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Biomass and dynamics of attached dead branches in the canopy of 450-year-old Douglas-fir trees

Hiroaki Ishii and Tomoko Kadotani

Abstract: The amount, physical characteristics, and spatial distribution of attached dead branches in the canopy of 450-year-old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) trees were studied over a 5-year period (1998–2003) to quantify their contribution to the canopy woody detritus pool of an old-growth Douglas-fir – western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) forest in the western Washington Cascades. We developed a five-class decay rating for attached dead branches. From the size distribution and relative amounts and vertical distribution of attached dead branches in the five decay classes, we inferred that death of large original branches had occurred in the recent past, followed by the production and death of epicormic branches. Tree height was an important variable for predicting branchwood dry mass per tree. We estimated that attached dead branches of Douglas-fir contributed 63.8% of the total canopy woody detritus pool of the stand. During the study period, $0.24\% \cdot \text{year}^{-1}$ of live branchwood mass died attached, and $0.37\% \cdot \text{year}^{-1}$ and $4.34\% \cdot \text{year}^{-1}$, respectively, of live- and dead-branch mass were lost due to branchfall and fragmentation. Because branch death and branchfall are stochastic processes, long-term monitoring in the canopy and on the ground is needed to understand the dynamics of canopy woody detritus.

Résumé : La quantité, les caractéristiques physiques et la distribution spatiale des branches mortes attachées dans la canopée de douglas de Menzies typiques (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) âgés de 450 ans ont été étudiées sur une période de 5 ans (1998–2003). L'objectif était de quantifier la contribution des branches mortes attachées au pool de débris ligneux de la canopée d'une forêt ancienne de douglas de Menzies typique et de pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.) dans la partie ouest de la chaîne des Cascades, dans l'État de Washington. Les auteurs ont développé un système d'évaluation à cinq classes de la décomposition des branches mortes attachées. À partir de la distribution des dimensions, des quantités relatives et de la distribution verticale des branches mortes attachées dans les cinq classes de décomposition, ils ont déduit que la mort des grosses branches originales était survenue récemment suivie par la production et la mort des branches adventives. La hauteur des arbres était une variable importante pour prédire la masse anhydre de matière ligneuse dans les branches par arbre. Ils ont estimé que les branches mortes attachées du douglas de Menzies typique représentent 63,8 % du pool total de débris ligneux de la canopée du peuplement. Durant la période de l'étude, $0,24\% \cdot \text{an}^{-1}$ de la masse de branches vivantes devenait des branches mortes attachées et $0,37\% \cdot \text{an}^{-1}$ de la masse de branches vivantes et $4,34\% \cdot \text{an}^{-1}$ de la masse de branches mortes étaient perdues via la chute des branches et la fragmentation. Parce que la mort et la chute des branches sont des processus stochastiques, un suivi à long terme dans la canopée et au sol est nécessaire pour comprendre la dynamique des débris ligneux de la canopée.

[Traduit par la Rédaction]

Introduction

Coniferous forests of the Pacific Northwest region of the United States have the highest potential for carbon accumulation in the world (Smithwick et al. 2002). Old-growth forests of this region contain enormous biomass (Waring and Franklin 1979; Franklin and Waring 1980) and represent the culmination of carbon (C) storage in ecosystems (Field and Kaduk 2004). Significant amounts of C are sequestered in both above- and below-ground biomass of old-growth coniferous forests. In addition to the great amount of living biomass, detrital biomass, or necromass (including woody detritus

and soil organic matter), accumulates with increasing forest age and contributes a significant amount to the total C store (Grier et al. 1981; Gholz 1982; Sollins 1982; Harmon et al. 1990). In a recent study, Harmon et al. (2004) estimated that detrital biomass accounted for 36% (22 092 g C·m⁻²) of the total C store (61 899 g C·m⁻²) in a 500-year-old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) – western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) forest in the western Washington Cascades (Wind River Canopy Crane Research Facility, WRCCRF). Of this, woody detritus contributed 43% (9550 g C·m⁻²) and mineral soil 42% (9300 g C·m⁻²). Their results indicate that quantification of the amount of woody detritus and its decomposition rate is an important and critical step in understanding C cycling of old-growth forests.

The amount of woody detritus on the forest floor, especially that of coarse woody debris (CWD, downed logs and snags), has been well documented for various forest types (Harmon et al. 1986), including coniferous forests of the Pacific Northwest (Spies et al. 1988; Tyrrell and Crow 1994;

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Stone et al. 1998). The amount and types of CWD are recognized as distinguishing characteristics of unmanaged, old-growth forests (Cline et al. 1980; Franklin et al. 1981; Spies and Franklin 1991). The canopy component of the above-ground woody detritus pool, however, has been much less studied. The canopy woody detritus pool consists mainly of dead branches that remain attached or suspended in the canopy of live trees. They are thought to fragment and decompose in the canopy and eventually fall to the ground, but the dynamics of canopy woody detritus are mostly unknown (Fonte and Schowalter 2004). Of the various components of tree biomass (stem wood, bark, foliage, live branches, dead branches, etc.), dry mass estimates of attached dead branches in the canopy have the largest uncertainty associated with them (Grier and Logan 1977; Gholz et al. 1979; Grier and Milne 1981; Gholz 1982; Gower et al. 1987), indicating that the canopy woody detritus pool is difficult to estimate accurately.

Harmon et al. (2004) and Grier and Logan (1977) estimate that fine woody litter including twigs and cones contribute as much as 32% of total litterfall in old-growth Douglas-fir – western hemlock forests of the Pacific Northwest. The high contribution of fine woody litter to total aboveground litterfall suggests that the woody detritus pool in the canopy of these forests may be quite large. Ishii and Wilson (2001) found that attached dead branches made up 21%–53% of the total number of branches of 450-year-old Douglas-fir trees at WRCCRF. In Douglas-fir trees, attached dead branches are first produced in significant amounts in the crown of young trees after crown closure when lower crown branches die and the live crown recedes upward with increasing tree height (Maguire and Hann 1990; Winter et al. 2002; Franklin and Van Pelt 2004). When the stand reaches old-growth stage, openings in the canopy created by individual tree mortality allow light to penetrate into the lower crown. This is thought to stimulate production of epicormic branches, especially from the axils of dead branches in the lower crown (Franklin and Van Pelt 2004). Ishii and Wilson (2001) found that epicormic branches occurred in all parts of the crown of old-growth Douglas-fir trees, contributing 15%–48% of the total number of live branches per tree. We observed that many of these epicormic branches may be relatively short lived and their death may result in a second phase of branch deaths in the course of Douglas-fir crown development. We also observed that both original and epicormic branches remain attached for long periods after death. This would result in accumulation of large amounts of woody detritus in the canopy of old-growth Douglas-fir – western hemlock forests as large old trees of Douglas-fir increase in age. Franklin et al. (1987) speculated that woody detritus, including heartwood and dead branches, may contribute as much as 90% of the total mass of mature trees.

Stand-level estimation of canopy woody detritus in old-growth Douglas-fir – western hemlock forests are based on allometric equations from a limited number of empirical studies (e.g., Fujimori et al. 1976; Grier and Logan 1977; Gholz et al. 1979; Gholz 1982; Snell and Max 1985). For example, using allometric equations developed by Gholz et al. (1979), Harmon et al. (2004) estimated that attached dead branches contributed 3.4% (320 of 9550 g C·m⁻²) of the C stored in woody detritus at WRCCRF. In addition, Harmon et al. (2004) assumed that, over their 5-year study period, there was no

net change in the canopy woody detritus pool, meaning that rates of production and loss of attached dead branches in the canopy are at equilibrium. However, the amount and accumulation rate of woody detritus in the canopy is likely to vary spatially depending on stand age and history and also fluctuate with time. Grier and Logan (1977) recognized that the history of mortality, including disturbance and periodic death events, cause large fluctuations in the amount of dead biomass of a stand and inferred that the accumulation of woody detritus may be a nonequilibrium process. The same could be said of dead branches in the canopy, that is, the amount and accumulation rate are dependent on the history of crown development and crown disturbances such as fire, herbivory, and crown dieback, which are stochastic in space and time. The canopy woody detritus pool may fluctuate with periods of accumulation and loss in relation to canopy development. Direct observations in the canopy are needed to establish reliable estimates of C stored in canopy woody detritus.

In this study, we describe the amount, physical characteristics, and spatial distribution of attached dead branches in the canopy of 450-year-old Douglas-fir trees. We developed a five-class decay rating for attached dead branches in the canopy, adapted from stages of deterioration of snags (Cline et al. 1980). We estimated dry mass of live and dead branches in the crown and their turnover rate over the 5-year study period. We also measured C and nitrogen (N) content of branches at different stages of decay. Based on these observations, we inferred the contribution of attached dead branches of Douglas-fir to the stand-level canopy woody detritus pool.

Materials and methods

Study site

The study was conducted in a 500-year-old, Douglas-fir – western hemlock forest at WRCCRF located in the Thornton T. Munger Research Natural Area, Gifford Pinchot National Forest, in southwestern Washington State, USA (45°49'N, 121°57'W; 371 m elevation). More than 42% (35.4 of 82.9 m²·ha⁻¹) of the stand basal area is dominated by Douglas-fir, with western hemlock contributing 32% (Shaw et al. 2004). Other tree species in the stand include (in order of basal area): western redcedar (*Thuja plicata* Donn ex D. Don), Pacific yew (*Taxus brevifolia* Nutt.), Pacific silver fir (*Abies amabilis* (Dougl. ex Loud.) Dougl. ex J. Forbes), and grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.). Shaw et al. (2004) give a detailed description of the study area.

Six Douglas-fir trees were selected for detailed measurement of crown characteristics (Table 1, after Ishii and Wilson 2001). The trees were located less than 100 m south of the 4 ha permanent research plot established around the canopy crane (Shaw et al. 2004). The study trees were selected to represent the size distribution of Douglas-fir trees within the research plot. Mean DBH (measured at 1.3 m above ground level) and tree height of Douglas-fir in the research plot are 111.0 cm and 52.0 m, respectively (Shaw et al. 2004). Douglas-fir is not regenerating in the understory of this forest, and the size-frequency distribution is nearly normal. The Douglas-fir trees in the stand are believed to be a cohort that established after a stand-replacing major disturbance in the area about 500 years ago (Franklin and DeBell

Table 1. Structural characteristics of the six old-growth Douglas-fir trees studied in southwestern Washington State (Wind River Canopy Crane Research Facility) in 1998.

Tree	Tree height (m)	DBH (cm)	Breast-height age (years)
Tallest	61.6	135.3	415
Tall	61.0	126.9	410
Tall-medium	58.7	153.5	—*
Medium-short	53.8	104.3	405
Short	51.3	87.1	395
Shortest	50.8	93.9	405

Note: Total basal area was 6.7 m².

*Breast-height age could not be accurately determined because of incomplete core sample.

1988). Breast-height age estimates of the six study trees ranged from 395 to 415 years. These estimates agree with ages of Douglas-fir stumps in nearby clearcuts (Franklin and DeBell 1988).

Measurement of live and dead branches in the canopy

The six study trees were climbed in June–July of 1998 using the single-rope technique (Moffett and Lowman 1995). All primary branches attached to the main stem (>0.5 m in length) were permanently tagged and distinguished as live (with foliage) or dead (without foliage). For each branch, branch height above ground (*h*, m) was measured using a tape measure that was stretched vertically along the main stem of the tree. Branch diameter (*d*, cm) was measured immediately outside the branch collar using diameter tape. Branch length (*l*, m) was measured by extending a 2.5 cm wide engineer's tape from the main stem to the farthest foliage for live branches and to the farthest point for dead branches. Measurements were not taken on branches in the top 1–2 m of each tree because they could not be reached safely.

The six trees were climbed for a second survey in June 2003 to document the death and loss of branches and branch parts from the canopy. All branches were identified by their tagged number and distinguished as live, dead, or broken at <0.5 m from the main stem since 1998. Branch *d* and *l* were remeasured using the same methods and tools as in 1998. Branches that were damaged as a result of climbing activity were disregarded. Attached dead branches were distinguished into the following five decay classes (DC1–DC5), adapted from stages of deterioration of snags (Cline et al. 1980) (Fig. 1):

- DC1: Recently dead branch with fine branching structure and bark still intact.
- DC2: General branching structure remains, but bark is beginning to slough.
- DC3: Branching structure is mostly gone. Bark is sloughing.
- DC4: Bark is mostly gone and the exposed wood is beginning to decay.
- DC5: Bark is completely gone and the exposed wood is deteriorating.

Tree-level estimation of live- and dead-branch mass in the canopy

To estimate dry mass of attached dead branches in the canopy, 5–13 sample branches were cut from each decay

class and brought back to the laboratory. All epiphytes (mainly mosses and lichens) were removed, and care was taken not to remove any bark. Fresh mass of each sample branch was measured to the nearest 0.5 g using a large digital balance (Pennsylvania 5600, Pennsylvania Scale Co., Leola, Pennsylvania). Sample sections (2–15 cm in diameter and 5–15 cm in length) were cut from each sample branch and weighed to the nearest 0.001 g using a precision digital balance (TS400D, Ohaus Corp., Florham Park, New Jersey). The sample sections were then dried to constant mass at 105 °C, and the dry mass was measured. The dry mass of each sample branch was calculated by multiplying the fresh mass of the sample branch by the dry mass / fresh mass ratio of its sample section.

Nonlinear least squares regression was used to find the best model for predicting dry mass of the sampled dead branches (m_D , g) from measurements of *d* and *l*. The following three-parameter allometric relationship was derived:

$$[1] \quad m_D = 36.71d^{1.56}l^{1.12} \quad (R^2 = 0.907, P < 0.01, n = 37)$$

As discussed later, this relationship did not vary among the different decay classes (ANCOVA, $F = 0.932$, $P = 0.458$). Therefore, eq. 1 was used to estimate dry mass of each attached dead branch (\hat{m}_D , g) in the six study trees from measurements of *d* and *l*. Because destructive sampling of live branches was restricted in the T.T. Munger Research Natural Area, eq. 1 was also used to estimate branchwood dry mass (excluding foliage) of each live branch (\hat{m}_L , g) from measurements of *d* and *l*.

Estimates of \hat{m}_L and \hat{m}_D for all live and attached dead branches were summed for each sample tree to obtain estimates of total branchwood dry mass of live and attached dead branches for each tree (\hat{M}_L and \hat{M}_D , respectively, kg). The following allometric equation was fit to \hat{M}_L in relation to DBH (*D*, cm), measured at 1.3 m above ground level, and tree height (*H*, m) of the six study trees:

$$[2] \quad \hat{M}_L = a D^b H^c$$

where *a*, *b*, and *c* are parameters estimated using nonlinear least squares regression. The same equation was applied to and the same parameters were estimated for \hat{M}_D .

C and N contents and dynamics of the canopy woody detritus pool

To estimate C and N content of attached dead branches, the oven-dried sample sections taken from sample branches in each decay class (DC1–DC5), were used to estimate C and N concentrations. Disks (5 mm in thickness) were cut from each sample section. The proportion of bark included in the disk samples was adjusted to represent that of the sample section. The disk samples were ground to a fine powder, and C and N concentrations (percent dry mass) were measured with an NC analyzer (Sumigraph NC-900, Sumika Chemical Analysis Service Ltd., Osaka, Japan). For estimation of C and N pools, decay class weighted mean C and N concentrations were calculated based on the dry mass contribution of each decay class. The estimated total dry mass of attached dead branches in the six study trees was multiplied by the decay class weighted mean C and N concentrations to obtain estimates of C and N pools in attached dead branches in the six study trees.

Fig. 1. Examples of different decay classes (DC1–DC5) of attached dead branches in the canopy of old-growth Douglas-fir trees in southwestern Washington State (Wind River Canopy Crane Research Facility).



We also assessed the dynamics of the canopy woody detritus pool. Equation 1 was applied to all branches surveyed in 1998 and 2003 and summed for each tree to obtain estimates of \hat{M}_L and \hat{M}_D for both years. We then calculated the net change in \hat{M}_D over the 5-year period as a result of input from the death of live branches and losses due to branchfall and fragmentation ($\text{kg}\cdot\text{year}^{-1}$). Using estimates of C and N concentrations, we calculated losses of C and N from the canopy woody detritus pool.

Comparison with previous studies

Previous studies relied on DBH as the only independent variable for estimating biomass of canopy components (Grier and Logan 1977; Gholz et al. 1979; Snell and Max 1985). We compared our method of tree-level estimation, which

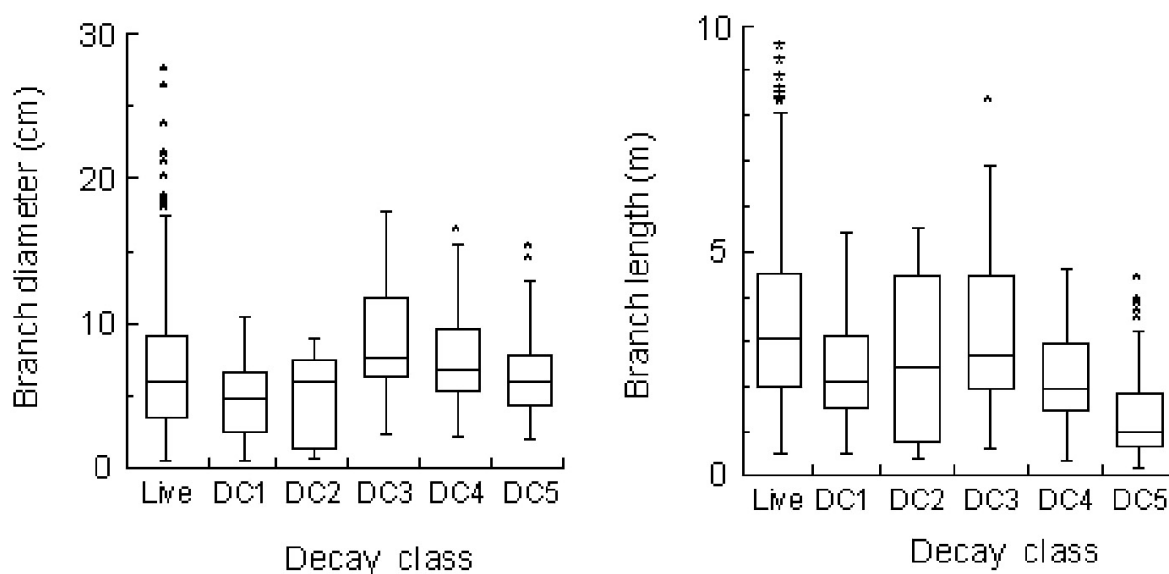
uses both diameter and tree height as independent variables, with those of previous studies. Grier and Logan (1977) developed equations for estimating branchwood dry mass of live and attached dead branches in the canopy of Douglas-fir trees in a 450-year-old Douglas-fir – western hemlock forest in western Oregon (watershed 10, H.J. Andrews Experimental Forest). Gholz et al. (1979) developed equations for estimating dry mass of tree components for many tree species in the Pacific Northwest region, which have been used to estimate primary production of different forest types in western Oregon (Gholz 1982). Snell and Max (1985) developed equations to estimate dry mass of live and attached dead branches in the crown of old-growth Douglas-fir trees in western Washington (Wind River Experimental Forest). Estimates based on equations from previous studies (Table 2)

Table 2. Equations for estimating branchwood dry mass of live and attached dead branches in the canopy of old-growth Douglas-fir trees in western Oregon and Washington, USA.

Equation	R^2	n	Source
[3] $\ln \hat{M}_L = -4.786 + 2.389 \ln D$	0.97	29	Grier and Logan 1977
[4] $\ln \hat{M}_D = -2.455 + 1.400 \ln D$	0.86	17	
[5] $\ln \hat{M}_L = -3.694 + 2.138 \ln D$	0.92	123	Gholz et al. 1979
[6] $\ln \hat{M}_D = -3.529 + 1.7503 \ln D$	0.84	85	
[7] $\ln \hat{M}_L = 4.0068 + 0.0206 D$	0.73	32	Snell and Max 1985
[8] $\ln \hat{M}_D = -10.6294 + 3.2692 \ln D$	0.79	32	

Note: \hat{M}_L , branchwood dry mass of live branches; \hat{M}_D , dry mass of attached dead branches. D , DBH.

Fig. 2. Box-whisker plots of the frequency distribution of diameter and length for live branches and attached dead branches (DC1–DC5) in the canopy of old-growth Douglas-fir trees in southwestern Washington State (Wind River Canopy Crane Research Facility). Box length is the interquartile range (the middle 50% of the data). The line inside the box is the median. The “whiskers” represent cases that are within 1.5 box lengths of the upper and lower edge of the box. Cases outside this range are plotted as asterisks.



were compared graphically with our estimates of \hat{M}_L and \hat{M}_D for the six study trees.

Results

Characteristics of dead branches in the canopy

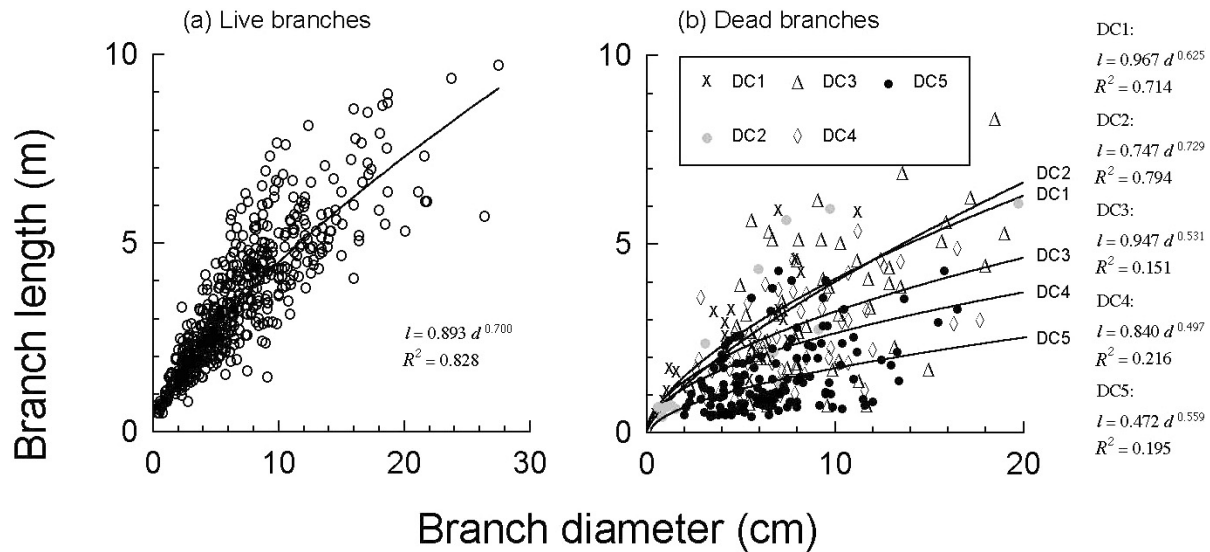
A total of 318 dead branches were measured in 1998 in the six study trees. Of these, 265 branches were remeasured in 2003 and 53 were broken at less than 0.5 m length from the main stem (branchfall). The diameter and length distributions of both live and attached dead branches in the canopy were positively skewed, with many small branches and few large branches (Fig. 2). For live branches, median diameter and length in 1998 were 5.9 cm and 3.0 m, respectively. For attached dead branches, median diameter and length increased from DC1 to DC3 and decreased from DC3 to DC5. The allometric relationship between branch diameter and length was significant for live branches and all decay classes of attached dead branches (Fig. 3). The relationship was strongest for live branches, followed by DC2 and DC1 branches, as indicated by high R^2 values. The diameter–length relationship became weaker as the variance in branch length increased from DC3 to DC5. The diameter–length relation-

ship also indicated that mean branch length for a given branch diameter decreased with increasing decay class from DC3 to DC5.

Of the five decay classes of attached dead branches, there were relatively few DC1 and DC2 branches in the six study trees: 2.6% and 4.4% of the total number of branches, respectively. The mass contribution of DC1 and DC2 branches were 1.8% and 6.7%, respectively, of the total dry mass of attached dead branches in the six study trees. DC3 contributed 19.4% of the total number of attached dead branches but its mass contribution was much greater (43.7%), reflecting the large size of individual branches in this decay class. DC4 branches contributed 20.2% of the total number and 21.4% of the total mass. DC5 was the most abundant, contributing more than half (53.5%) of the total number of attached dead branches, but its mass contribution was only a quarter of the total (26.5%), reflecting the relatively small size of individual branches in this decay class.

The vertical distribution of live branches was top heavy (Fig. 4). The greatest number of branches was found in the top 90% of tree height, and the maximum dry mass occurred at 70%–80% of tree height. In contrast, the greatest number and dry mass of attached dead branches occurred at 50%–

Fig. 3. Branch diameter in relation to branch length for live (a) and attached dead branches (b) in the canopy of old-growth Douglas-fir trees in southwestern Washington State (Wind River Canopy Crane Research Facility). Lines indicate significant allometric relationships represented by the equations shown for each branch type ($P < 0.05$).



60% of tree height. DC1 and DC2 branches were found widely throughout various heights in the crown, while DC3–DC5 branches occurred in greater number and dry mass in the middle to lower crown.

Tree-level estimates of live- and dead-branch mass in the canopy

Total branchwood dry mass of both live and attached dead branches increased with increasing tree size (Fig. 5a). The following equations were derived for total branchwood dry mass in relation to D (cm) and H (m) for the six study trees:

$$[9] \quad \hat{M}_L = 1.061 \times 10^{-7} D^{1.84} H^{3.31} \quad (R^2 = 0.984)$$

$$[10] \quad \hat{M}_D = 3.141 \times 10^{-5} D^{1.89} H^{1.54} \quad (R^2 = 0.914)$$

The scaling exponents indicate the relative influence of D and H on estimates of branchwood dry mass. The scaling exponent for H in eq. 9 was larger than for D . The scaling exponent for H in eq. 10 was slightly smaller than for D .

Equations from previous studies for estimating \hat{M}_L based only on D (Table 2) were in good agreement with each other (Fig. 5a). Our estimates of \hat{M}_L for the six study trees were comparatively smaller. For the tall-medium tree ($D = 153.5$ cm), estimates based on previous studies were 146%–173% of our estimates. Equations from previous studies for estimating \hat{M}_D were highly variable. Our estimates agreed best with eq. 8 (Snell and Max 1985). However, their estimate for the tall-medium tree was 151% of our estimate.

The allometric relationship between \hat{M}_L and \hat{M}_D of the six study trees was approximated by the following equation (Fig. 5b):

$$[11] \quad \hat{M}_D = 1.081 \hat{M}_L^{0.787} \quad (R^2 = 0.961)$$

The scaling exponent was less than one, indicating that the rate of increase in \hat{M}_D slows with increasing \hat{M}_L . The relationships between \hat{M}_L and \hat{M}_D from previous studies were

highly variable amongst each other and did not agree with our estimates.

C and N contents and dynamics of the canopy woody detritus pool

C concentration of attached dead branches showed no directional trend with decay class (Table 3), though C concentrations of DC2 and DC3 branches were higher than those of DC1, DC4, and DC5 branches (ANOVA, $F = 5.36$, $P < 0.01$). N concentration decreased with increasing decay class ($F = 2.89$, $P = 0.04$) such that N concentration of DC1 branches was higher than those of DC3, DC4, and DC5 branches ($P < 0.04$). Decay class weighted mean concentrations based on the relative proportions of dry mass in each decay class were 46.45% for C and 0.115% for N.

During the 5-year study period, 6.99 kg·year⁻¹ of live branches died attached and 10.76 kg·year⁻¹ were lost because of branchfall and fragmentation from the six study trees. These amounts corresponded to mean annual losses of 0.24% and 0.37%, respectively, of the total branchwood dry mass of live branches. Three large live branches ($d = 5.9$ – 13.9 cm, $l = 4.2$ – 5.3 m) were broken in the tallest tree and the tall-medium tree during the winter of 1999–2000, contributing 8.1% (4.38 of 53.80 kg over the 5-year period) of branchfall and fragmentation of live branches. The amount of branchfall and fragmentation of attached dead branches was greater than for live branches (Table 4). During the winter of 2000–2001, a neighboring snag fell down, damaging the lower crown of the shortest tree and causing many dead branches in the lower crown to break. In addition, a large dead branch ($d = 16.5$ cm, $l = 1.6$ m) was broken in the tallest tree. During the 5-year study period, we observed decreases in \hat{m}_D for 65% of the total number of attached dead branches of the six study trees. Nearly half (45%) of the attached dead branches showed decreases in length greater than 0.1 m. The amount of dry mass loss was relatively low for DC1 and DC2 and higher for DC3–DC5. Percent annual loss was low for DC1–DC3 and higher for DC4 and DC5.

Fig. 4. Vertical distribution of the number and dry mass of live and attached dead branches in the canopy of old-growth Douglas-fir trees in southwestern Washington State (Wind River Canopy Crane Research Facility). Relative height in tree is the height above ground of each branch divided by tree height. For the live branches, bars represent percentages relative to the total for all live branches in the six study trees. For the dead branches, bars represent percentages relative to the total for all attached dead branches in the six study trees distinguished by decay class.

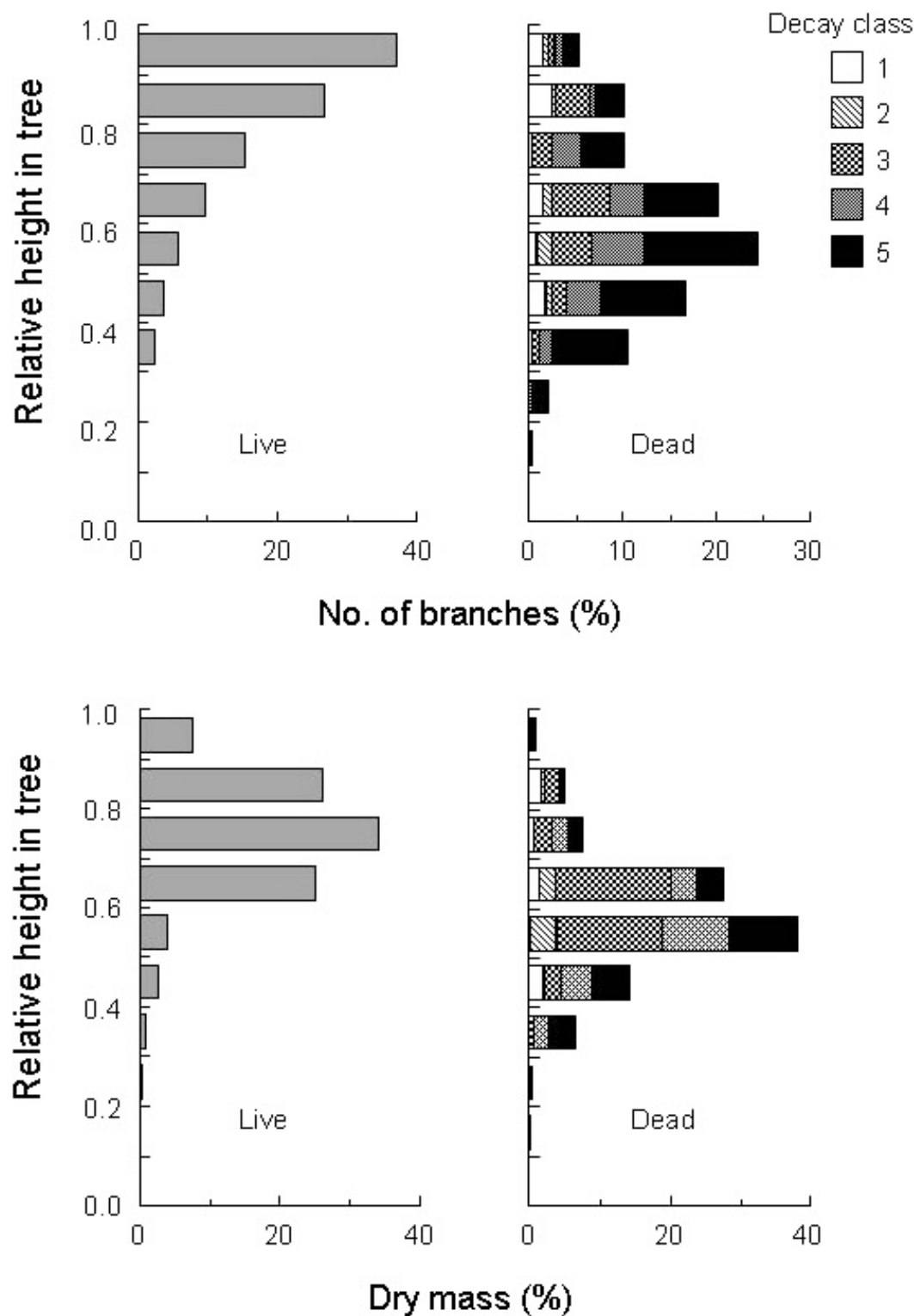


Fig. 5. Comparison of estimates of total branchwood dry mass of live and attached dead branches in relation to DBH (a) and the relationship between total branchwood dry mass of live branches and that of attached dead branches per tree (b). Estimates for the six old-growth Douglas-fir trees in southwestern Washington State (Wind River Canopy Crane Research Facility) are shown as data points. Equations for estimating branchwood dry mass from DBH from previous studies are shown as lines.

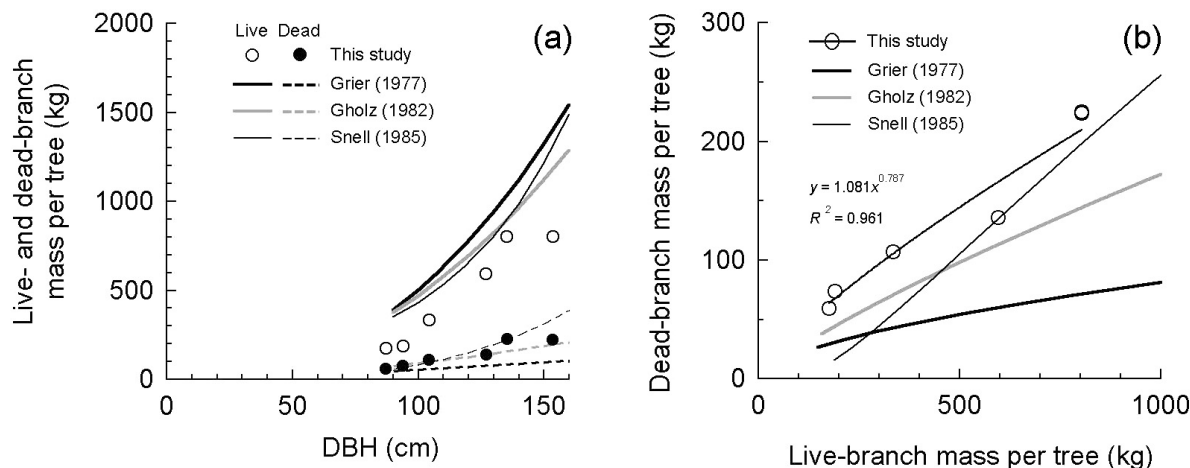


Table 3. Carbon (C) and nitrogen (N) concentration of attached dead branches in the canopy of old-growth Douglas-fir trees in southwestern Washington State (Wind River Canopy Crane Research Facility).

Decay class	% dry mass	
	C	N
DC1	45.86 (0.32)a	0.155 (0.007)a
DC2	47.79 (0.35)b	0.131 (0.014)ab
DC3	47.31 (0.27)b	0.110 (0.010)b
DC4	45.32 (0.56)a	0.107 (0.011)b
DC5	45.63 (0.47)a	0.121 (0.009)b
Decay class weighted mean	46.45	0.115

Note: Figures in parentheses indicate 1 SE. Values labeled with the same letter are not significantly different from each other (ANOVA followed by Tukey's test, $P < 0.05$). The mean concentrations weighted by decay class are based on dry mass estimates in each decay class (see text).

Together, branchfall and fragmentation of attached dead branches resulted in the loss of $35.94 \text{ kg} \cdot \text{year}^{-1}$ of dead-branch mass, corresponding to a mean annual loss of 4.34%. Using estimates of C and N concentrations in each decay class (Table 3), we estimated that branchfall and fragmentation of attached dead branches resulted in losses of $16.69 \text{ kg C} \cdot \text{year}^{-1}$ and $41.33 \text{ g N} \cdot \text{year}^{-1}$ from the six study trees.

Discussion

Characteristics of dead branches in the canopy

Means et al. (1992) found that size of logs on the forest floor decreased progressively with increasing decay class in a 450-year-old Douglas-fir forest in the H.J. Andrews Experimental Forest, Oregon, and inferred that large trees constituted recent deaths and that smaller logs decayed more rapidly. In this study, diameter of attached dead branches were smaller for DC1 and DC2 compared with those for DC3–DC5, suggesting that small, presumably young branches constituted recent branch deaths, while death of large-diameter branches had occurred in the recent past. Branch

Table 4. Estimates of annual dry mass loss of attached dead branches between 1998 and 2003 in the canopy of old-growth Douglas-fir trees in southwestern Washington State (Wind River Canopy Crane Research Facility).

Decay class	Dry mass loss ($\text{kg} \cdot \text{year}^{-1}$)
DC1	0.43 (3.15)
DC2	1.72 (3.31)
DC3	9.78 (2.93)
DC4	9.82 (5.20)
DC5	9.14 (4.19)
Branch fall	5.05 (0.61)
Total	35.94 (4.34)

Note: Losses due to fragmentation were distinguished respectively by decay class determined in 2003. Decay class could not be determined for broken branches (branchfall). Figures in parentheses for each decay class, branch fall, and total indicate percent annual losses relative to dry mass estimates in 1998.

length progressively decreased from DC3 to DC5, reflecting fragmentation of attached dead branches with the progression of decay in the canopy.

The relationship between diameter and length also indicated that DC1 and DC2 branches maintained relatively good allometric relationships. However, as decay progressed from DC3 to DC5, the diameter–length relationship became weaker as the result of more variable branch lengths. Ishii et al. (2000a) showed that stochastic events such as breakage and partial death of live branches in old-growth Douglas-fir trees contributed to weaker allometric relationships compared with branches of young trees. From our observations in the canopy, we inferred that as decay progressed from DC3 to DC5, the bark and sapwood were lost and higher order axes and branch tips were broken, leaving only a short, heartwood core of the branch attached to the main stem. The stochasticity of branchwood fragmentation and sloughing is

likely to contribute to increasing the variability in branch sizes as decay progresses in the canopy.

The total number of branches increased with increasing decay class and was greatest for DC5, suggesting that dead branches remain attached for long periods and accumulate in the canopy of old-growth Douglas-fir trees. Large branches in DC3 and DC4 together contributed 65.1% of the total mass of attached dead branches in the canopy. These mainly occurred in the middle to lower crown of the study trees and comprised large original branches that died in the recent past. Comparatively smaller branches in DC1 and DC2 occurred widely throughout all canopy heights and comprised small epicormic branches that died relatively recently. Ishii and Wilson (2001) observed that several epicormic branches sprouted from the axils of old original branches that had died. Others have observed these sprays of epicormic branches to often form in the lower crown following the death of original branches, resulting in a downward extension of crown depth as trees reach the old-growth stage (Franklin and Van Pelt 2004, their Fig. 3). These epicormic branches may eventually be thinned and a few dominant branches remain. From the size distribution and relative amounts and vertical distribution of attached dead branches in the five decay classes, we inferred that death of large original branches had occurred in the recent past, followed by production of epicormic branches. Currently, the trees seem to be at the stage of crown development where death of epicormic branches is occurring.

Many of the Douglas-fir trees in this stand have reached maximum tree height and crown volume (Ishii et al. 2000b, 2003). Winter et al. (2002) showed that height growth rate decreased considerably after about 250 years in old-growth Douglas-fir, while diameter growth continued indefinitely. This suggests that respiratory surface area continues to increase in old Douglas-fir trees even after foliage amount culminates. This would result in a decreasing ratio of productive to nonproductive tissue, leading to decreased crown productivity (Remphrey and Davidson 1992). Self-pruning of branches is one mechanism that reduces the amount of nonproductive woody tissue (Maguire and Hann 1987; Gerrish 1990). The death of large original branches in the middle to lower crown of the study trees probably contributed to large reductions in the amount of nonproductive woody tissue. In old Douglas-fir trees, self-pruning of original branches followed by epicormic branching may work to maintain crown productivity by increasing the ratio of productive to nonproductive tissue.

Tree-level estimates of live- and dead-branch mass in the canopy

For CWD on the forest floor, wood density generally decreases with the progress of decomposition (Harmon et al. 1986). Studies of wood decay on the forest floor have shown that wood density of Douglas-fir logs on the forest floor decreases with increasing decay class (Sollins 1982; Sollins et al. 1987). In contrast, our analysis indicated that the relationship between size and dry mass of attached dead branches in the canopy did not change with decay class (eq. 1). Abiotic decomposition processes such as fragmentation and sloughing are presumed to be more dominant in the canopy than on the forest floor (Fonte and Schowalter 2004). The constant size–

dry mass relationship of attached dead branches suggests that there is a threshold density below which fragmentation and sloughing occur, such that the density of the branchwood left attached to the tree remains constant regardless of decay class.

Grier and Milne (1981) contend that allometric equations for predicting biomass components from DBH for a given species tend to be widely applicable. In the absence of alternatives or resources for developing site-specific equations, many researchers have applied allometric equations from the literature beyond the range of data and conditions from which they were derived. There have also been efforts to derive “universal” equations for predicting various biomass components for a given region (e.g., Gholz et al. 1979 for the Pacific Northwest, USA). The results of this study indicated that this practice may lead to widely variable estimates of biomass, C, and nutrient stores. When applied to the six study trees, estimates of total branchwood dry mass of live branches (\hat{M}_L) based on equations from previous studies were consistently higher than our estimates. One reason for the lower estimates in this study may be because our equation for estimating branchwood dry mass of individual live branches (\hat{m}_L) was derived from the relationship between branch size and dry mass of dead branches (eq. 1). Live branches include more fine axes and twigs that are not found on dead branches. Our estimates of \hat{M}_L may have been greater had we been able to sample live branches separately and developed separate equations for estimating \hat{m}_L . Another reason for the comparatively smaller estimates in this study may be because the Douglas-fir trees used in previous studies were taller than our six study trees. The six study trees fell within the range of diameters covered by previous studies. However, the diameter–height relationship may be different. Grier and Logan (1977) sampled trees up to 76.5 m tall. Gholz et al. (1979) and Snell and Max (1985) only give diameter ranges for their sample trees, but their trees may also be taller than our study trees. Equation 9 indicated that H was more important than D in predicting \hat{M}_L . Of the six study trees, D was greatest (153.5 cm) for the tall-medium tree, but this tree was the third tallest. Our estimate of \hat{M}_L for the tall-medium tree based on eq. 9 was much smaller than estimates based on equations from previous studies. Our results suggested that estimates of \hat{M}_L based on diameter alone may result in large discrepancies if applied to stands with different diameter–height relationships and that tree height is an important predictor variable in estimating biomass of canopy components.

Grier and Logan (1977) estimated that mean dry mass of attached dead branches per tree was 39.9 kg for a 450-year-old Douglas-fir – western hemlock forest at H. J. Andrews Experimental Forest. Our estimates ranged between 57.2 and 225.0 kg·tree⁻¹ and best agreed with eq. 8 (Snell and Max 1985), whose study was conducted in the same region. However, as with \hat{M}_L , our estimate of \hat{M}_D for the tall-medium tree was lower than that predicted by eq. 8. The large variability found among previous studies reflected the uncertainty associated with estimation of \hat{M}_D . In addition to directional processes of crown development such as self-pruning and epicormic branching, stochastic processes such as crown disturbance influence branch mortality rates. The implications of this study are limited because of the small sample size (six trees). However, we showed that direct ob-

servations in the canopy can elucidate the effects of crown developmental history on canopy detritus stores and help to refine estimates of the canopy woody detritus pool.

Although the rate of increase in \dot{M}_D decreased with increasing \dot{M}_L , the positive slope of the relationship and the presence of numerous DC5 branches in the canopy suggested continuous accumulation of attached dead branches in the crown of old-growth Douglas-fir trees with increasing tree size. Grier et al. (1981) found that dry mass of attached dead branches was four times as large ($7.9 \text{ Mg}\cdot\text{ha}^{-1}$) in 180-year-old mature *Abies amabilis* stand than in the 23-year-old young stand ($2.0 \text{ Mg}\cdot\text{ha}^{-1}$) in the Washington Cascades. These observations suggest that the canopy woody detritus pool accumulates with increasing stand age. Studies of CWD on the forest floor have shown that Douglas-fir snags and logs are relatively more resistant to decay than western hemlock and the true firs (*Abies* spp.) (Graham and Cromack 1982; Erickson et al. 1985; Sollins et al. 1987). Similarly, attached dead branches in the canopy of old Douglas-fir trees may persist for many years, contributing an increasing amount to the stand-level canopy woody detritus pool.

C and N contents and dynamics of the canopy woody detritus pool

Harmon et al. (2004) estimated that the total C store for attached dead branches in this stand was $318 \text{ g C}\cdot\text{m}^{-2}$. Using the decay class weighted mean C concentration (46.45%), we estimated that C stored in attached dead branches of the six study trees in 1998 was 384.5 kg. If we extrapolate this estimate to the stand level using the ratio of basal area of the study trees (6.7 m^2) to the stand total ($35.4 \text{ m}^2\cdot\text{ha}^{-1}$), our stand-level estimate for C stored in attached dead branches of Douglas-fir is $203.1 \text{ g C}\cdot\text{m}^{-2}$. This accounts for 63.8% of the stand total estimated by Harmon et al. (2004). Large old trees of Douglas-fir contribute more than 42% of the total basal area of this stand. In addition, the decay rate of Douglas-fir wood is very slow. For example, logs and snags of Douglas-fir contributed 45.8% (1920 of $4190 \text{ g C}\cdot\text{m}^{-2}$) of the total C store in logs and 75.1% (2170 of $2890 \text{ g C}\cdot\text{m}^{-2}$) of the total C store in snags (Harmon et al. 2004). Similarly, attached dead branches in the crown of old Douglas-fir trees may contribute a large proportion of the total canopy woody detritus pool in this stand.

Our results showed that fragmentation and branchfall of attached dead branches resulted in loss of biomass from the canopy woody detritus pool. Harmon et al. (2004) estimate that $3 \text{ g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ was transferred from the canopy to the forest floor as a result of fragmentation and branchfall of attached dead branches in this stand. If we extrapolate our estimate of C loss from the canopy of the six study trees to the stand-level using the same calculations as before, our stand-level estimate of C transfer from the canopy to the forest floor is $8.82 \text{ g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$. This estimate may be too high because not all losses due to branchfall and fragmentation resulted in transfer to the forest floor and some pieces may remain suspended in the canopy. Observations made in the canopy need to be combined with measurements of litterfall made on the forest floor to account for suspended woody detritus. On the other hand, Harmon et al. (2004) conducted experiments using branches hung near the forest floor to es-

timate the rate of mass loss of attached dead branches due to fragmentation (M. Harmon, personal communication, June 2004). Abiotic processes such as fragmentation and sloughing are thought to dominate in the decomposition of attached dead branches in the canopy (Fonte and Schowalter 2004). We observed that loss of higher order axes and reduction in branch length were the main causes of fragmentation of attached dead branches. It may be difficult to reproduce these processes to the degree to which they actually occur in the canopy using suspended samples. Our results suggested that rates of dry mass and C loss due to fragmentation in the canopy may be greater than previously thought. More long-term observations of branch dynamics in the canopy combined with measurements of litterfall on the forest floor are needed to confirm this result.

Our results also suggested that fragmentation and branchfall of attached dead branches resulted in loss of N from the canopy woody detritus pool. Although N content of branchwood is very low, significant amounts fall from the canopy to the forest floor each year in temperate coniferous forests (Grier and Logan 1977; Harmon et al. 2004). For example, Sollins et al. (1980) estimated that $0.38 \text{ g N}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ was transferred from the canopy to the forest floor in the form of fine woody litter at watershed 10, H.J. Andrews Experimental Forest. In this study, N concentration of attached dead branches increased with increasing decay class probably because, as decay progresses, fragmentation and sloughing results in the loss of bark and sapwood, both of which have high N concentrations. Because the occurrence of tree and snag falls is sporadic, fine woody litter resulting from fragmentation of attached dead branches may be important as a constant source of N-rich substrate for fungi and other decomposers that use woody litter on the forest floor. Researchers have found that fungal colonization of branchwood occurs in the canopy even before branches fall to the forest floor (e.g., Swift et al. 1976; Chapela and Boddy 1988a, 1988b). Because characteristics of the forest canopy has important implications for nutrient cycling in forest ecosystems (Prescott 2002), the supply of woody detritus from the canopy to the forest floor through fragmentation and branchfall deserves more attention in nutrient cycling studies (Edmonds 1987).

Harmon et al. (2004) assumed there was no net change in the canopy woody detritus pool during their 5-year survey of C stores in this stand. However, as with tree mortality, branch death is a stochastic process influenced by stand history and crown development, such as the timing of crown closure and the types and frequency of crown disturbances. Tree mortality is highly variable through time and causes large fluctuations in stand biomass (Grier and Logan 1977; Franklin et al. 1987). Several studies point out the importance of disturbance history in determining the amount of CWD (Lambert et al. 1980; Spies et al. 1988; Webb 1989). Similarly, branch mortality in the canopy may be highly variable, with fluctuations resulting from periodic death events (Maguire 1994). During our 5-year study, we observed that disturbances such as a falling snag can cause large amounts of branchfall and fragmentation. These observations suggest that the canopy woody detritus pool may not be a steady-state system. Clark et al. (2001) found that annual variation in the amount of branchfall can be very high in tropical forests and recom-

mended that measurements over 5- to 10-year periods may be necessary to obtain reliable "background" rates. This study represents the first effort to make direct long-term observations in the canopy to investigate the dynamics of the canopy woody detritus pool.

Conclusions

Buchmann and Schultze (1999) found that net ecosystem flux rates of CO₂ were lowest in stands younger than 20 years and highest in intermediate-aged stands (30–80 years). Rates in stands older than 160 years fell in between these two age-classes, suggesting that old-growth stands may not be at equilibrium with respect to C balance. If old-growth forests are a C sink, primary production rates may be higher or decomposition and respiration rates may be lower than the current estimates. Accumulation of woody detritus both on the forest floor and in the canopy may contribute to increasing C storage as stands increase in age because decomposition rate of woody detritus is slow and there is considerable accumulation as CWD on the forest floor and as attached and suspended woody detritus in the canopy. Randerson et al. (2002) stress the importance of considering all possible sources of C flux in and out of ecosystems to accurately estimate net ecosystem production (NEP). Because "background" rates of stochastic processes such as tree mortality and branch death are difficult to quantify in short-term investigations, long-term monitoring is needed to understand these processes in more detail.

Various studies (e.g., Cline et al. 1980; Harmon et al. 1986) propose that management of woody detritus is important for maintaining plant and wildlife habitat in old-growth forests. Our study indicated that a significant amount of woody detritus exists in the canopy of old-growth Douglas-fir trees. Because various structural components in the canopy, including attached dead branches, are used as habitat by canopy-dwelling organisms, epiphytes, and decomposers, we contend that canopy woody detritus is an important component of managing habitat for old-growth conditions.

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