic mean dbh and stocking density.

For both sets of model runs, we used two sets of harvest utilization parameters. The minimum case (the one that left the least residue) corresponded to current conditions, whereas the maximum case (the one that left the most residue) corresponded to the 1930–1940 utilization standards. As our main emphasis for these tests was the effect of size class distribution, we assumed all trees were Douglas-fir.

Species composition.—Sensitivity of the model to species composition was evaluated by comparing the amount of aboveground biomass remaining on a site for stands composed of only Douglas-fir to those with varying proportions of common species associated with Douglas-fir. These comparisons were for the current or minimum utilization standards. Substituted species included Pacific silver fir (*Abies amabilis*), western redcedar, and western hemlock. Size class distributions representative of old-growth, mature, and second-growth stands were used in this test. We performed species replacements one species at a time, and evenly for each size class (i.e., if western hemlock comprised 20% of the stand then it comprised 20% of each size class).

Model corroboration

We compared predicted aboveground residual mass to literature reports for 1990 and historical time periods. Although the values reported are subject to much error because of changes in sampling methods over time, these values represent our best historical record of the amount of mass left after harvesting. Model runs

TABLE 6. Timber utilization standards for different time periods in the Pacific Northwest.

Time period	Stump height (m)	Minimum top diameter (cm)	Minimum tree diameter (cm)*	Model estimate of woody residue left (%)†	
				Mature	Old-growth
1910–1920	6.00	43	62	75–77	62–66
1930–1940	1.75	40	52	64–67	57–63
1940–1945	1.00	30	40	49–53	52–58
1945–1950	0.60	30	40	47–52	51–57
1950–1977	0.60	20	28	40–45	49–55
1981–1985	0.45	14	20	36–41	47–54

* Minimum tree diameter was estimated from the taper equations by solving for the diameter at breast height that yielded a log >4.87 m long with a top diameter equal to the minimum top diameter.

† The range represents the percent left on slopes of 0 and 100%. All woody tree parts including the bole, branches, and coarse roots were considered.

TABLE 7. Historical changes in aboveground woody residues left under timber harvest in the Pacific Northwest.

Time period	Woody residues left (Mg/ha)			Source
	Observed	Predicted‡		
		S = 0	S = 100	
1920–1930	143	127	165	Hodgson (1930)
1920–1930	280	127	165	Rapraeger (1932)
1930–1940	90	98	140	Grondal (1942)
1940–1945	243	248	284	Matson and Granthum (1947)
1940–1950	315	378	447	Pool (1950)
1970–1975	81	73	117	Koss et al. (1977)
1975–1980	103*	171	197	Howard (1981)
1975–1980	73†	87	96	Howard (1981)
1985–1990	89	134	156	Willamette National Forest (unpublished data)

* Old-growth and second-growth mixture.
† Second-growth only.
‡ Values include only the parts reported and not total residues as in Table 6 predicted residue mass is given separately for slope steepness (S [%]) = 0 and 100.

were performed, with the size class structure and species composition of individual stands used to provide a measure of variability. Unfortunately, the exact nature of the stands sampled for residues was not reported. We therefore had to make assumptions concerning the size class and age of these stands. We used old-growth stands for predicting residual mass for the pre-1970 periods. After 1970, a mixture of second- and old-growth stands were harvested in the region. For the 1970–1980 period, we assumed a 70% old-growth and 30% second-growth mixture. For the 1980–1990 period, we assumed that equal proportions of old growth and second growth were harvested (50:50 mixture). Because literature reports varied in the types of residue included, we removed the materials not reported from the model output before we made the comparisons. For example, none of the reported values included stumps, therefore, stump mass was not included in the predicted values.

RESULTS

Historical changes in utilization standards

Stump height.—The height of stumps has decreased greatly with time (Table 6). Early this century, some stumps were up to 6.0 m tall (Gibbons 1918), and stumps 3.0–4.0 m tall were not unusual (Conway 1982). Reports of that time indicate that >10% of the stand volume was left in stumps (Gibbons 1918). Between 1920 and 1930, stump height was reduced to 1.00–1.75 m, amounting to 6–7% of the total bole volume. Reported values for both periods are lower than predicted by HARVEST, but this is to be expected because they are based on board-foot and not cubic volume. The advent of the chainsaw in the 1940s led to another drop in stump height to 0.6 m (Pool 1950); today, stumps are commonly 0.35–0.45 m tall.

Top and tree diameter.—The historical record of

minimum top diameter and minimum tree diameter is less clear than for stump height (Table 6). In the 1910s, the average diameter of logs left as unmerchantable after harvest was 43 cm (Hanzlik et al. 1917). During the 1920s, it was common to leave logs <35–56 cm in diameter, depending upon the length (Hodgson 1930). The degree of utilization has increased since that period, with diameters decreasing to 30 cm from the 1930s to 13–15 cm today.

Woody biomass removed.—The changes in stump height and minimum diameters have led to an increased proportion of woody biomass removed during harvest in both mature and old-growth forests. Under early utilization standards, a greater proportion of woody biomass was left after harvest of mature stands than of old-growth stands (Table 6). As utilization standards have increased over time, the reverse is now true, with harvest of older stands leaving proportionally more woody detritus. As the proportion of mature stands harvested has also increased over time, this may lead to an even greater reduction in the proportion of woody detritus left after harvest. This trend is unlikely to continue, however, as the recent shift to harvesting smaller, second-growth stands may lead to a slight increase in the fraction left as woody detritus of from 36–41% in mature stands to 42–44% in second-growth stands.

Model corroboration

Predicted aboveground residue mass for both 0 and 100% slopes was significantly correlated with the reported mass of residues (Table 7). Using the average of the extremes of slope gave a correlation of $r = 0.78$ ($P < 0.05$, $N = 9$). Many of the HARVEST predictions were higher than the reported values when the observed mass was <150 Mg/ha. This may have been caused either by the subsequent removal of detritus after log-
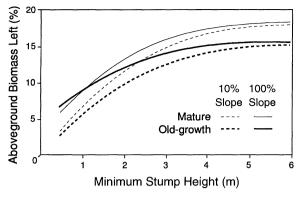
FIG. 2. Proportion of aboveground biomass left in stumps as a function of stump height.

ging or by the exclusion of some types of woody detritus from the inventories.

Sensitivity analysis

Utilization standards.—As stump height increases, the proportion of aboveground biomass left as stumps increases to an asymptote of 15–18%, depending upon the slope steepness (Fig. 2). Moreover, there appears to be an interaction between slope steepness and size class structure in determining the proportion of biomass left as stumps. When stump height was low, slope steepness caused more of a difference than size class structure. In contrast, at higher stump heights, slopes were quite similar and the primary difference was between mature and old-growth forests.

The proportion of aboveground biomass left as tops and in unharvested trees in mature and old-growth stands increases exponentially with minimum diameter (Fig. 3). Although little residue is left in tops or unharvested trees under current standards, as much as 25–75% of the aboveground biomass was left in these forms during the 1910s. Together, the changes in top diameter and minimum tree diameter harvested have made the largest difference in the amount of above-

ground biomass removed from harvested stands over the last 80 yr.

Size class structure.—Although size-class distribution influences the absolute biomass (Fig. 4), it does not greatly affect the proportion of biomass left under current utilization standards (Fig. 5). For example, among all the types of distributions, the proportion of aboveground mass left as residue in second-growth, mature, and old-growth stands varied only 1–5 percentage points.

The model was more sensitive to diameter size class structure when utilization standards decreased (Fig. 5). Under 1930–1940 utilization standards, the difference in proportions of residual mass for old-growth stands for all the distributions was 5–9 percentage points. In mature stands, however, the quadratic mean estimate was more than twice that of the other distributions (100 vs. 40%). This indicates that when the minimum tree diameter or top diameter approaches the quadratic mean, this method gives erroneous results.

Species composition.—The proportion of aboveground biomass left as residue varied with species (Fig. 6). These differences are caused primarily by differences in the breakage and decay functions among species and are therefore most evident in older, larger stands. For example, replacing half the Douglas-fir with western redcedar in a second-growth stand increases the proportion of aboveground biomass left after harvest from 30 to 40%. A similar substition for an old-growth stand changes the proportion from 35 to 65%. Interestingly, replacing Douglas-fir with almost any other associated species will increase the proportion of aboveground biomass left after harvest.

Although sensitive to species composition, HARVEST was not particularly sensitive to the type of size class distribution used. Comparing actual distributions and quadratic mean diameter on a flat surface for mixed-species stands indicated that the proportion of residue left after harvest varied 1–4 percentage points for all age classes. At 100% slope, differences were
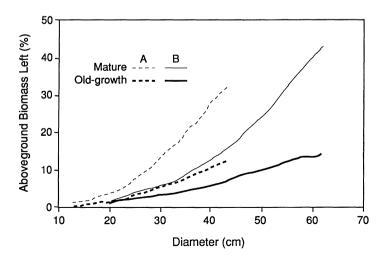

FIG. 3. Proportion of aboveground biomass left in tops (A) and unharvested trees (B) as a function of diameter.
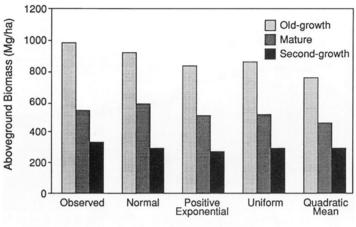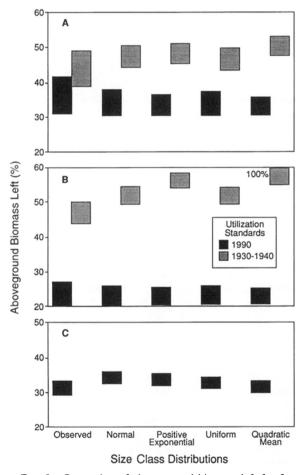
FIG. 4. Aboveground biomass estimated from different size class distributions having the same stocking density and quadratic mean diameter at breast height.
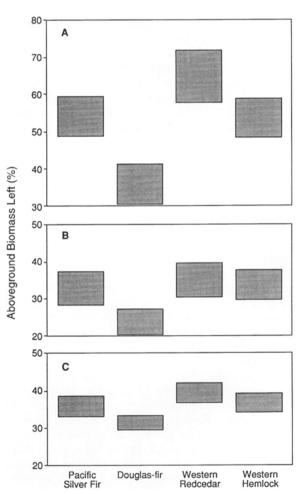

FIG. 5. Proportion of aboveground biomass left for five types of size-class distributions: (A) old-growth, (B) mature, and (C) second-growth stands. Second-growth stands are not shown for 1930–1940 because with these utilization standards, the trees were too small to be harvested. The lower and upper ends of the range indicated by shaded area correspond to 0 and 100% slope, respectively.

FIG. 6. Effect of species composition on the proportion of aboveground biomass left using 1990 utilization standards. Douglas-fir stands consisted of only this species. Other stands were composed of 50% Douglas-fir and 50% of the species noted. The lower and upper ends of the range indicated by shaded area correspond to 0 and 100% slope, respectively.
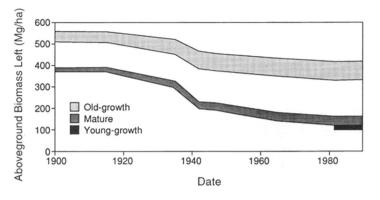
Fig. 7. Predicted changes in the mass of woody detritus left above ground after timber harvest from 1910 to 1990.

larger, ranging from 7–10, 2–5, and <2 percentage points in old-growth, mature, and second-growth stands, respectively.

DISCUSSION

Our review of published reports indicates many inconsistencies in diameter limits and types of material inventoried, which limit the value of these data. When adjusted for these methodological differences, the predictions of the HARVEST model are well correlated to these data. The model indicates that the amount of material left after logging harvest has changed greatly over the last 80 yr (Fig. 7). In 1910, the typical harvest of an old-growth stand would have left 500–540 Mg/ha of the aboveground woody organic matter or 52–56% of the preharvest aboveground biomass. This is quite similar to the amount that would be left by a catastrophic fire or windthrow (Agee and Huff 1987, Spies et al. 1988). The sheer quantity of wood left was put in context by Hodgson (1930), who calculated that the mass of sound wood left after harvest in western Oregon and Washington forests during the 1920s exceeded the entire amount cut for pulp over the entire United States! Although current utilization standards are much higher, a considerable mass (380–445 Mg/ha or 33–41% of the preharvest aboveground biomass) of wood residue is still left above ground after harvest of old-growth forest. Changes in age class structure of forests also mean that less woody residue is left today than in the past. We estimate that 100–115 Mg/ha, or 31–35% of the preharvest above-ground biomass, is left after a second-growth forest is harvested today.

Old-growth stands are often considered to have the highest woody-detritus biomass, an idea that seems to have developed from the analysis of old-field succession (Triska and Cromack 1980). Even with today's timber utilization standards, however, harvest increases aboveground woody detritus mass 2–3 fold, assuming an old-growth, preharvest woody-detritus level of 150–200 Mg/ha (Harmon and Hua 1991). Timber harvest at the turn of the century or natural disturbances would have caused an even larger increase. If belowground woody roots are also considered, it becomes quite obvious that forests recently disturbed by fire, wind, or timber harvest contain the greatest amount of woody detritus.

The historical shift in the amount of residue left in Pacific Northwest forests has changed their ecological function over succession. One way to assess this change in terms of carbon sequestration is to calculate the time required for the new stand to store as much carbon as would be released by the decomposition of woody residue added by harvest. Assuming a medium-to-high level of site productivity (Site Index 2–3), an old-growth stand harvested in 1910 would reach this balance in 60 yr. In contrast, a recently harvested old-growth stand would reach this balance in 45 yr unless the increase in utilization standards has decreased the size of woody detritus to the point that decomposition rates have increased. To some degree, this decrease in the time required for trees to offset the carbon released from residue decomposition may be misleading. A more complete accounting of the type of forest products produced from the harvested material is required before one can determine if forests harvested at the turn of the century release more carbon than those more recently harvested. More detailed examination of the effects of woody residues on ecosystem behavior would be gained by linking the HARVEST model to stand dynamics, carbon, and nutrient cycling models.

Sensitivity analysis of HARVEST indicates that when detailed size-class structure data are lacking, the quadratic mean dbh of a stand can be used to estimate the proportion of aboveground mass left as woody residue. This method becomes less reliable as minimum tree size increases or as the quadratic mean dbh decreases. Under these situations, better results may be obtained by using either a normal or a uniform size class distribution, which requires estimating not only the mean tree size, but also the stocking density.

Mixed-species stands are also problematical, especially if the age or size class distribution of the species differs. When species-specific size class data are not known, it may be possible to estimate woody residue mass by using the quadratic mean dbh of each species. Species effects are likely to be greatest in the largest, oldest stands, where species-specific decay and breakage differences are mostly likely to be expressed.

The primary limitation to the use of the HARVEST model for historical reconstructions is the lack of detailed information on exactly how utilization standards have changed. For some parameters, such as stump height, this record may still be present in the field for several more decades. Another factor that needs to be considered is residue removal during harvest. This may explain, in part, why HARVEST estimates of residue for 1975–1980 were 66–91% higher than reported values. This is a period when yarding of unmerchantable material (YUM) was prevalent. Including this harvest of unmerchantable logs and pieces in the model may be required before the most realistic historic patterns of residue amounts can be reconstructed.

LITERATURE CITED

Agee, J. K., and M. H. Huff. 1987. Fuel succession in a western hemlock/Douglas-fir forest. Canadian Journal of Forest Research 17:697–704.

Aho, P. E. 1977. Decay of grand fir in the Blue Mountains of Oregon and Washington. United States Department of Agriculture Forest Service Research Paper PNW-229.

Ausmus, B. S. 1977. Regulation of wood decomposition rates by arthropod and annelid populations. Ecological Bulletin (Stockholm) 25:180–192.

Avery, T. E., and H. E. Burkhart. 1983. Forest measurements. McGraw-Hill, New York, New York, USA.

Bier, J. E., R. E. Foster, and P. J. Salisbury. 1946. Studies in forest pathology. IV. Decay of Sitka spruce on the Queen Charlotte Islands. Canadian Department of Agriculture Technical Bulletin 56.

Bier, J. E., P. J. Salisbury, and R. A. Wadie. 1948. Studies in forest pathology. V. Decay in fir Abies lasiocarpa and A. amabilis, in the upper Fraser region of British Columbia. Canadian Department of Agriculture Technical Bulletin 66.

Boyce, J. S. 1920. The dry-rot of incense cedar. United States Department of Agriculture Bulletin 871.

———. 1932. Decay and other losses in Douglas-fir in western Oregon and Washington. United States Department of Agriculture Technical Bulletin 286.

Boyce, J. S., and J. W. B. Wagg. 1953. Conk rot of old-growth Douglas-fir in western Oregon. Forest Research Laboratory Bulletin 4, Oregon State University, Corvallis, Oregon, USA.

Boyle, J. R., and A. R. Ek. 1972. An evaluation of some effects of bole and branch pulpwood harvesting on site macronutrients. Canadian Journal of Forest Research 2: 407–412.

Breadon, R. E. 1957. Butt-taper tables for commercial tree species of British Columbia. British Columbia Forest Service Forest Survey Notes 3, Victoria, British Columbia, Canada.

British Columbia Forest Service. 1966a. Butt-taper tables for coastal tree species. British Columbia Forest Service Forest Survey Notes 7, Victoria, British Columbia, Canada.

———. 1966b. Net volume loss factors. British Columbia Forest Service, Forest Survey Notes 8, Victoria, British Columbia, Canada.

Buckland, D. C., R. E. Foster, and V. J. Nordin. 1949. Studies in forest pathology. VII. Decay in western hemlock and fir in the Franklin River area British Columbia. Canadian Journal of Research C 27:312–331.

Conway, S. 1982. Logging practices. Revised edition. Miller Freeman, San Francisco, California, USA.

Corn, P. S., and R. B. Bury. 1991. Terrestrial amphibian communities in the Oregon Coast Range. Pages 305–317 in Wildlife and vegetation of unmanaged Douglas-fir forests. United States Department of Agriculture Forest Service General Technical Report PNW-GTR-285.

Cramer, O. P., editor. 1974. Environmental effects on forest residues management in the Pacific Northwest. United States Forest Service General Technical Report PNW-24.

Detwiler, R. P., and C. A. Hall. 1988. Tropical forests and the global carbon budget. Science 239:42–47.

Englerth, G. H. 1942. Decay of western hemlock in western Oregon and Washington. Yale School of Forestry Bulletin 50.

Etheridge, D. E. 1958. Decay losses in subalpine spruce on the Rocky Mountain Forest Reserve, Canada. Forestry Chronicle 34:116–131.

Fahey, T. J., J. W. Hughes, M. Pu, and M. A. Arthur. 1988. Root decomposition and nutrient flux following whole-tree harvest in northern hardwood forests. Forest Science 34: 744–768.

Foster, R. E., J. E. Browne, and A. T. Foster. 1958. Studies in forest pathology. XIX. Decay of western and amabilis fir in the Kitimat region of British Columbia. Canadian Department of Agriculture Publication 1029.

Foster, R. E., H. M. Craig, and G. W. Wallis. 1954. Studies in forest pathology. XII. Decay of western hemlock in the upper Columbia region, British Columbia. Canadian Journal of Botany 32:145–171.

Foster, R. E., and A. T. Foster. 1951. Studies in forest pathology. VIII. Decay of western hemlock on the Queen Charlotte Islands, British Columbia. Canadian Journal of Botany 29:479–521.

Fowells, H. A. 1965. Silvics of forest trees of the United States. United States Department of Agriculture Forest Service Agricultural Handbook 271.

Garman, S. L., S. A. Acker, J. L. Ohmann, and T. A. Spies. 1995. Asymptotic height-diameter equations for twenty-four tree species in western Oregon. Oregon State University, Forest Research Laboratory Research Contribution 10.

Gibbons, W. H. 1918. Logging in the Douglas-fir region. United States Department of Agriculture Forest Service Contribution Bulletin 711.

Gore, J. A., and W. A. Patterson III. 1986. Mass of downed wood in northern hardwood forests in New Hampshire: potential effects of forest management. Canadian Journal of Forest Research 16:335–339.

Gosz, J. R., G. E. Likens, and F. H. Bormann. 1973. Nutrient release from decomposing leaf and branch litter in the Hubbard Brook Forest, New Hampshire. Ecological Monographs 43:173–191.

Grondal, B. L. 1942. Logging waste and its potential value in pulp manufacture. Pacific Pulp and Paper Industry 16: 18–21.

Hanzlik, E. J., F. S. Fuller, and E. C. Erickson. 1917. A study of breakage, defect, and waste in Douglas-fir. Forest Club Annual, University of Washington V:32–39.

Harcombe, P. A., M. E. Harmon, and S. E. Greene. 1990. Changes in biomass and production over 53 years in a coastal Picea sitchensis-Tsuga heterophylla forest approaching maturity. Canadian Journal of Forest Research 20:1602–1610.

Harmon, M. E., and C. Hua. 1991. Coarse woody debris dynamics in two old-growth ecosystems. BioScience 41: 604–610.

Harmon, M. E., W. K. Ferrell, and J. F. Franklin. 1990. Ef-

fects on carbon storage of conversion of old-growth forests to young forests. Science **247**:699–702.

Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack, Jr., and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research **15**:133–302.

Hinds, T. E., F. G. Halksworth, and R. W. Davidson. 1960. Decay of subalpine fir in Colorado. United States Department of Agriculture Forest Service Rocky Mountain Forest and Range Experiment Station Paper **51**.

Hodgson, A. H. 1930. Logging waste in the Douglas-fir region. Pacific Pulp and Paper Industry and West Coast Lumberman **56**:6–13.

Houghton, R. A., J. E. Hobbie, J. M. Melillo, B. Moore, B. J. Peterson, G. R. Shaver, and G. M. Woodwell. 1983. Changes in the carbon content of terrestrial biota and soils between 1860 and 1980: a net release of CO_2 to the atmosphere. Ecological Monographs **53**:235–262.

Howard, J. O. 1973. Logging residue—volume and characteristics. United States Department of Agriculture Forest Service Resource Bulletin **PNW-44**.

———. 1981. Logging residue in the Pacific Northwest: characteristics affecting utilization. United States Department of Agriculture Forest Service Research Paper **PNW-289**.

Howard, J. O., and J. K. Bulgrin. 1986. Estimators and characteristics of logging residue in California. United States Department of Agriculture Forest Service Research Paper **PNW-355**.

Howard, J. O., and C. E. Fiedler. 1984. Estimators and characteristics of logging residue in Montana. United States Department of Agriculture Forest Service Research Paper **PNW-321**.

Kimmey, J. W. 1956. Cull factors for Sitka spruce, western hemlock, and western redcedar in southeast Alaska. United States Department of Agriculture Forest Service Alaska Forest Research Center Station Paper **6**.

Koss, W., J. Van Gorkom, and B. D. Scott. 1977. Residue, roundwood and the Washington pulp industry. State of Washington Department of Natural Resources Report 35, Olympia, Washington, USA.

Mattson, E. E., and J. B. Grantham. 1947. Salvage logging in the douglas-fir region of Oregon and Washington. Oregon Forest Products Laboratory Bulletin **1**.

Mattson, K. G., and W. T. Swank. 1989. Soil and detrital carbon dynamics following forest cutting in the southern Appalachians. Biology and Fertility of Soils **7**:247–253.

Mattson, K. G., W. T. Swank, and J. B. Waide. 1987. Decomposition of woody debris in a regenerating, clear-cut forest in the southern Appalachians. Canadian Journal of Forest Research **17**:712–721.

Means, J. E., H. A. Hansen, G. J. Koerper, M. K. Klopsch, and P. B. Alaback. 1994. Software for computing plant biomass—Biopak users guide. United States Department of Agriculture Forest Service General Technical Report **PNW-GTR-340**.

Meinecke, E. P. 1916. Forest pathology in forest regulation. United States Department of Agriculture Bulletin **275**.

Pool, C. G. 1950. An analysis of falling and bucking. Timberman **51**(7):78–82.

Rapraeger, E. F. 1932. Tree breakage and falling in the Douglas-fir region. Timberman **33**:9–13, 24.

Snell, J. A. K., and J. K. Brown. 1980. Handbook for predicting residue weights of Pacific Northwest conifers. United States Department of Agriculture Forest Service General Technical Report **PNW-103**.

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

Triska, F. J., and K. Cromack, Jr. 1980. The role of wood debris in forests and streams. Pages 171–190 *in* R. H. Waring, editor. Forests: fresh perspectives from ecosystem analysis. Proceedings of the 40th Annual Biology Colloquim, Oregon State University Press, Corvallis, Oregon, USA.

Weir, J. R., and E. E. Hubert. 1919. A study of rots in western white pine. United States Department of Agriculture Bulletin **799**.

Welsh, H. H., and A. J. Lind. 1991. The structure of the herpofaunal assemblage in the Douglas-fir/hardwood forests of northwestern California and southwestern Oregon. Pages 395–413 *in* Wildlife and vegetation of unmanaged Douglas-fir forests. United States Department of Agriculture Forest Service General Technical Report **PNW-GTR-285**.