Decomposition of coarse woody debris originating by clearcutting of an old-growth conifer forest[1]

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Abstract: Decomposition constants (k) for above-ground logs and stumps and sub-surface coarse roots originating from harvested old-growth forest (estimated age 400-600 y) were assessed by volume–density change methods along a 70-y chronosequence of clearcuts on the Wind River Ranger District, Washington, USA. Principal species sampled were *Tsuga heterophylla* and *Pseudotsuga menziesii*. Wood and bark tissue densities were weighted by sample fraction, adjusted for fragmentation, then regressed to determine k by tissue type for each species. After accounting for stand age, no significant differences were found between log and stump density within species, but *P. menziesii* decomposed more slowly ($k = 0.015 \cdot y^{-1}$) than *T. heterophylla* ($k = 0.036 \cdot y^{-1}$), a species pattern repeated both above- and below-ground. Small-diameter (1-3 cm) *P. menziesii* roots decomposed faster ($k = 0.014 \cdot y^{-1}$) than large-diameter (3-8 cm) roots ($k = 0.008 \cdot y^{-1}$), a pattern echoed by *T. heterophylla* roots (1-3 cm, $k = 0.023 \cdot y^{-1}$; 3-8 cm, $k = 0.017 \cdot y^{-1}$), suggesting a relationship between diameter and k. Given our mean k and mean mass of coarse woody debris stores in each stand (determined earlier), we estimate decomposing logs, stumps, and snags are releasing back to the atmosphere between 0.3 and 0.9 Mg $C \cdot ha^{-1} \cdot y^{-1}$ (assuming all coarse woody debris is *P. menziesii*) or 0.8-2.3 Mg $C \cdot ha^{-1} \cdot y^{-1}$ (assuming all coarse woody debris is *T. heterophylla*). Including coarse roots increases these loss calculations (averages of all decomposition classes for the study year) to 0.5-1.9 Mg $C \cdot ha^{-1} \cdot y^{-1}$ or 1.0-3.5 Mg $C \cdot ha^{-1} \cdot y^{-1}$, respectively. Our results support substitution of log k in C flux models when stump k is unknown. Substitution of log k for coarse root k could, however, substantially overestimate C flux back to the atmosphere from these forests.
Keywords: carbon storage, coarse woody debris, decomposition, logs, roots, stumps.

Résumé : Nous avons déterminé les constantes de décomposition (k) des arbres pour les troncs et les souches sur le sol ainsi que pour les grosses racines dans le sol. L'étude s'est déroulée dans une forêt ancienne exploitée dont l'âge a été estimé entre 400 et 600 ans. Les constantes ont été déterminées par des méthodes de changements de volume et de densité le long d'une chronoséquence de coupes forestières s'étalant sur une période de 70 ans dans le district de Wind River Ranger, dans l'État de Washington, aux États-Unis. Les principales espèces échantillonnées étaient *Tsuga heterophylla* et *Pseudotsuga menziesii*. Les densités du bois et de l'écorce ont été pondérées en fonction des fractions de l'échantillonnage, ajustées pour la fragmentation, puis soumises à une régression pour déterminer la valeur de k par type de tissu pour chaque espèce. Après avoir tenu compte de l'âge du peuplement, nous n'avons trouvé aucune différence significative entre la densité des troncs et des souches pour une même espèce. Toutefois, *P. menziesii* se décompose plus lentement ($k = 0,015 \cdot an^{-1}$) que *T. heterophylla* ($k = 0,036 \cdot an^{-1}$), que ce soit sur ou sous la surface du sol. Les racines de petit diamètre (1 à 3 cm) de *P. menziesii* se décomposent plus rapidement ($k = 0,014 \cdot an^{-1}$) que celles de plus grand diamètre (3 à 8 cm; $k = 0,008 \cdot an^{-1}$). Ce patron se répète chez les racines de *T. heterophylla* (racines de 1 à 3 cm de diamètre : $k = 0,023$ an^{-1}; racines de 3 à 8 cm : $k = 0,017 \cdot an^{-1}$), ce qui suggère qu'une relation existe entre le diamètre et la constante de décomposition. À partir des constantes moyennes et des masses moyennes des gros débris ligneux déterminées dans chaque peuplement, nous avons estimé que les troncs, les souches et les racines émettent entre 0,3 et 0,9 Mg de $C \cdot ha^{-1} \cdot an^{-1}$ vers l'atmosphère chez *P. menziesii* et entre 0,8 et 2,3 Mg de $C \cdot ha^{-1} \cdot an^{-1}$ chez *T. heterophylla*. Le fait d'inclure les grosses racines dans ces calculs contribue à hausser les valeurs estimées. Elles s'étendent de 0,5 à 1,9 Mg $C \cdot ha^{-1} \cdot an^{-1}$ chez *P. menziesii* et de 1,0 à 3,5 Mg $C \cdot ha^{-1} \cdot an^{-1}$ chez *T. heterophylla*. Il serait possible de substituer la constante de décomposition des troncs dans les modèles de flux de carbone lorsque la constante des souches est inconnue. La substitution de la constante de décomposition des troncs par celle des grosses racines pourrait néanmoins avoir pour effet de surestimer grandement les flux de carbone vers l'atmosphère dans ces forêts.
Mots-clés : décomposition, gros débris ligneux, puits de carbone, racines, souches, troncs.

Nomenclature: Willis, 1988.

Introduction

Despite widespread clearcutting of boreal, temperate, and tropical forests and the high loads of coarse woody debris (CWD) generated by this type of landscape management (Howard, 1981; Harmon, Garman & Ferrell, 1996), few studies address decomposition of CWD originating from clearcutting. Decomposition constants (k) for CWD in clearcuts and young stands are thus generally unknown and consequently must be inferred when needed from those derived from fallen logs in older, closed-canopy forests, which have been reasonably well studied across a range of closed forest types and ages (Harmon *et al.*, 1986; Harmon *et al.*, 2001; Yatskov, Krankina & Harmon, 2003). Such inferences may be inappropriate, however, because clearcuts impose a different environ-

ment on wood decomposition than do closed canopies. Moreover, length, orientation, and decomposition-class distribution of logs and stumps resulting from clearcutting differ from those of logs and snags in forests that have never been harvested. Uncertainty in estimating decomposition constants is also high for coarse roots, which are even less well studied than logs (Yavitt & Fahey, 1982; Chen, Harmon & Griffiths, 2001). Distinct above- *versus* below-ground effects exerted on decomposition (Harmon *et al.,* 1986) also raise doubts about whether above-ground, log-derived decomposition constants apply to woody pools in the soil column such as coarse roots.

Lack of study of CWD originating from clearcuts thus hinders accurate modelling of woody decomposition throughout succession, but also has other consequences. For example, estimation of net ecosystem productivity (NEP, or difference in ecosystem carbon [C] gains and losses over time) is affected, because assessing forest C fluxes depends on knowing the *in situ* decomposition constant, as well as the store of C in CWD, both of which in turn affect classification of ecosystems as sources or sinks of CO_2 relative to the atmosphere. Because an estimated 80% (454 Pg) of terrestrial vegetation C is stored as forest biomass, roughly half as live trees and CWD (Dixon *et al.,* 1994), the consequences of managing forests with biased *k* estimates are not trivial. Harvesting an old-growth stand with a full-tree mass of 364 Mg C·ha^{-1} (Smithwick *et al.,* 2002), for example, leaves an estimated 74 Mg C·ha^{-1} as stumps and coarse roots to decompose to CO_2. Thus, when CWD loads generated by harvesting forests are high, estimates of *k* biased by even a few percent can influence estimates of C flux back to the atmosphere by several Mg C·ha^{-1}·y^{-1}. Bias of this magnitude rivals net primary productivity (NPP) of some forest age classes (Turner & Long, 1975; Law *et al.,* 2001), thus confounding whether such stands are C sources or C sinks.

We derived our preliminary estimates of *k* from a chronosequence of regenerating stands, originating from clearcutting of old growth, by evaluating density changes of CWD. While deriving estimates of *k* from direct observations of stands through time would be ideal, such an approach is impractical for several tree species dominating Pacific Northwest forests because decomposition of wood from these species takes many decades. We thus instead substituted space for time, using a chronosequence of stands to derive less precise but quicker estimates. We asked several questions, including 1) is *k* estimated from CWD originating from clearcutting old growth similar to *k* estimated from intact old growth; 2) how does *k* of above-ground CWD (*e.g.,* stumps and logs) compare to *k* of sub-surface coarse roots; and 3) are *k* of stumps and logs similar? We sampled logs, stumps, and roots (the principal CWD pools remaining after a stand-destroying disturbance; Tinker & Knight, 2000) from Douglas-fir (*Pseudotsuga menziesii)* and western hemlock (*Tsuga heterophylla*), as well as a limited number of logs from western red cedar (*Thuja plicata*) and *Abies* sp. (likely *A. amabilis* [Pacific silver fir]). A set of conifer stumps not identifiable to species by our methods (hereafter identified as Group 3 but also likely *Abies* sp.), but drawn from our chronosequence, were also sampled to maximize our stump and log counts of a given age.

Study region

Data were collected from forest stands within the USDA Forest Service Wind River Ranger District, Gifford Pinchot National Forest, approximately 20 km north of the Columbia River Gorge in southwest Washington State, USA. This study was part of a larger, integrated project already in progress at the well-studied T. T. Munger Research Natural Area (RNA), so stand selection was confined to a roughly 10- × 10-km region centred on the RNA (45° 49' N, 121° 58' W). Elevation ranges approximately between 335 m and 1,200 m in this region, and soils are classified as well-drained Stabler series Andic Haplumbrept (Franklin *et al.,* 1972) derived from recent volcanic tephra (Franklin & DeBell, 1988). The district lies in the Cascade Mountains rain-on-snow zone. Winters are temperate and wet; summers are warm and dry. Mean precipitation recorded at the Wind River Ranger Station (1936-1972) is 250 cm·y^{-1}, with less than 10% falling between June and September (Franklin & DeBell, 1988). Mean annual temperature is 8.7 °C (Wind River Canopy Crane data). Based on ring counts from stumps and trees inside or adjacent to the RNA, old-growth forests in this area originated approximately 500 y ago (DeBell & Franklin, 1987). This age class is common over large regions of the Central Cascades in Oregon and Washington and is attributed to vast, stand-destroying fires that swept across the Central Cascades during a climatically dry period *ca* 1490 (Franklin & Waring, 1979). Vegetation of the study region is dominated by *P. menziesii–T. heterophylla* forests. RNA vegetation is transitional between *T. heterophylla* and *A. amabilis* zones (Franklin & Dyrness, 1973). Harvested stands regenerated by combinations of replanting and natural seeding.

Methods

Stand selection

Stands sampled were USDA Forest Service harvest units regenerating from commercial clearcutting and drawn from the Gifford Pinchot Oracle database, as described earlier (Janisch & Harmon, 2002). Candidate stands were grouped into decadal age classes (1940-1949, 1950–1959, etc.) with stand age based on harvest date, then final selection criteria were applied. Final stand-selection criteria, complementing criteria outlined earlier for other project goals (Janisch & Harmon, 2002; Janisch & Harmon, unpubl. data), were the following:

Elevation: Stands were between approximately 360 m and 900 m. The lower elevation limit was the valley floor. The upper elevation limit was selected to avoid the transition zone from *Pseudotsuga*-dominated to *Abies*-dominated forest.

Size: Generally only stands able to contain a 200-m transect plus 100-m perimeter buffers (*i.e.,* 400 m per side) were considered, because estimating CWD *k* was a sub-objective of a larger project investigating NEP (Janisch & Harmon, 2002). Stand dimensions were estimated from scaled USDA Forest Service orthophotos.

Presence of cut logs: Changing definitions of marketable wood diameter and quality over time (Harmon, Garman & Ferrell, 1996) resulted in nearly complete log

removal from some stands. These sites were avoided unless other sites of similar ages with logs were not available.

Aspect: Generally, stands from our complete 500-y, 36-stand chronosequence of second growth and old growth (constructed to meet other project objectives [Janisch & Harmon, 2002], which included stands of approximately north, south, and flat aspect for each of the first five decades) were sampled to derive our estimates of log, stump, and root k.

The age range for younger stands in the chronosequence (years of harvest 1945-1993) reflects clearcutting history on the district and stands available within the elevation band considered. Additional stands, clearcut after fire in 1928, were added to extend log and stump sampling further in time. This resulted in a stand age sequence of 7, 16, 22, 26, 31, 34, 45, 50, and 71 y post-harvest, from which 50 stumps and 41 logs were sampled. When possible, roots were sampled from the same stands. However, given the difficulty in excavating coarse roots, root life spans in soil, and a need for root samples from recently dead trees (not available at clearcut stands in our elevation band due to USDA Forest Service timber sale patterns), some stands were interchanged. Roots were thus sampled from 41 stumps from stands aged 0, 3, 7, 16, 22, 40, and 50 y. Roots aged 0 and 3 y were sampled from root wads of boles broken (but not windthrown) by winter storms.

As in any chronosequence, it is possible that spatial variation rather than temporal variation influenced our results. For example, cooler temperatures rather than short length of time a material is exposed to decomposition may cause decomposition rate to decline. It is also true that, due to forest practices, elevation (a proxy for temperature) and stand age in the study region are somewhat correlated. However, as we discuss below, it is unlikely our estimates of average decomposition rates are confounded by temperature effects.

LOG AND STUMP SELECTION

Logs were defined as downed dead tree boles with at least one cut end. Stumps were distinguished from snags by the presence of a cut upper surface, indicating commercial harvest of the bole. To reduce edge effects on k and to avoid perimeter slash, landings, and multiple-age cohorts resulting from road building, sampling was restricted to logs and stumps at least 20 m inside stand edges. Consistency of within-stand CWD cohort decomposition classes was visually assessed following definitions developed by Sollins (1982). Stands where broad or multiple-age cohorts appeared to be present were not sampled unless cohorts were widely separated in time or could be explained by known stand history, such as experimental thinning of primary forest (age 400-600 y) that occurred on the district *ca* 1940 (USDA Forest Service, 1951). To avoid snags felled by saw during harvest and left *in situ*, logs and stumps judged to have had heart rot at harvest, friable heartwood, woodpecker holes, or other indications of advanced decomposition (Harmon, Nadelhoffer & Blair, 1999) atypical of the sampling cohort were not sampled. Living stumps (those showing tissue growth over a cut surface) were also avoided. Logs

and stumps originating via post-harvest mortality and thinning were excluded by size and decomposition class and not sampled. Characteristics such as bark thickness and degree of furrowing, as well as stump growth form, were used to identify species.

STUMP SAMPLING

Because cut wood surfaces provide entry points for decomposition organisms and are thus generally zones of advanced decomposition (Meredith, 1973; Harmon & Sexton, 1996), the top 20-30 cm of each stump was removed by chainsaw and discarded. Each stump was then assessed for sections best representative of overall decomposition and fragmentation (Harmon *et al.,* 1986). Three cuts, two vertical (pith to cambium [or bark]) and one horizontal (through the disc of the stump), were made by chainsaw to remove a 30° - 40° (bark surface curvature) pie-shaped wedge of each stump. Pith-to-bark radii, thickness, and angle of each wedge were then recorded so that density could be calculated. Shells of bark and branch stubs (both resistant to decomposition) were used to estimate green (live) radii in cases where sapwood had fragmented (Harmon & Sexton, 1996). Total wedge weight (field-wet) was obtained to the nearest 0.5 g on a portable scale, then bark and wood tissues were separated. Sapwood and heartwood were not subdivided. Wood sub-samples were collected from each wedge as pith-to-cambium strips of tissue with an approximate field-wet mass of 200 g. When available, bark samples of similar mass were collected. Samples were sealed in plastic bags, transported to the lab within 48 h, and dried at 55 °C to constant mass.

LOG SAMPLING

Selection of representative logs was as for stumps. Zones of advanced decomposition associated with cut wood surfaces, game trails, crushing by falling trees, and other factors were avoided. Logs longer than approximately 3 m were sampled at two representative points; all others were sampled at a single point. Discs 10-15 cm thick were collected from logs by surveying a log for representative soundness, then making two vertical, parallel cuts through the log across its diameter. Where log diameter exceeded twice the working chain saw bar length (75 cm), logs were sampled by removing a wedge as for stumps (above). Log tissue sub-sampling, sample processing, and adjustments for sloughed sapwood was as for stumps.

ROOT SAMPLING

Four of the seven stands sampled for stumps and logs, plus three additional stands of age 0, 3, and 40 y (see above), were used for sampling coarse roots. Selection was restricted to the cohort population outlined above, with two to five stumps selected from each species at each stand. Living stumps were not sampled. Methods followed those of Chen, Harmon, and Griffiths (2001). Two dominant roots from each stump were excavated, stump butt to root tip, by hand shovel during summer 1999. After excavation, complete (wood + bark) 10- to 20-cm-long sections of root were removed by saw. Three to twelve root sections were sampled per stump and sorted into small (1-3 cm) and large (3-8 cm) classes based

on average diameter. Average diameter and longitudinal length of each section were calculated as the mean of three measurements of each dimension. Percent bark remaining was visually estimated, then bark was collected from each section. Bark from highly decomposed roots was not always fully recovered during excavation, but this was not expected to strongly influence estimation of k (Chen, Harmon, & Griffiths, 2001). After stripping all bark, root measurements were repeated to determine wood dimensions. Samples were then returned to the lab and dried at 65 °C to constant mass.

DENSITY

Density was determined as mass per unit volume (Swift, Heal & Anderson,1979; Harmon, Nadelhoffer & Blair, 1999), calculated as dry mass divided by green volume for each sample. For stumps and logs, dry-mass fraction was calculated as dry sub-sample mass divided by wet sub-sample mass, with total disc or wedge dry mass as the product of total wet (field) mass and dry-mass fraction. Root sample masses were determined directly from the entire sample. Volumes of stump samples (also some logs) were calculated as for a pie-shaped wedge of uniform average thickness:

$$V_w = \left[\frac{\theta}{360}\right] \times \pi \times \left(\left[\frac{(R_1 + R_2)}{2}\right]\right)^2 \times \left[\frac{T_1 + T_2}{2}\right] \qquad [1]$$

where V_w equals volume, θ equals wedge angle, R_1 and R_2 equal pith-to-outer-bark radii, and T_1 and T_2 are wedge thicknesses at pith and sapwood, respectively. Volume of each root section and log sample (except wedge-cut logs) was calculated as for a cylinder:

$$V_c = \frac{\pi \times (D^2 \times L)}{4} \qquad [2]$$

where V_c equals volume, D equals average diameter, and L equals average longitudinal length.

Bark volume was calculated as whole root (wood + bark) volume minus wood volume, adjusted for resin cores (*i.e.,* resin-saturated sections of roots resistant to decomposition; Chen, Harmon & Griffiths, 2001). Sapwood was only just beginning to slough from our oldest stump and log age classes, so adjustments to volume for fragmentation were negligible.

To account for differences in tissue k (Harmon & Sexton, 1996), density was calculated separately for each bark and wood sample as total dry weight divided by total sample volume, then combined into a single, tissue-weighted density for each stump or log. To adjust for log taper and density variation, a second weighting was applied when two samples were collected from a single log (Harmon & Sexton, 1996). Bark, wood, and resin-core densities of each individual root sample were calculated as total oven-dry weight divided by total green volume. Average root density was calculated as mean wood, bark, and resin-core densities for each sample, weighted by proportion of total root sample volume.

DATA ANALYSIS

We first compared densities of logs and stumps for each species, then assessed main and interaction effects.

Main and interaction effects of species, stand age, and position on density were evaluated by multiple linear regression, where density was raw density of each sample or its natural log transformation, species was an indicator variable, stand age was y since clearcutting, and position was an indicator variable distinguishing logs from stumps.

We then calculated k by several methods. First, decomposition constants and intercepts for our log and stump data were derived by fitting a single-exponential statistical model (Olson, 1963; Means, Cromack & MacMillan, 1985) of the form:

$$D_t = D_0\left(e^{-kt}\right) \qquad [3]$$

to each species (non-linear regression, SAS Institute, 1999), regressing density against time. Root parameter estimates were determined similarly. Because *P. menziesii* green wood could not be sampled (see above), we then re-estimated k for this species by non-linear regression using its published density ($D_0 = 0.45$ g·cm^{-3}; USDA Forest Products Laboratory, 1974). To assess linear *versus* non-linear model fit, we repeated the analysis using linear regression. Finally, to assess temporal variation, k of individual stumps and logs were calculated as (Olson, 1963)

$$k = \frac{-\left[\ln\left[(D_t)/(D_0)\right]\right]}{t} \qquad [4]$$

where D_t equals density at time t, D_0 equals green-wood density (USDA Forest Products Laboratory, 1974), and t equals y since clearcutting. Equation [4] was also used to explore effects of fragmentation on k using green-wood densities for *P. menziesii* and *T. heterophylla* (0.42 g·cm^{-3}). Due to small sample size, k for each *Abies* ($n = 2$) and *T. plicata* ($n = 1$) log was calculated by Equation [4] rather than regression. D_0 for these two species was assumed equivalent to sound (free of decay) green wood and bark, assigned as 0.310 g·cm^{-3} (*T. plicata* wood), 0.417 g·cm^{-3} (*Abies* wood), and 0.50 g·cm^{-3} (*Abies* bark) (USDA Forest Products Laboratory, 1974; Harmon, 1992). *Thuja plicata* bark, which is very thin, had already sloughed by the year of our study and thus was not sampled. Because the species identity of Group 3 was unclear, green-wood density of *P. menziesii* was used in calculations.

Results

LOGS AND STUMPS

After accounting for stand age, the regression slopes of log density and stump density within each species were not significantly different (*P. menziesii*, $P = 0.316$; *T. heterophylla*, $P = 0.805$), so these data were combined by species for remaining analyses. Based on non-linear regression results for combined stumps and logs, *P. menziesii* decomposed most slowly ($k = 0.007$·y^{-1}, SE = 0.002) and *T. heterophylla* decomposed most rapidly ($k = 0.036$·y^{-1}, SE = 0.008) (Table I), though some R^2 values are low. Repeating the regression for *P. menziesii* using its accepted green-wood density increased k to 0.015·y^{-1} (SE = 0.001). Group 3 (stumps from the unidentified species) was intermediate ($k = 0.013$·y^{-1}, SE = 0.005; $P = < 0.0001$). In contrast, coefficients by linear regression were 0.002·y^{-1},

TABLE I. Coefficients of single-exponential regressions used to estimate decomposition for above-ground logs and stumps and below-ground roots. Conclusions about relative above-ground *versus* below-ground decomposition rates were inferred by combining the adjusted k of *P. menziesii* logs and stumps with Y_0 and k for other species and types of CWD (see text). Data from a chronosequence of previously clearcut stands originating from harvested old growth at Wind River, Washington, USA. SE are in parentheses.

| C store | Species | Diameter (cm) | Density | Regression Coefficients[a] | | | | k (adjusted) |
				Y_0	k	R^2	n	
Logs and stumps[b]								
	P. menziesii		0.45[h]	0.348 (0.034)	0.007 (0.002)	0.15	45	0.016[d] 0.015[g]
	T. heterophylla		0.42[h]	0.439 (0.048)	0.036 (0.008)	0.51	25	0.042[d]
	unknown		—	0.312 (0.046)	0.013 (0.005)	0.28	18	0.031[d]
Roots[c]								
	P. menziesii	1-3	0.6[e,f]	0.51	0.014 (0.005)	0.73*	19	0.022[i]
		3-8	0.53[e,f]	0.40	0.008 (0.002)	0.31*	21	0.019[i]
	T. heterophylla	1-3	0.45[e]	0.36	0.023 (0.004)	0.56*	9	0.043[i]
		3-8	0.38[e]	0.33	0.017 (0.003)	0.77*	21	0.025[i]

[a] Regressions are of the form $Y_t = Y_0 e^{-kt}$ where Y_t is density t years after clearcutting, Y_0 is green-wood density, and k is the decomposition rate constant.
[b] Each data point represents the weighted mean of bark and wood samples from an individual log or stump.
[c] Each data point represents the mean of 4-12 samples.
[d] Mean of individually calculated log and stump k.
[e] Mean density of green-wood samples.
[f] One sample only.
[g] Based on non-linear regression setting Y_0 = accepted published values (listed in table).
[h] Accepted published green-wood densities.
[i] Mean of individually calculated root k.
* $P < 0.01$.

$0.009 \cdot y^{-1}$, and $0.003 \cdot y^{-1}$ for *P. menziesii*, *T. heterophylla*, and Group 3, respectively. Wood k from the single *T. plicata* log was $0.013 \cdot y^{-1}$. Mean bark and wood k for the first *Abies* log were $0.004 \cdot y^{-1}$ and $0.072 \cdot y^{-1}$, respectively. For the second, wood k was $0.069 \cdot y^{-1}$. The density range for logs and stumps within a given species and age class was broad (Figure 1). Regression of individual k (logs and stumps, *P. menziesii* and *T. heterophylla*) against log diameter indicated a small but significant inverse effect of diameter ($P = 0.005$).

Linear regression of log-transformed density against time indicated green-wood density of *P. menziesii* (-0.939 [back transformed: 0.391 Mg·m^{-3}], SE = 0.208) differed significantly from *T. heterophylla* and Group 3 ($F = 10.32$, $P = 0.002$). Intercepts of *T. heterophylla* (-1.283 [back transformed: 0.277 Mg·m^{-3}], SE = 0.219) and Group 3 (-1.266 [back transformed: 0.281 Mg·m^{-3}], SE = 0.107) were not significantly different ($F = -0.0161$, $P = 0.881$), but were not combined because the species composition of Group 3 was uncertain. In contrast, green-wood densities by non-linear regression for *P. menziesii* (0.348 Mg·m^{-3}, SE = 0.034), *T. heterophylla* (0.439 Mg·m^{-3}, SE = 0.048), and Group 3 (0.332 Mg·m^{-3}, SE = 0.046) all differed significantly ($P < 0.0001$). In our evaluation of temporal variation in k (each *P. menziesii* and *T. heterophylla* log and stump) individual log k ranged from 0.004 to $0.04 \cdot y^{-1}$ (*P. menziesii*) and 0.002 to $0.05 \cdot y^{-1}$ (*T. heterophylla*); stump k ranged from 0.002 to $0.03 \cdot y^{-1}$ and 0.01

to $0.09 \cdot y^{-1}$, respectively (Table II). Generally, individual k increased until approximately 20 y post harvest, then declined until approximately 30 y post harvest, then remained relatively constant (Figure 2). Averages of individually calculated stump and log k were $0.016 \cdot y^{-1}$ for *P. menziesii*, $0.042 \cdot y^{-1}$ for *T. heterophylla*, and $0.031 \cdot y^{-1}$ for Group 3.

Both linear regression model fitting (-0.0109, SE = 0.0024, $P < 0.001$ back transformed) and automated model selection (stepwise: $F = 12.19$, $P < 0.001$, $C_{(p)}$ = 5.567, $R^2 = 0.229$) indicated stand age and species were the only significant main effects on density (additional variables were plot-level slope, aspect, and elevation). Interaction between stand age and *T. heterophylla* was significant (-0.020, SE = 0.009, $P = 0.031$), but at the expense of individual variable significance. Elevation and stand age were somewhat correlated (Pearson's, -0.581), but k of individual logs and stumps were only weakly correlated with age (-0.332) and uncorrelated with elevation (-0.052) and aspect (-0.045).

COARSE ROOTS

Root k varied significantly by size and species (Table I, Figure 3). Small-diameter roots (1-3 cm) of *P. menziesii* decomposed faster ($0.014 \cdot y^{-1}$) than large-diameter roots ($0.008 \cdot y^{-1}$), though 1-3 cm roots were denser. Roots of *T. heterophylla* showed a similar pattern (1-3 cm: $k = 0.023 \cdot y^{-1}$; 3-8 cm: $k = 0.017 \cdot y^{-1}$). Small-diameter *P. men-*
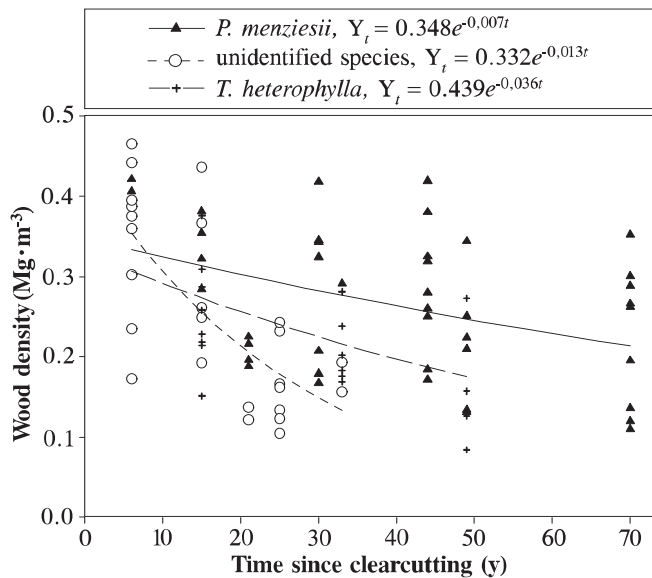
FIGURE 1. Decomposition trajectories of coarse woody debris for three Pacific Northwest conifer species [*Pseudotsuga menziesii, Tsuga heterophylla,* unidentified sp. (likely *Abies* sp.)]. Exponential decay parameter estimates were derived by non-linear regression of densities for individual stumps and logs against time. Data from above-ground logs and stumps along a chronosequence of conifer-dominated stands regenerating after clearcutting and fire at Wind River, Washington, USA.

ziesii roots (1-3 cm) decomposed slightly more slowly than logs and stumps (assuming green-wood density to be 0.45 g·cm^{-3}), while 3-5 cm roots decomposed approximately half as fast. Analogous results for *T. heterophylla* were about 0.6 and 0.5 times as fast. Decomposition rate ratios between species (*T. heterophylla*: *P. menziesii*) for 3-8 cm roots (2.1) and for stumps and logs (2.4) were thus similar but somewhat different for 1-3 cm roots (1.6). As with stumps and logs, our regression-based estimates of green-root densities were lower relative to those derived from green-root samples by mass-volume methods (Table I).

Discussion

REGENERATING CLEARCUTS *VERSUS* CLOSED-CANOPY FOREST

One of our questions concerned the degree to which decomposition of CWD varies between clearcut and closed-canopy forest. Similar respiration rates in clearcut *versus* closed-canopy environments for logs of *P. menziesii* and *T. heterophylla* have been reported from comparable forest (Marra & Edmonds, 1996), though species *k* differed, consistent with other results (Graham & Cromack, 1982; Marra & Edmonds, 1994). Our mean above-ground *k* for old-growth *P. menziesii* logs and stumps originating from clearcuts (0.015·y^{-1}) was slightly higher than *k* for old-growth *P. menziesii* logs (0.014·y^{-1}) inside the nearby T. T. Munger RNA, (Harmon *et al.,* 2004). Our *k* for old-growth *T. heterophylla* logs and stumps in clearcuts (0.036·y^{-1}), however, was twice that for old-growth logs of the same species inside the RNA (0.018·y^{-1}; Harmon *et al.,* 2004). As the RNA is within our study area, its general climatic conditions are likely similar to those in regenerating stands we sampled; differences in *k* are thus possibly due to microclimate. Our pre-

TABLE II. Range of individual log and stump decomposition constants (*k*)[a] based on bulk densities *t* years after clearcutting and green-wood densities of 0.45 g·cm^{-3} (*Pseudotsuga menziesii*) and 0.44 g·cm^{-3} (*Tsuga heterophylla*). Data from a chronosequence of previously clearcut stands originating from harvested old growth at Wind River, Washington, USA.

Stand age (years since clearcutting)	Range of *k*			
	Elevation (m)[b]	*P. menziesii*	*T. heterophylla*	*n*[c]
7	554	0.011 – 0.017	0.003 – 0.160	9
16	853	0.011 – 0.031	0.002 – 0.056	5, 5
22	632	0.033 – 0.041	0.056 – 0.062	4, 2
26	560	0.026	0.026 – 0.058	1, 7
31	633	0.009 – 0.033	0.025 – 0.032	7, 2
34	890	0.013	–	1
45	597	0.004 – 0.021	–	10
50	646	0.005 – 0.025	–	6
71	370	0.004 – 0.020	–	9

[a] Calculated as $-k = \{\ln[(D_t)/(D_0)]/t\}$ where D_t is density *t* years after clearcutting, D_0 is initial density, and *k* is the decomposition rate constant.
[b] Stand midpoint estimated from USGS 7.5 min quadrangles and digital DEM.
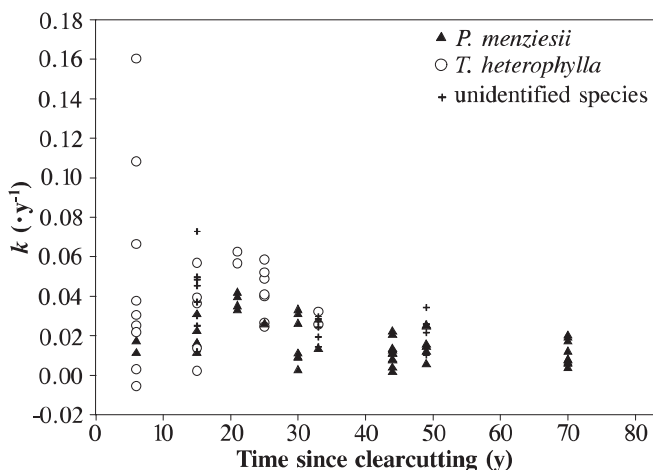[c] Stump and log sample size for *P. menziesii*, *T. heterophylla* in each stand.

FIGURE 2. Decomposition constants (*k*) for individual logs and stumps, calculated using Equation 4 (see text). For *T. heterophylla* and *P. menziesii*, *k* generally increased 7-20 y post-disturbance, declined 20-30 y post-disturbance, then remained relatively constant between 35-70 y. The fact that decomposition is a multi-stage, multi-*k* process has been described previously by vector analysis (Harmon, Krankina & Sexton, 2000). Data from the unidentified species (likely *Abies* sp.) are insufficient to assess whether its decomposition is multi-stage, but the distribution generally follows that of the other two species. Several age 7 y *T. heterophylla* samples exhibit *k* 10x higher than our regression-derived *k*, indicating that very rapid decomposition may sometimes follow disturbance. Data from above-ground logs and stumps along a chronosequence of conifer-dominated stands regenerating after clearcutting and fire at Wind River, Washington, USA.

liminary comparison thus indicates higher decomposition rates for CWD in clearcuts than under closed forest canopies, even though the period of maximal environmental difference between these two environments is generally brief and occurs early in the decomposition process, when wood density changes are thought to be minor.

One limitation of our approach is that initially open conditions, such as those resulting from clearcutting, are

modified by vegetation growth as a stand regenerates. Differences in k between second growth and the nearby RNA are thus likely smaller than between old growth and stands remaining open, as after regeneration failure. A more precise experiment that controls vegetation growth would refine estimates of differences between these contrasting environments.

DECOMPOSITION CONSTANTS AMONG FORMS OF CWD

Another major question we considered was the degree to which type and location of CWD influenced decomposition rates. We found log and stump decomposition rates to be similar. Relative to other studies of stumps, our log-stump k were less than those observed for *Pinus sylvestris* (e.g., ~ $k = 0.06 \cdot y^{-1}$; Sierota, 1997) and *Picea* sp. (~ $k = 0.08 \cdot y^{-1}$; Käärik & Rennerfelt, 1957) but within the range observed for *Larix olgensis* and *Pinus koraiensis* ($0.01–0.05 \cdot y^{-1}$; Heal, Bo-rong & Guang-shan, 1983). Relative to other studies of logs, *P. menziesii* k was higher than the $0.010 \cdot y^{-1}$ for several species and stand ages reported by Sollins *et al.* (1987) and the $0.0063-0.007 \cdot y^{-1}$ reported by Means, Cromack, and MacMillan (1985); these earlier data neglect fragmentation, however, and thus possibly underestimate k. Other studies from Pacific Northwest forests report k intermediate to our *P. menziesii* and *T. heterophylla* results, but sometimes combine species, and methodologies vary (Sollins, 1982, $[0.028 \cdot y^{-1}$, indirect methods]; Spies, Franklin & Thomas, 1988, $[0.029 \cdot y^{-1}$, chronosequence–mass loss methods]), so direct comparison is not possible. Our derived log and stump k for *T. heterophylla* was somewhat higher than that from other regional chronosequence studies of this species ($0.008-0.03 \cdot y^{-1}$: Grier,

1978; Sollins *et al.,* 1987), but our derived k for *Abies* sp. was within the range of published values (*A. balsamea* $[0.029 \cdot y^{-1}]$: Lambert, Lang & Reiners, 1980; *A. concolor* $[0.049 \cdot y^{-1}]$: Harmon, Cromack & Smith, 1987).

We found large differences between above- and below-ground CWD decomposition, indicating that applying log k to coarse roots, even within a species, would strongly bias estimated mass loss. Coarse roots of *P. menziesii* decomposed more slowly than those of many other species reported ($0.02-0.06 \cdot y^{-1}$: Yavitt & Fahey, 1982; Chen, Harmon & Griffiths, 2001). Patterns between species k for above-ground CWD were echoed below ground, indicating species effects are exerted in both environments.

IMPLICATIONS FOR C SOURCES AND SINKS

To estimate yearly C fluxes (adjusted for regenerating stand age) from logs, stumps, and snags along our chronosequence, stand-level mean CWD masses (Table III) were combined with green-wood densities and mean species k in Equation [3]. Applying methods of our previously published C flux analysis (Janisch & Harmon, 2002), we estimate logs, stumps, and snags in these stands are releasing C back to the atmosphere at 0.5-0.9 Mg $C \cdot ha^{-1} \cdot y^{-1}$ (assuming all CWD is *P. menziesii*) or 0.8-2.3 Mg $C \cdot ha^{-1} \cdot y^{-1}$ (assuming all CWD is *T. hetero-*

TABLE III. Estimated upper and lower limits on stand-level annual C flux from logs, stumps, snags, and roots assuming all CWD is either a slow decomposing species (*Pseudotsuga menziesii*) or a fast decomposing species (*Tsuga heterophylla*). Data from a chronosequence of previously clearcut coniferous stands dominated prior to harvest by old-growth *P. menziesii* and *T. heterophylla* at Wind River, Washington, USA.

Stand age (years since clearcutting)	Total CWD stores [a,b] (Mg $C \cdot ha^{-1}$)	Losses per year $k = 0.015$[c] and $k = 0.011$[d] (Mg $C \cdot ha^{-1} \cdot y^{-1}$)	Losses per year $k = 0.036$[e] and $k = 0.020$[f] (Mg $C \cdot ha^{-1} \cdot y^{-1}$)
6	129.58	1.65	3.44
11	109.54	1.41	2.89
14	126.03	1.64	3.39
16	78.23	1.02	2.13
17	77.85	0.98	1.93
22	129.19	1.67	3.36
23	48.30	0.64	1.31
26	55.02	0.70	1.33
30	69.38	0.89	1.73
31	198.50	1.29	2.57
34	54.32	0.70	1.33
35	77.24	1.03	2.10
36	145.45	1.86	3.54
39	64.16	0.84	1.64
41	100.73	1.30	2.47
44	58.85	0.77	1.49
45	89.94	1.16	2.17
49	35.49	0.48	0.96

[a] Logs > 1 m length, stumps, snags ≥ 10 cm largest diameter.

[b] Assuming wood is 50% carbon.

[c] If all above-ground CWD is assumed to be *P. menziesii*.

[d] Average k of small and large diameter *P. menziesii* roots applied to total root mass.

[e] If all above-ground CWD is assumed to be *T. heterophylla*.

[f] Average k of small and large diameter *T. heterophylla* roots applied to total root mass.
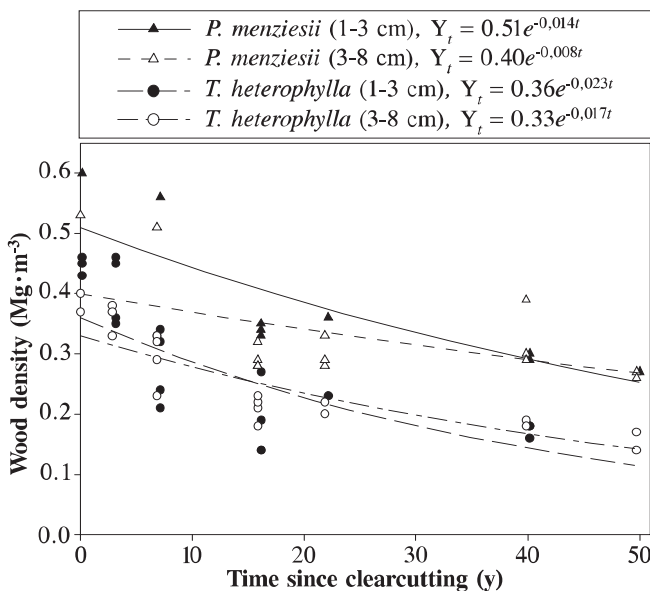

FIGURE 3. Decomposition trajectories for small (1-3 cm) and large (3-8 cm) diameter sub-surface roots of two Pacific Northwest conifer species (*P. menziesii* and *T. heterophylla*). Exponential parameter estimates were derived by non-linear regression of empirically derived densities against time. Data from roots attached to stumps along a chronosequence of conifer-dominated stands regenerating after clearcutting and fire at Wind River, Washington, USA.

Legend for Figure 3:
- *P. menziesii* (1-3 cm), $Y_t = 0.51e^{-0.014t}$
- *P. menziesii* (3-8 cm), $Y_t = 0.40e^{-0.008t}$
- *T. heterophylla* (1-3 cm), $Y_t = 0.36e^{-0.023t}$
- *T. heterophylla* (3-8 cm), $Y_t = 0.33e^{-0.017t}$

Axis labels: Wood density (Mg·m^{-3}); Time since clearcutting (y)

phylla). Adding coarse roots (assumed equivalent to 20% bole mass) increases these fluxes to 0.5-1.9 Mg C·ha^{-1}·y^{-1} or 1.0-3.5 Mg C·ha^{-1}·y^{-1}, respectively (given mean species root k). As *P. menziesii* dominated many chronosequence stands prior to harvest, true fluxes are likely closer to the lower range.

Given these fluxes, NPP of roughly 1-4 Mg C·ha^{-1}·y^{-1}, well within the NPP range for aggrading regional stands (Law *et al.,* 2001; Acker *et al.,* 2002; Janisch & Harmon, unpubl. data) would maintain stands near C balance or as C sinks throughout much of succession. However, our calculated C losses account only for fluxes from CWD left in a stand after logging. In contrast, transfer of C back to the atmosphere in fire-killed stands might be fivefold higher, offsetting NPP of the regenerating stand for many decades (Janisch & Harmon, 2002).

LIMITATIONS ON OUR ESTIMATES OF K

Chronosequences provide rapid estimates of long-term decomposition rates, but have several limitations. Given that space was substituted for time, for example, site rather than temporal factors may be causing differences we observed. Because clearcutting on the district historically began in lowland drainages and moved upslope to ridges, ages of stands (*i.e.,* number of years since clearcutting) sampled in our study are somewhat correlated with elevation (a proxy for temperature differences). We found little correlation between stand age and k of individual logs, or between k and elevation, however, so it is unlikely our estimates of decomposition constants were systematically biased due to environmental differences.

Between-site differences in slope, aspect, and elevation might also have caused much of the unexplained variation in our regressions, but our sampling was insufficiently systematic to fully test these effects as proxies for moisture balance and temperature, and thus ultimately on k. Effects of environmental differences on CWD decomposition constants are not well understood, but at regional and global levels these effects can be relatively small for species with high decay resistance (Yatskov, Krankina & Harmon, 2003). Using the Q10 principle and results from Yatskov, Krankina, and Harmon (2003), a preliminary prediction of microclimate effects is possible, however. Assuming temperature to be the primary environmental variable differing among sites, a two- to three-fold increase in k with each 10 °C increase in mean annual temperature, and a temperature lapse rate of ≈2.2 °C per 350 m, decomposition constants should vary 15 to 25% across our set of stands. This range of variation is much smaller than the two-fold differences in decomposition between species we and others (Abbott & Crossley, 1982; Harmon & Sexton, 1996) have observed.

Lack of knowledge about initial conditions can also influence the precision of chronosequences. Incorrect stand age or inclusion of long-dead snags in our data, for example, could bias our independent variable, time. Temporal error is likely small, however, given our density analysis, CWD selection criteria, and testing of harvest dates (Gifford Pinchot Oracle Vegetation Activity Database, Rev. 1.1) by increment coring regenerating trees. Initial conditions preceding and following clearcutting may also

have caused unexplained variation. Generally, stands were burned after clearcutting as a silvicultural treatment, but in one case wildfire burned the stand prior to clearcutting. Exclusion of this stand does not greatly influence our conclusions, however, and all stands re-initiated under open canopies with charred surfaces.

In our analysis we used a single exponential model to estimate decomposition rates. This model was an adequate predictor of green-wood density for *T. heterophylla* logs and stumps, but not for *P. menziesii* as our estimated green-wood densities are 13-34% too low compared to published values (Harmon, Nadelhoffer, & Blair, 1999). This may indicate *P. menziesii* underwent a phase of rapid decomposition 1-10 y after clearcutting, a period earlier than our youngest available stand, or that more highly decomposed (*e.g.,* lower density) CWD samples from older stands overly influenced the regression. Thus, our adjusted k (Table III), based on accepted green-wood density, likely better approximates the true value. Similarly, green-root densities calculated empirically were higher than corresponding density estimates derived as regression coefficients. As we had few green roots, however, and root k are still poorly known, we based our comparisons of roots to other forms of CWD on regression coefficients because regression makes use of the most data. We also found some evidence that decomposition rate increased then decreased with time (Figure 2), indicating distinct decompositional phases. Future resampling of logs and stumps used in our chronosequence might clarify this temporal pattern and help explain the initially rapid phase of decomposition some logs seemed to undergo.

Management implications and conclusions

Despite the combined effect of initially open- then closed-canopy environments experienced by CWD originating from clearcutting, decomposition of CWD in clearcuts proceeded at higher rates than under intact old growth. Decomposition of above- and below-ground wood was influenced by tree species and, at least for roots, by their diameter. The small but significant relationship between diameter and k we found for logs is consistent with recent meta-analysis where diameter explained substantial variation in k (Mackensen, Bauhus & Webber, 2003), though diameter–k relationships for logs have been reported as positive, negative, and non-existent. Such mixed results may indicate diameter effects are small and thus require large data sets to detect. Sampling boles from short-rotation stands, generally of smaller diameter than old growth, may answer this question.

We also found that interchanging log and stump k within a species would not seriously bias estimates of C flux from above-ground CWD, but substituting log k for root k, even within a species, could alter C flux calculations enough to confound periods when stands are C sources relative to the atmosphere with periods when they are C sinks. The generality of interchanging log for stump k, or differences between k of clearcuts and closed canopies, however, is not yet clear as a majority of CWD decomposition studies to date have emphasized *P. men-*

ziesii in Pacific Northwest (USA) and British Columbia (Canada) forests (Mackensen & Bauhus, 1999). Data from other species within and beyond the coastal conifer zone of western North America would clarify our results, as would more controlled experiments in which species, diameter, position, and microclimate are examined.

Such refinements to estimates of CWD decomposition constants could aid identification of ecosystems and management scenarios for maximizing C storage. The large effect of species on *k*, for example, suggests stand-level CWD C stores, as well as landscape-scale C fluxes, might be controlled by altering tree species composition silviculturally. Changes to state and federal forestry practices rules, such as those governing minimum rotation length and CWD mass left after harvest, could also influence C stores and fluxes. Though we found decomposition of CWD in regenerating clearcuts to be more rapid than under the closed canopy of nearby old growth, net overall C released back to the atmosphere from a landscape dominated by short-rotation stands could remain constant relative to a landscape dominated by old growth. This is because short rotations generate much less CWD than does clearcutting old growth (Harmon, Garman & Ferrell, 1996; Janisch & Harmon, 2002), but multiple short rotations may occur during the several centuries needed to regenerate late-successional forest.

Acknowledgements

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