

Successional changes in live and dead wood carbon stores: implications for net ecosystem productivity

J. E. JANISCH^{1–3} and M. E. HARMON¹

¹ Department of Forest Science, Richardson Hall, Oregon State University, Corvallis, OR 97331, USA

² Present address: Environmental Assessment Program, Washington Department of Ecology, 300 Desmond Drive, Lacey, WA 98503, USA

³ Author to whom correspondence should be addressed (jack.janisch@orst.edu)

Received April 17, 2001; accepted September 1, 2001; published online January 2, 2002

Summary If forests are to be used in CO₂ mitigation projects, it is essential to understand and quantify the impacts of disturbance on net ecosystem productivity (NEP; i.e., the change in ecosystem carbon (C) storage with time). We examined the influence of live tree and coarse woody debris (CWD) on NEP during secondary succession based on data collected along a 500-year chronosequence on the Wind River Ranger District, Washington. We developed a simple statistical model of live and dead wood accumulation and decomposition to predict changes in the woody component of NEP, which we call NEP_w. The transition from negative to positive NEP_w, for a series of scenarios in which none to all wood was left after disturbance, occurred between 0 and 57 years after disturbance. The timing of this transition decreased as live-tree growth rates increased, and increased as CWD left after disturbance increased. Maximum and minimum NEP_w for all scenarios were 3.9 and –14.1 Mg C ha^{–1} year^{–1}, respectively. Maximum live and total wood C stores of 319 and 393 Mg C ha^{–1}, respectively, were reached approximately 200 years after disturbance. Decomposition rates (*k*) of CWD ranged between 0.013 and 0.043 year^{–1} for individual stands. Regenerating stands took 41 years to attain a mean live wood mass equivalent to the mean mass of CWD left behind after logging, 40 years to equal the mean CWD mass in 500-year-old forest, and more than 150 years to equal the mean total live and dead wood in an old-growth stand. At a rotation age of 80 years, regenerating stands stored approximately half the wood C of the remaining nearby old-growth forests (predominant age 500 years), indicating that conversion of old-growth forests to younger managed forests results in a significant net release of C to the atmosphere.

Keywords: biomass accumulation, carbon sequestration, coarse woody debris, CWD, disturbance, negative to positive, NEP, succession.

Introduction

As atmospheric CO₂ concentrations increase and concern over greenhouse-gas-related climate change deepens, forests are being considered as a means to remove and store accumulating

atmospheric carbon (C) (Iverson et al. 1993, Marland 2000). Opinion on this strategy (Schlamadinger and Marland 1998, Schulze et al. 2000) and the role of CO₂ in current global temperature trends (e.g., Hensen et al. 2000) has varied. Climate-related forest migration and response lags (Davis 1986), as well as potential direct and indirect climate effects on forest growth and decomposition (Rogers et al. 1993, Körner 1996), further point toward uncertainties in the future C storage capacity of forests.

If forests are to be used to manipulate atmospheric CO₂ concentration, there is a need to consider these systems in terms of net ecosystem productivity (NEP) in addition to net primary productivity (NPP). This is because forests simultaneously sequester C through growth and lose C through decomposition and heterotrophic respiration. Net ecosystem productivity, which accounts for these competing processes, can thus be defined as the rate of change in ecosystem C storage over time (Aber and Melillo 1991), or:

$$\text{NEP} = dC/dt. \quad (1)$$

When NEP is negative, the ecosystem is a CO₂ source relative to the atmosphere. When NEP is positive, the system is a CO₂ sink. The NEP status of a stand thus varies over time depending on which process dominates.

Stand NEP status also depends on mass and decomposition rate of coarse woody debris (CWD) and mass and net C uptake rate of live trees. Many stand development models have focused on simple logistic growth and decomposition functions because interpretations are biologically meaningful. Models of this type include smooth logistic growth (Odum 1969), shifting mosaic (Bormann and Likens 1979), dampened oscillation (Peet 1981) and related patterns of live tree biomass accumulation. In general, these models predict that live biomass increases rapidly following stand initiation, peaks or plateaus during stand maturation, and finally stabilizes or declines in late-successional phases. For the CWD component, chronosequence studies in wave-regenerated *Abies balsamea* (L.) Mill. (Lang 1985), *Pinus contorta* Dougl. ex Loud (Romme 1982) and *Pseudotsuga menziesii* (Mirb.) Franco forests

(Spies et al. 1988) have reported U-shaped temporal patterns in the mass of the CWD pool. These patterns result from gradual decomposition of high CWD loads usually generated by disturbance (Howard 1981, Harmon et al. 1996a) and gradual regeneration of these stores as the replacement stand matures. Interaction of these U-shaped dynamics of CWD stores and the pattern of live-tree biomass accumulation (e.g., Whittaker and Woodwell 1969, Pare and Bergeron 1995, Johnson et al. 2000, Wirth et al. 2002) imply four phases of NEP during secondary succession: (1) a period of disturbance, such as fire or logging, that reduces living woody biomass and adds detritus from harvested or burned trees to the pre-harvest detrital load of the stand; (2) a period dominated by C loss (negative NEP) associated with decomposition of dead wood existing prior to disturbance and added by the disturbance; (3) a period dominated by C uptake as stand regeneration sequesters C as live wood (NEP switches from negative to positive); and (4) a gradual decrease of uptake to balance between C gain and C loss as the stand ages (NEP approaches zero). Based on published parameters (Grier and Logan 1977, Harmon et al. 1986) and simple exponential models of these dynamics, a negative NEP phase of approximately 20–30 years is predicted following conversion of Pacific Northwest, old-growth conifer forest to secondary forest by clear-cutting.

Although Pacific Northwest forest soils store an estimated 35% of the total system C (Smithwick et al. 2002), this C is released slowly relative to the time scale of forest disturbance and succession (Johnson and Curtis 2001). Thus, because a large fraction of non-soil forest C is stored in live boles and CWD (Smithwick et al. 2002), these components may largely govern forest C fluxes even though other C pools relevant to NEP exist in forest ecosystems. This paper thus examined C gains and losses from tree boles and CWD, referred to here as NEP_w . These C stores, together with the successional dynamics, suggest four questions: (1) How do live wood C stores change during succession? (2) How do CWD C stores change during succession? (3) Does interaction of biomass accumulation and CWD decomposition result in negative NEP_w following clear-cutting, and if so, for how long? (4) Can these dynamics be used to place extreme positive and negative limits on NEP_w ? To answer these questions, we developed a simple statistical model pairing functions of live wood accumulation and CWD decomposition dynamics. We parameterized the model by measuring live tree boles and CWD along a chronosequence of 36 forest stands. Chronosequences suffer from substitution of space for time (e.g., Grier 1978, Harmon and Sexton 1996), sensitivity to the fate of CWD pools during harvest, and other liabilities. When mass-based, however, these methods may offer advantages over the currently favored method of eddy covariance for investigating NEP (e.g., Moncrieff et al. 1997, Constantin et al. 1999). This is because eddy covariance stand choice criteria are not required, actual masses of live and CWD C pools can be compared, CWD stores taken off-site can be estimated, and estimation of C pool mass before, during, and after harvest allows prediction of NEP and C accumulation throughout succession.

Study region

Data were collected from forest stands within the USDA Forest Service Wind River Ranger District, about 20 km from the Columbia River Gorge in southwest Washington State. Because this study was part of an integrated project already in progress at the T.T. Munger Research Natural Area, stand selection was confined to a region approximately 10×10 km, centered on the Research Natural Area ($45^{\circ}49' N$, $121^{\circ}58' W$). Elevation ranges between about 335 and 1200 m. Soils are classified as well-drained Stabler series Andic Haplumbrept (Franklin et al. 1972) derived from recent volcanic tephra (Franklin and 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 year^{-1} (Franklin and DeBell 1988), with less than 10% falling between June and September (Franklin and DeBell 1988). Mean annual temperature at the Research Natural Area is $8.7^{\circ} C$ (Wind River Canopy Crane data). Based on ring counts from stumps and tree cores collected inside or adjacent to the Research Natural Area, these forests originated about 500 years ago (DeBell and 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 around 1490 (Franklin and Waring 1979). Vegetation of the study region is dominated by *P. menziesii*–*Tsuga heterophylla* (Raf.) Sarg. forest. The Research Natural Area vegetation is transitional between *T. heterophylla* and *Abies amabilis* Dougl. ex Forbes zones (Franklin and Dyrness 1973). Other evergreen tree species include *A. amabilis*, *Abies grandis* (Dougl. ex D. Don) Lindl., *Abies procera* Rehd., *Thuja plicata* Donn ex D. Don, *Taxus brevifolia* Nutt. and *Pinus monticola* Dougl. ex D. Don. Deciduous tree species are present in many stands as minor components and include *Cornus nuttallii* Audubon, *Acer macrophyllum* Pursh and *Alnus rubra* Bong. Shrub species include *Berberis nervosa* Pursh, *Gaultheria shallon* Pursh, *Acer circinatum* Pursh, *Ceanothus* sp., *Vaccinium parvifolium* Smith and *Vaccinium membranaceum* Dougl. ex Hook.

Methods

Stand selection

This study is observational with no true replication. Stands are defined as forested sites used as harvest units by the U.S. Forest Service (USFS). Stands ranged in age from 5 to 400–600 years and formed three general groups: (1) clear-cut, regenerating stands aged 5–50 years post-harvest; (2) 75–150-year-old stands regenerating from commercial harvest or stand-destroying wildfire; and (3) 400–600-year-old old-growth stands. Groupings are artifacts of available stand ages or methodological needs (described below) and are used only for ease of discussion.

Candidate stands were derived from district maps compiled

from harvest date GIS layers (Gifford Pinchot Vegetation Database, Rev. 1.1). The second phase of stand selection was based on six selection criteria. (1) Age: Candidate stands were grouped into decadal age classes (1940–1949, 1950–1959, etc.) with stand age based on harvest date. At least three stands were selected from each decade to produce the chronosequence. (2) Aspect: To represent the range of site productivity, one stand each of northerly, southerly and flat (valley floor) aspect were selected in each decade. (3) Elevation: Selected stands lie roughly between 760 and 360 m (the valley floor). The upper elevation limit was selected to avoid the transition zone from *Pseudotsuga*-dominated forest to *Abies* sp.-dominated forest. (4) Size: Preference was given to stands large enough to contain a 200-m transect and 100-m edge buffers (at least 400 m per side). Stand dimensions were estimated from scaled USFS orthophotos. (5) Stand canopy homogeneity: USFS orthophotos of candidate stands were examined for interior swamps, experimental plantings and other features interfering with plot placement. (6) Old-growth/second-growth stand pairing: An effort was made to select second-growth stands adjacent to or near old-growth stands. This was done because minimum merchantable-log diameter (Hanzlik et al. 1917, Hodgson 1930, Conway 1982), stump height (Gibbons 1918, Pool 1950, Conway 1982) and total non-merchantable mass of CWD (slash) have changed over time (Harmon et al. 1996a, 1996b). Old-growth stands may thus provide an estimate of pre-clear-cut CWD mass in adjacent regenerating stands.

After initial selection, other Group 1 stands were added to produce a final chronosequence with age gaps no larger than 5 years for the first 50 years of stand development (1945–1993). Three more stands were then added between harvest dates 1960 and 1970 because an initial analysis predicted that NEP_w switched from negative to positive in this age range. The upper age limit (1945 harvest) for Group 1 stands was chosen because full-scale clear-cutting began in the district around 1940. The lower age limit (1993 harvest) was determined by available stand ages. Age classes at 70, 110 and 150 years post-disturbance (Group 2) were added to examine whether live biomass curves of developing stands followed growth trajectories implied by old-growth biomass and to partially fill the +400-year gap between Group 1 and old-growth (Group 3) stands. Final totals were 18, nine and nine stands in Groups 1, 2 and 3, respectively. Old-growth stands represented remaining tracts of 400–600-year-old forest in the district.

Transect design

All stands were sampled for live trees and CWD based on plots along a transect. Transect bearings generally followed the long axis of each stand but varied with stand shape and area. With the exception of one two-plot transect, each transect consisted of three concentric circular plots with 50–100 m between plot centers. To reduce edge effects (Chen and Franklin 1992, Mesquita et al. 1999), outer plot radii were located at least 50–100 m from stand boundaries. Plot number, plot-to-plot distances and buffer widths varied with stand area, shape or composition. Locations of Plots 2 and 3 were determined by

bearing and distance from Plot 1. Plots straddling old roads, seasonal drainages and thinning boundaries were moved. Two concentric sample zones of radii 12.6 and 17.8 m surrounded each point, providing sample areas equal to 0.05 ha for live trees and 0.1 ha for CWD biomass. Plot radii were measured by calibrated Sonin® and meter tape.

Live trees

At each plot, all live trees with DBH (diameter breast height) ≥ 5 cm were tagged at breast height with pre-numbered aluminum tags. Breast height was defined as 1.4 m above the soil surface on the upslope side of the trunk. Trees near plot perimeters were tagged if more than half of the tree bole was inside the plot. The DBH was measured to the nearest 0.1 cm just above the aluminum tag with commercial metric D-tapes. The DBH was then converted directly to bole wood mass and bark mass using species-specific BIOPAK allometric regression equations (Means et al. 1994) based on both regional (Central Cascades) and specific forests.

For all species, C of live tree bole and bark was assumed to be 50% of bole and bark mass (Swift et al. 1979). Calculated masses were slope adjusted at the plot level by a correction factor (cf):

$$cf = 1/(\cos(\text{atan}(\text{slope}/100))), \quad (2)$$

where slope is in degrees. Corrected live tree mass is reported as the product of uncorrected mass and the correction factor. For this study, vine maple (*Acer circinatum*) was defined as a shrub.

Coarse woody detritus

Three principle forms of aboveground CWD were sampled: logs, stumps and snags. Logs were defined as downed tree boles at least 1 m in length and 10 cm in diameter at the largest end. Only sections of logs inside plots were measured. Stumps were defined as standing cut tree boles at least 10 cm in diameter. Snags were defined as standing, uncut, dead trees at least 10 cm in DBH. Stumps and snags near plot perimeters were counted if more than half of the bole was inside the plot. Each log, stump and snag was assigned a decay class rank from 1 (least decayed) to 5 (most decayed) (Sollins 1982). When bark and growth character permitted identification, each log, stump and snag was identified to species. The CWD mass of an unknown species or genus was calculated based on *P. menziesii* densities. Logs, stumps and snags entering the CWD pool from the regenerating stand through mortality and thinning (hereafter referred to as de novo CWD) were separated from pre- and post-clear-cutting material inherited from old-growth stands. Inherited material measured in 1998 is hereafter referred to as legacy CWD.

Log center and end diameters were measured by caliper to the nearest 1 cm. Log lengths were measured to the nearest 0.1 m by tape measure or calibrated Sonin®. Stump diameter was measured just below the cut by caliper to the nearest 1 cm. Stump height was measured to the nearest 0.1 m with a meter stick. Snag basal diameter and accessible top diameters were

directly measured to the nearest 1 cm by caliper. Snag heights ≤ 3 m were measured directly to the nearest 0.1 m. For snags > 3 m in height, top diameters and heights were estimated visually by calibrating against a known height or diameter at the base of the snag (Harmon and Sexton 1996). Logs and stumps were assumed to have bark. Log volumes were calculated by Newton's method. Stump volume was calculated by estimating DBH from measured stump height and diameter, estimating basal diameter from DBH, and then calculating volume from DBH and basal diameter (Harmon and Sexton 1996). Stump hollow volumes were calculated as above and subtracted from the total. Snag volumes were calculated as frustums of cones based on height and diameters. Legacy CWD C mass was calculated as the product of volume and density, adjusted by decomposition class (Graham and Cromack 1982, Sollins et al. 1987, Harmon and Sexton 1996) and assuming 50% C content. Legacy CWD volume was then used to calculate the initial CWD mass, defined as:

$$\text{Initial CWD mass} = \text{legacy CWD volume} \times 0.45 \text{ Mg m}^{-3}, \quad (3)$$

where density (0.45 Mg m^{-3}) is green wood density of each species (e.g., Anonymous 1999). This approximates the mass of CWD loads left immediately after clear-cutting because dimensions of CWD are largely preserved until decay Class 4 (Means et al. 1985). Regression lines were fit through the set of initial CWD masses to test for a time bias in amounts of residual slash left by changing harvest practices (Harmon et al. 1996b). Slope correction of CWD mass was as for live trees.

Model

A Chapman-Richards function (Equation 3) was fit to data describing biomass accumulation in tree boles following stand initiation (Richards 1959) as:

$$L_t = L_{\max}(1 - e^{-k_L t})^{r_L}, \quad (4)$$

where L_t is live tree biomass at time t , L_{\max} is maximum (asymptotic) live tree biomass, k_L is an empirically derived growth constant and r_L is a shaping parameter. Mean live tree parameters (L_{\max} , k_L , r_L) were estimated by nonlinear regression (PROC NLIN, SAS statistical software package, Version 7, SAS Institute, Cary, NC) to the set of 36 mean stand-level live tree mass (Mg ha^{-1}) estimates calculated with Equation 4. Confidence limits were calculated as ± 2 SEs from the mean. For model fitting, old-growth stands were assigned an age of 500 years.

Mass loss from legacy CWD was modeled by a negative exponential function (Kira and Shidei 1967):

$$D_t = D_0(e^{-k_D t}),$$

where D_t is legacy CWD mass at time t after clear-cutting, D_0 is mean legacy CWD mass on site, and k_D is an empirically derived decomposition constant. Legacy CWD parameters

(D_0 , k_D) were estimated by nonlinear regression to Equation 5 based on the set of mean legacy CWD masses (Mg ha^{-1}) from Group 1 stands. To examine variation in CWD decomposition rates among individual Group 1 stands, k -values for each stand were calculated as:

$$k = \frac{-\ln(\text{legacy CWD mass} / \text{initial CWD mass})}{\text{time}}, \quad (6)$$

where legacy and initial CWD are as defined above and time is number of years since clear-cutting.

Accumulating de novo CWD mass was also modeled by a Chapman-Richards function. De novo parameters (N_{\max} , k_N , r_N) were estimated by nonlinear regression to Equation 4 based on de novo CWD masses from Groups 1 and 2 and current CWD loads from Group 3. All parameters for live trees, mortality and CWD were allowed to vary without bound under the Marquadt algorithm in the SAS statistical software package, Version 7. Total CWD mass was calculated as:

$$\text{TD}_t = D_t + N_t, \quad (7)$$

where N_t is de novo CWD, D_t is legacy CWD and TD_t is total CWD stores.

Woody component of NEP

The NEP_w was calculated as the sum of live and CWD stores:

$$\text{NEP}_w = \Delta L + \Delta D = (L_{t+1} - L_t) + (\text{TD}_{t+1} - \text{TD}_t), \quad (8)$$

and is presented as mean, upper extreme and lower extreme for four scenarios. In Scenario 1, all on-site CWD is assumed to be removed by clear-cutting (CWD mass = 0) and off-site decomposition is ignored. Although this scenario is unrealistic, it sets an extreme upper limit on positive NEP_w . Scenario 2 combines the range of initial CWD loads in Group 1 stands with live bole mass accumulation. It reflects the pattern of NEP_w following clear-cutting of old-growth forest but neglects off-site stores. Scenario 3 is a variation on Scenario 2, pairing live bole mass accumulation with CWD loads measured in old-growth stands. This scenario was included because the range of CWD loads in old-growth stands, although relatively unaffected by logging, may differ from the range of CWD loads in second-growth stands. Finally, in Scenario 4, all trees in an old-growth stand were assumed to be killed by fire and allowed to undergo in situ decomposition. Paired with C accumulation during stand regeneration, this scenario sets an extreme negative limit on NEP_w . Mean NEP_w curves were generated by inserting growth and decomposition parameters (L_{\max} , D_0 , N_0 , k -values) generated by nonlinear regression (Table 1) into Equation 8. Upper and lower boundaries around each mean curve represent extremes of live and CWD data—e.g., maximum CWD mass + maximum old-growth live biomass, and minimum CWD mass + minimum old-growth live biomass, where the range of CWD mass varies by scenario. Decomposition rate (k_D), growth rate (k_L), and live tree shaping parameter (r_L) were held constant for all curves. De

Table 1. Parameters used to fit NEP_w curves. In each case, curves are calculated as mean live C stores + mean legacy CWD C stores + mean de novo C stores, upper live C stores + upper CWD C stores + mean de novo C stores, and lower live C stores + lower legacy CWD C stores + mean de novo C stores. Data, collected from the Wind River Ranger District, Washington, were fit with a Chapman-Richards function and simple exponential decomposition model ($y = De^{-kt}$), where D is initial CWD mass, k is an empirically derived decomposition constant (Equation 6) and t is time since disturbance, and all parameters were allowed to vary.

Parameter	Growth	Decomposition				De novo
	Scenario 1–4 ¹	Scenario 1 ²	Scenario 2 ³	Scenario 3 ⁴	Scenario 4 ⁵	Scenario 1–4 ¹
<i>Mean</i>						
L_{max}	319					
k_L	-0.017					
r_L	2.09					
D_0		0	76	74	393.5	
k_d			-0.025	-0.025	-0.025	
N_{max}						74.3
k_N						-0.025
r_N						11.13
<i>Upper limit</i>						
L_{max}	451.5					
k_L	-0.017					
r_L	2.09					
D_0		0	118.5	160.5	612	
k_d			-0.025	-0.025	-0.025	
<i>Lower limit</i>						
L_{max}	184.5					
k_L	-0.017					
r_L	2.09					
D_0		0	42	32	216.5	
k_d			-0.025	-0.025	-0.025	

¹ The range of current old-growth live tree C stores. The same in all cases.

² All legacy CWD removed by logging. Live tree and de novo C stores accumulate.

³ The range of calculated initial CWD C stores.

⁴ The range of current old-growth CWD C stores.

⁵ All live trees killed by catastrophic fire and moved into on-site CWD stores. Limits are high killed live + high CWD and low killed live + low CWD C stores.

novo CWD parameters were the same in all scenarios because CWD accumulations was modeled as converging on mean old-growth CWD stores.

Results

Live tree stores ranged from 184.5 to 451.5 Mg C ha⁻¹ (mean ± SE: 315.4 ± 30.8 Mg C ha⁻¹) across the nine old-growth stands. Live tree mass was low in stands for the first 10 years of succession then increased rapidly until age 75–85 years (Figure 1). Beyond this age, growth declined slowly and converged on an asymptotic maximum mass (319 ± 16.40 Mg C ha⁻¹, $F = 183.68$, $P < 0.0001$). The fitted growth parameter (k_L) was 0.017 ± 0.005 year⁻¹, indicating that maximum live tree stores were reached in approximately 200 years. The fitted shaping parameter (r_L) was 2.09 ± 0.72.

Mean initial CWD mass in Group 1 stands was 76 ± 7.4 Mg C ha⁻¹ (range: 42–119 Mg C ha⁻¹, $n = 19$) and not significantly different from mean CWD mass in old-growth stands in 1998 (mean: 74 ± 12.7 Mg C ha⁻¹, range: 32–160 Mg C ha⁻¹, $n = 9$)

($t = -0.13$, $P = 0.89$). A small negative trend (i.e., time bias from harvest practices) among reconstructed initial CWD loads of Group 1 stands (Figure 2) was not significant either by linear (time = -1.03 ± 0.88, $t = -1.16$, $P = 0.26$) or quadratic (time = -0.02 ± 0.02, $t = -1.04$, $P = 0.312$) regression of mass against time. The fitted Group 1 legacy CWD C storage (D_0) was 55 ± 9.58 Mg C ha⁻¹ ($F = 81.11$, $P < 0.000$) (Figure 2).

Legacy CWD C stores declined with increasing stand age across Group 1 with a fitted mean decomposition rate (k_d) of 0.010 ± 0.006 year⁻¹ ($n = 18$) (see Figure 3 for distribution of mean CWD across all stands). This was lower than the calculated mean decomposition rate of individual stands of 0.025 year⁻¹ (range: 0.013–0.043 year⁻¹) and other reported values for *P. menziesii* in the region of about 0.03 year⁻¹ (Sollins 1982, J.E. Janisch et al., unpublished data). Because of this, the NEP_w was based on mean decomposition rate of individual stands. Mean fitted asymptotic de novo mass (N_0), accumulation rate (k_N) and shaping parameter (r_N) were 74 ± 6.65 Mg C ha⁻¹ ($F = 50.73$, $P < 0.001$), 0.025 ± 0.013 year⁻¹ and 11.13 ± 14.31, respectively (Figure 4). Regression of

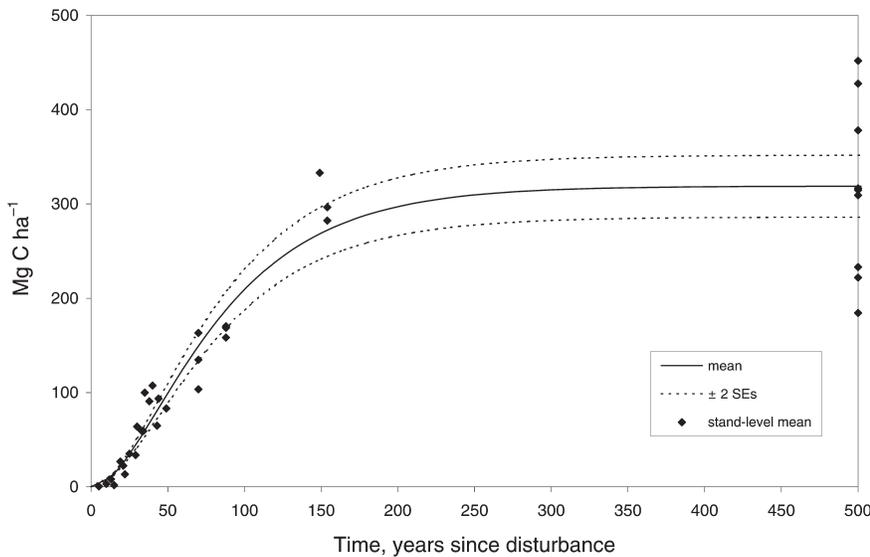


Figure 1. Live tree bole C stores along a 500-year chronosequence of 36 *Pseudotsuga-Tsuga* dominated forest stands. The x-axis is years since disturbance, or age of the stand. The y-axis is live bole C stores in each stand. Data were fit using a Chapman-Richards function where all parameters were allowed to vary. Data were collected from the Wind River Ranger District, Washington.

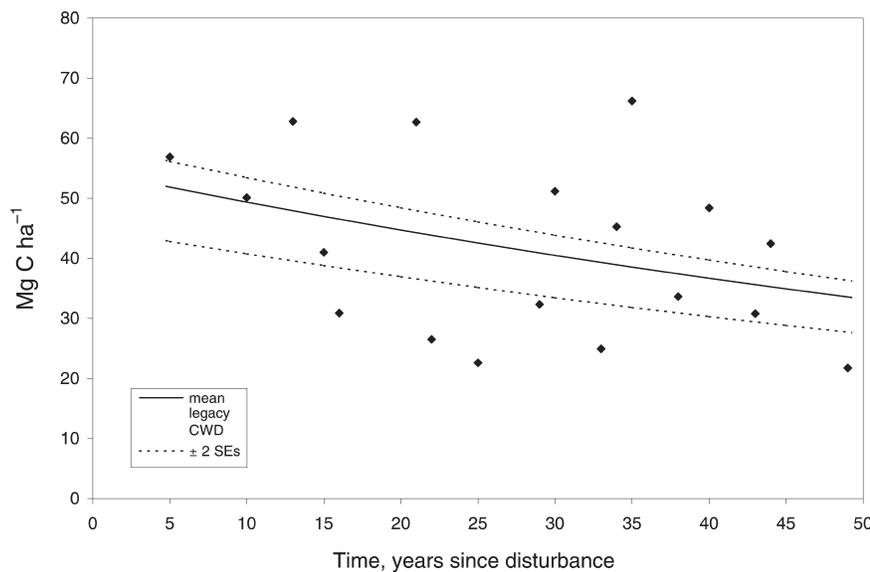


Figure 2. Change in estimated initial CWD C stores (stands < 60 years old; Group 1) using a simple exponential decomposition model ($y = De^{-kt}$). The weak time bias indicated in mass of CWD C left on-site after clear-cutting was not statistically significant. The x-axis is years since disturbance, or age of the stand. The y-axis is estimated initial CWD C stores in each stand. Data were obtained from *Pseudotsuga-Tsuga* dominated second-growth stands in the Wind River Ranger District, Washington.

old-growth live tree mass against old-growth CWD mass suggests a weak but not significant positive correlation between increasing live tree mass and increasing CWD mass ($+0.19 \pm 0.14$ Mg C ha⁻¹ CWD per 1 Mg C ha⁻¹ live tree mass, $n = 9$, $t = 1.41$, $P = 0.200$).

Given these results, at a rotation age of 80 years, a regenerating stand would store 172 Mg C ha⁻¹ live wood (mean) and 28 Mg C ha⁻¹ CWD (mean, including de novo CWD). This is 193 Mg C ha⁻¹ below old-growth rates ($L_0 +$ mean old-growth CWD). Given a rotation age of 60 years, a regenerating stand would store a mean of 125 Mg C ha⁻¹ in live wood and 21 Mg C ha⁻¹ CWD. This amounts to a reduction of 247 Mg C ha⁻¹ relative to old-growth stands, consistent with past modeled conversions of old-growth forests to regenerating forests (Harmon et al. 1990). Maximum C stores (live + dead) of 393 Mg C ha⁻¹ were reached about 200 years after disturbance.

The transition from negative to positive NEP_w depended strongly on growth rate and decomposition rate as well as the fate of CWD and harvested wood. In Scenario 1, where all CWD was assumed to be removed, stands functioned as net sinks of atmospheric CO₂ from Year 0 (Figure 5). In Scenario 2 (Figure 6), where CWD loads are reorganized by clear-cutting, stands functioned as CO₂ sources for 12–14 years. Given the range of CWD masses in old-growth stands (Scenario 3, Figure 7), it took 10–20 years for stands to become CO₂ sinks. When an old-growth stand was assumed to be killed by fire and decomposed in situ (Scenario 4), the transition took 50–56 years (Figure 8). The NEP_w ranged from a negative extreme of -14.1 Mg C ha⁻¹ year⁻¹ in Scenario 4 to a positive extreme of 3.9 Mg C ha⁻¹ year⁻¹ in Scenario 1.

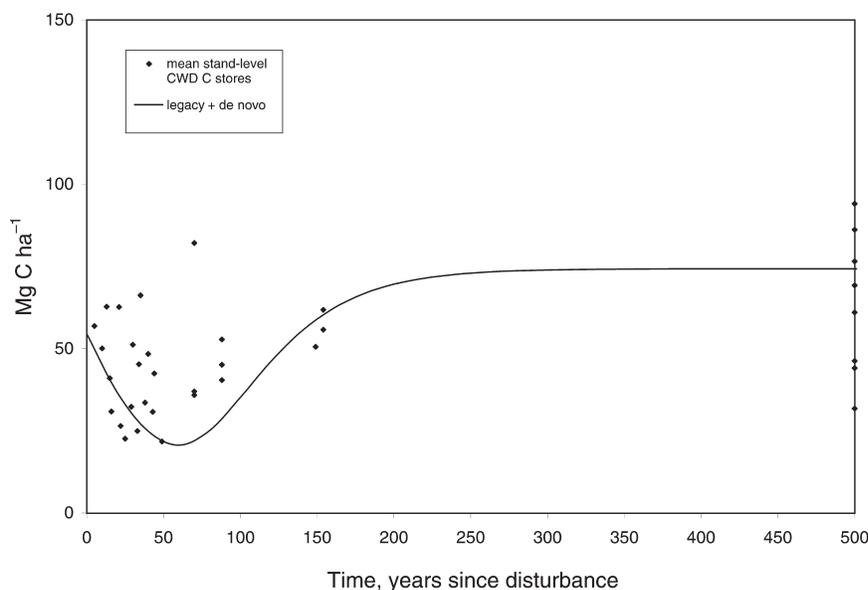


Figure 3. Total CWD C stores along a 500-year chronosequence of 36 *Pseudotsuga-Tsuga* dominated forest stands. Curve represents the sum of two separate functions: decline in legacy CWD C stores after clearcutting due to decomposition ($y = De^{-kt}$) and accumulation of de novo CWD following stand regeneration (Chapman-Richards function). The x -axis is years since disturbance (t), or age of the stand. The y -axis is CWD C stores in each stand. Data were collected from the Wind River Ranger District, Washington.

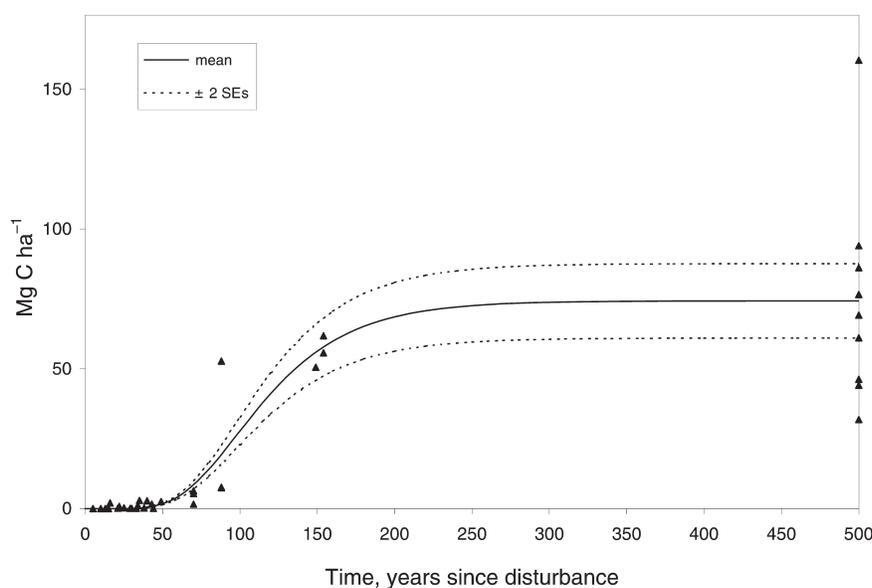


Figure 4. Change in de novo CWD C stores along a 500-year chronosequence of *Pseudotsuga-Tsuga* dominated stands in the Wind River Ranger District, Washington. Data was fit using a Chapman-Richards function. Mean old-growth CWD C mass was used as an asymptotic mass in the model. The x -axis is years since disturbance, or age of the stand. The y -axis is mean CWD C stores in each stand.

Discussion

Regional live wood and CWD

Mean live bole C stores in old-growth stands (319 Mg C ha^{-1}) were consistent with estimates from the Wind River Research Natural Area (302 Mg C ha^{-1} , M.E. Harmon, unpublished data), the H.J. Andrews Experimental Forest ($295\text{--}585 \text{ Mg C ha}^{-1}$, Grier and Logan 1977), and the regional mean of 296 Mg C ha^{-1} (Smithwick et al. 2001), but higher than values for other regional coniferous forests (158 Mg C ha^{-1} (*Tsuga mertensiana*, 225 years, Boone et al. 1988), $222.5 \text{ Mg C ha}^{-1}$ (*A. amabilis*, 180 years, Grier et al. 1981) and 234 Mg C ha^{-1} (*A. amabilis-T. mertensiana*, 417 years, Krumlik and Kimmins 1976)). Our estimates of CWD C stores are generally at

the lower end of the range reported for Oregon *P. menziesii*-dominated forests (127 Mg C ha^{-1} , Means et al. 1992; $29.5\text{--}325.8 \text{ Mg C ha}^{-1}$, Grier and Logan 1977; $95.5 \text{ Mg C ha}^{-1}$, M.E. Harmon, unpublished data) and coastal British Columbia *T. plicata*-dominated old-growth forests (182 Mg C ha^{-1} , Keenan et al. 1993). Compared with second-growth stands, old-growth live and CWD stores were more variable, consistent with the idea that, as stand age increases, there is more time for stochastic variation to be expressed (Eberhart and Woodard 1987, Sturtevant et al. 1997). Alternatively, variable regeneration times relative to the initiating disturbance could push old-growth stands apart in time (Tappeiner et al. 1997), leading to increased variation between such stands when treated as the same age class. Some of the increased variation with forest

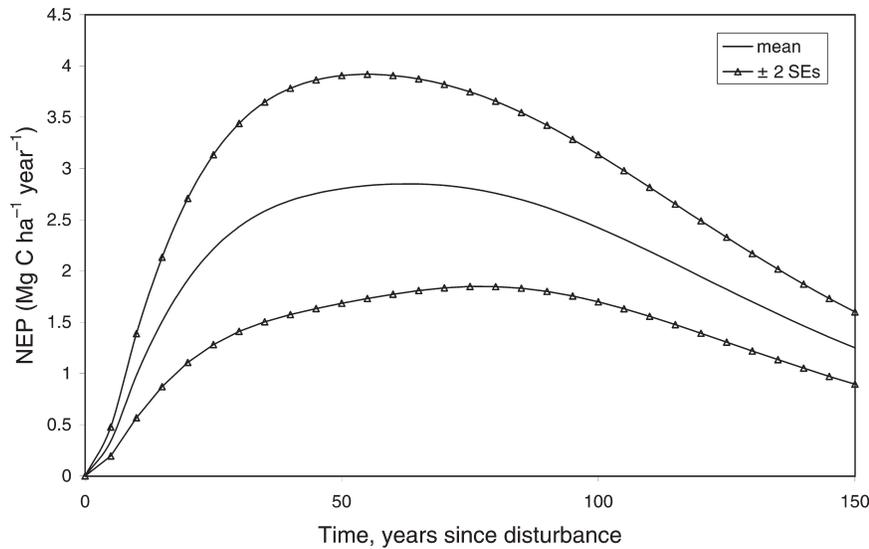


Figure 5. Predicted NEP_w dynamics over time (on site) during secondary succession. This scenario (Scenario 1) shows live tree biomass accumulation (stand regeneration), assuming that all CWD C stores are removed by logging and/or burning. Curves represent changes in NEP_w based on mean growth rate derived from a Chapman-Richards function and mean asymptotic live tree mass \pm 2 SE. Predicted NEP_w values are based on data from a chronosequence of *Pseudotsuga-Tsuga* dominated stands in the Wind River Ranger District, Washington.

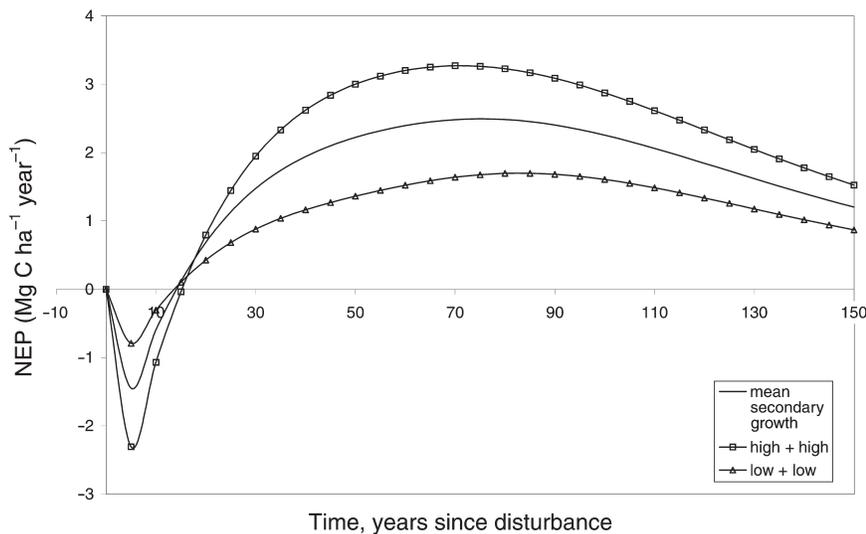


Figure 6. Predicted NEP_w dynamics over time (on site) during secondary succession when legacy CWD C stores were paired with live bole regeneration (Scenario 2). The solid curve describes NEP_w over succession based on mean legacy CWD C mass and mean asymptotic live bole mass. Dashed curves describe pairings of extremes of the ranges of live and CWD C stores. Totals include de novo CWD, but not stores removed from the site by clear-cutting. Predicted NEP_w values are based on data from a chronosequence of *Pseudotsuga-Tsuga* dominated stands in the Wind River Ranger District, Washington.

age may have been related to the small plot area used to sample old-growth stands.

Initial CWD mass

Lack of significant time bias in initial CWD was unexpected given changes in utilization and residual slash management reported elsewhere (Harmon et al. 1996b). This suggests that differences in initial CWD masses may be a function of old-growth CWD masses and site variables controlling production and decomposition. The weak positive correlation between increasing live tree mass and increasing CWD mass may reflect this pattern, suggesting that more studies are warranted.

Lack of a significant difference between initial Group 1 CWD loads and old-growth CWD mass does not, however, mean that CWD was unaffected by disturbance. Initial CWD mass in harvested stands, for example, included stumps, and by excluding them, mean Group 1 CWD stores declined to 57 Mg C ha^{-1} relative to old-growth CWD stores of 74.4 Mg C

ha^{-1} . This indicates a rapid period of loss of CWD from the site. A second effect of harvest is indicated by the narrower range of initial CWD mass in Group 1 stands relative to the range of 1998 old-growth CWD (37–99 Mg C ha^{-1} for Group 1 versus 67–281 Mg C ha^{-1} for old growth). This suggests that clear-cutting both reduces initial CWD loads relative to old-growth stands and reduces variability in CWD loads between harvested stands.

Live biomass accumulation

Although studies of aggrading live tree biomass appear to support some models of stand development (Siren 1955, Zackrisson et al. 1996), because we did not sample 200–400-year and +400-year age classes, it is unclear which hypothesis (e.g., smooth logistic growth, shifting mosaic, etc.) applies to this region. Other chronosequence data in the Pacific Northwest suggests a decline in live tree biomass beyond Age 400 years (T.A. Spies, U.S. Forest Service, personal communication),

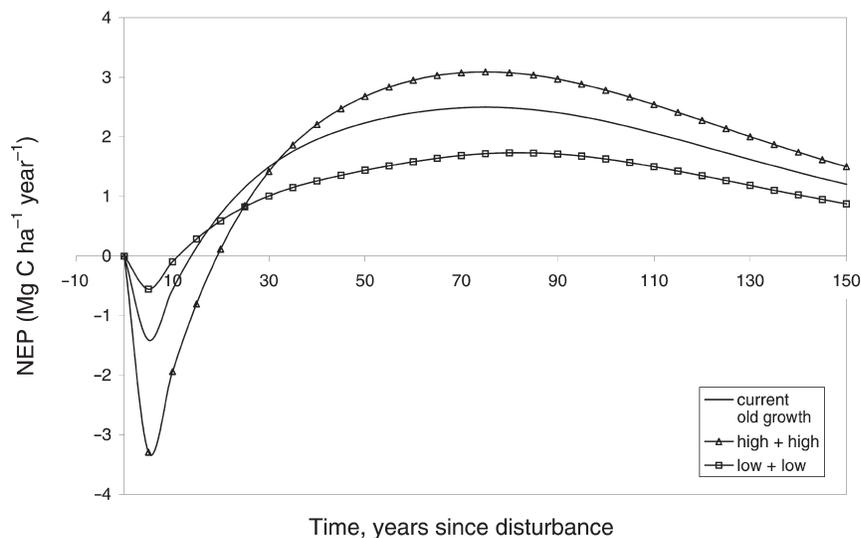


Figure 7. Predicted NEP_w dynamics over time (on site) during secondary succession for scenario when decomposition of old-growth CWD C stores is paired with live bole regeneration (Scenario 3). As with Scenario 2 (Figure 6), the transition from negative to positive NEP_w occurred approximately 14 years after clear-cutting. However, the curves, which show pairings of means and extremes of the ranges of live and CWD old-growth C stores, show a wider range than Scenario 2, indicating that CWD stores are homogenized by clear-cutting. Carbon stores removed from the site by clear-cutting are not included. Predicted NEP_w values are based on data from a chronosequence of *Pseudotsuga-Tsuga* dominated stands in the Wind River Ranger District, Washington.

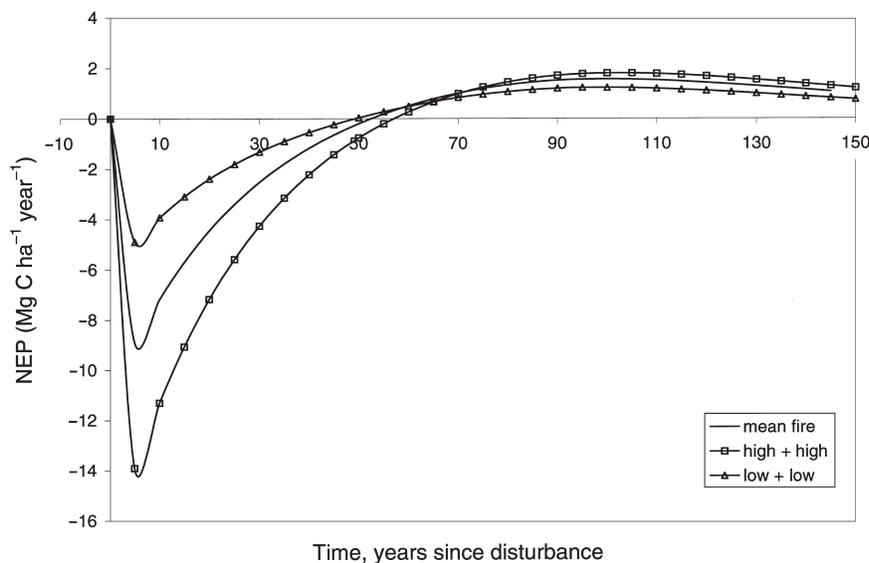


Figure 8. Predicted NEP_w dynamics over time (on site) during secondary succession for Scenario 4, in which all live trees in an old-growth stand are assumed to be killed by fire and allowed to decompose in situ. When these stores remained on-site, the transition from negative to positive NEP_w took approximately 50 years. Curves were generated by combining simple exponential decomposition models, Chapman-Richards functions, and empirically derived parameters. Predicted NEP_w values are based on data from a 500-year chronosequence of *Pseudotsuga-Tsuga* dominated stands in the Wind River Ranger District, Washington.

whereas time series data in old-growth forests suggest that biomass remains relatively constant (Franklin and DeBell 1988). Our data indicate that regrowth biomass approximates that found in old-growth forests by about 200 years after disturbance. Actual time series data showing biomass saturation by 150 years (Acker et al. 2000) and little change in old-growth live tree mass (Bible 2001) suggest that an asymptotic mass limit characteristic of the Chapman-Richards function is reasonable. Addition of other age stands and remeasurement of all stands over the next 10–20 years may help clarify the biomass accumulation dynamics of Pacific Northwest conifer forests.

NEP and initial conditions

The influence of initial conditions on NEP_w was investigated

through a hierarchical set of four scenarios. In general, NEP_w followed the pattern suggested by Odum (1969)—a negative phase followed by a positive phase followed by convergence on zero. When all legacy CWD was assumed to be oxidized or moved off-site during clear-cutting, there was no negative period of NEP_w because on-site CWD stores were zero (Scenario 1, Figure 5). In addition to setting an absolute positive limit on NEP_w , this scenario shows how short-term estimates of NEP_w and C accumulation are misleading if stand history is neglected. For example, given pre-harvest C stores of 300 Mg C ha^{-1} in live tree boles, approximately 95% is removed by harvest and 50% (142 Mg C ha^{-1}) of this is lost to the atmosphere during the first year (Harmon et al. 1996a). These initial losses would not be reflected in NEP_w were such a stand measured later in succession. The CO_2 debt might be further deepened in

this scenario by complete oxidation of CWD stores inherited from the harvested old-growth stand, implying a negative NEP_w pulse in excess of 200 Mg C ha^{-1} within the first year after harvest. Scenario 2 (Figure 6) predicts NEP_w during regeneration of a clear-cut stand using the range of initial CWD observed. This scenario had a short negative lag period but is also unrealistic because wood moved off-site during harvest and CWD oxidized as burned slash is not counted. Unless this C is preserved in decomposition-free, long-term storage (and some was already lost to burning), CO_2 flux to the atmosphere and the negative NEP_w phase are underestimated. Scenario 3 (Figure 7), like Scenario 2, predicts NEP_w during regeneration of a clear-cut. Unlike Scenario 2, however, the range of CWD stores in intact old-growth forest, rather than the range of CWD stores left by clear-cutting, are used to model NEP_w . Because clear-cutting both reduces (burning, removal of CWD stores inherited from the harvested stand) and increases (addition of stumps, unmerchantable boles, and other components from harvested live trees) stand CWD stores, Scenario 3 avoids some of the changes in this pool confounded by logging. Compared with Scenario 2, the source-to-sink transition is delayed longer following disturbance, the source-to-sink interval is wider, and the negative NEP_w phase is deeper. However, as with Scenario 2, the negative phase of NEP_w is still underestimated because harvested wood lost during manufacturing is not accounted for. Finally, off-site pools are not an issue in Scenario 4 because all stores remained on site. When an old-growth stand is completely killed by fire, all live wood stores move immediately into the CWD pool. If these CWD stores then decompose in situ, the mass and life span of this CWD load is so great that the negative NEP_w phase during secondary succession is protracted (50–56 years) and deepened ($-14.1 \text{ Mg C ha}^{-1} \text{ year}^{-1}$), and the positive NEP_w phase is dampened (peaking at $1.79 \text{ Mg C ha}^{-1} \text{ year}^{-1}$) relative to other scenarios. Although the role of Scenario 4 as an extreme negative limit on NEP_w is obvious, Scenario 4 also clarifies the underlying C flux signal of harvested stands, which has often been confused by the multiple fates and decomposition rates of material taken off site. Thus, if off-site C stores decompose and old-growth forests with high C storage are converted to short-rotation forests that do not attain C stores equivalent to those of the forest they replace, there is a net loss of terrestrial C to the atmosphere (Harmon et al. 1996a, 1996b). Overall, these results are consistent with modeled predictions of changes in C storage and 15–30 year negative NEP_w phases following conversion of old forest to younger forest (Harmon et al. 1990). To avoid the problem of how to treat disturbance and the fate of C removed from the site, net biome production (NBP) has been proposed as an extension of NEP (Schulze et al. 2000). We believe that NEP could also be used in this context, provided that conservation of mass is observed so that artificial C sinks are not created (e.g., NEP measured in stands is adjusted for C stores moved off-site).

NEP and carbon storage

The number of years NEP_w is negative is largely irrelevant,

however, because there is little relationship between the length of time that NEP_w is negative and the total mass loss from decaying CWD. If, for example, slash burning oxidized all CWD left by logging, NEP_w of the regenerating stand would register as positive immediately after replanting even though $> 50 \text{ Mg C ha}^{-1}$ was released and the mass of the replanted stand was trivial. Second, because CWD is ultimately oxidized unless it enters some form of permanent storage, stands should be treated as CO_2 sources at least until regenerating live tree mass balances the CO_2 debt generated by clear-cutting. This point is critical because if the C fixation rate exceeds the C loss rate, stands with absolute CO_2 debts relative to pre-harvest C storage will register as CO_2 sinks during “instantaneous” or short-term monitoring of NEP_w . When NEP_w accounting includes decomposition of all CWD, the source-to-sink transition changes to 27–57 years (Scenario 2), 38–165 years (Scenario 3) and 105–200+ years (Scenario 4) (based on mean live tree growth versus range of CWD). Further, Scenario 4 upper C storage limits are approachable only by accumulating both de novo CWD C and live bole C. Thus, C flux resulting from harvest disturbance, as well as C stores in second-growth stands relative to C stores in old-growth stands that they replace, must be included in assessing how forest management can mitigate increasing atmospheric CO_2 concentration. Given this outlook, conclusions about what constitutes a C sink, such as forest regrowth in the north temperate zone counterbalancing C released by tropical deforestation (Jarvis and Dewar 1993, Trans 1993, Gifford 1994), may need to be reassessed relative to old-growth forest baseline stores.

Improving NEP estimates

Considering whole-tree storage rather than just boles and bark would improve our NEP_w estimates, increasing the maximum NEP_w calculated by approximately one-third. Inclusion of herbaceous and shrub understory would also increase NEP, but to a smaller degree given their low maximum biomass. Including fine woody debris, forest floor litter and subsurface CWD pools would have reduced NEP during the negative phase by as much as $4\text{--}8 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ for all scenarios. Accumulations in forest floor litter might also add to the positive phase of NEP, whereas the fine subsurface woody detritus pools probably would not because the mass added by disturbance is much greater than the old-growth mass of these pools. Neglecting only soil C would thus provide an estimate at the ecosystem level, assuming that soil C is as unresponsive to disturbance as noted by Johnson and Curtis (2001). To reduce potential positive bias, NEP calculations could also reflect live-tree bole hollows and heart rot, which can be 8–14% of old-growth *T. heterophylla* “live” volume (Foster and Foster 1951). A further refinement would be the inclusion of lag-time parameters in the decomposition model, which could affect how negative NEP becomes, but not the magnitude of the CO_2 debt.

Because growth and decomposition rates strongly influence the NEP_w transition, better confidence intervals and upper and lower NEP_w limits could be estimated by Monte Carlo methods in which all parameters are allowed to co-vary. A true mor-

tality function describing mass of trees entering the CWD pool throughout succession could also be used. However, modeling mortality as logistic de novo mass accumulation may be a reasonable simplification because high seedling mortality contributes little CWD mass relative to mature tree mortality.

Management implications and conclusions

Publications considering forests as a means of atmospheric CO₂ mitigation have reached contradictory conclusions (Harmon et al. 1990, Marland and Marland 1992) depending on whether calculations consider CWD loads (Harmon et al. 1990, Fischlin 1996), substitution of wood for fossil fuels (Matthews 1992, 1994), afforestation, or conversion of old-growth forest to secondary forest (Schlamadinger and Marland 1996). There is also evidence that longer rotations, underplanting and other silvicultural manipulations of existing stands do little to improve CO₂ mitigation and are less effective than afforestation (Kuersten and Burschel 1993). The latter conclusions are supported by the low storage and high fluxes associated with conversion to short-rotation forests relative to intact old-growth forest indicated here. Conversely, afforestation on a scale to achieve appreciable CO₂ mitigation is limited by available land area (Shroeder and Ladd 1991). Given these limits, optimizing forest C storage appears to mean preserving old-growth forests and stopping deforestation or moving forest products into decomposition-free permanent storage.

Mass-based methods of estimating NEP also deserve more attention, particularly if the results of these methods run contrary to flux-based estimates. Although the legitimacy of flux tower and chamber-based measurement of NEP (e.g., Arneeth et al. 1998, Schmid et al. 2000) are not disputed here, key events in a stand's history, such as stand-destroying wildfire, may rapidly release high percentages of stored stand C. Because these events may span only days or weeks, a short period of time relative to potential stand life spans of several centuries or longer, there is a high probability that short-duration monitoring, regardless of method, will miss these rapid changes in C stores. Thus, estimates of NEP_w, and consequently conclusions about C sources, C sinks and C accumulation drawn from short-term flux measurements, should be interpreted cautiously.

Finally, descriptions of forest CWD C stores across a range of forest types have improved (Grier and Logan 1977, Harmon et al. 1995), but assessment of the sources and fates of these stores is still needed. Our results indicate that the more CWD is left on site, the more negative NEP_w becomes, the longer before NEP_w switches from negative to positive, and the lower the maximum NEP_w. When off-site and burned CWD stores are accounted for and C accumulation is summed over time, logging old-growth *Pseudotsuga-Tsuga* forests creates a CO₂ debt that may persist for more than 150 years, even when old-growth forests are replaced with vigorously growing secondary forest. If stand history is not considered, NEP-based determinations of whether stands function as CO₂ sources or sinks can be misleading. This is because C stores in old-growth

stands may differ vastly from C stores in second-growth stands that replace them, because woody biomass exported from a site may not be reflected in NEP, and because substantial fractions of stand C stores may be lost in rapid pulses easily missed by short-term monitoring.

Acknowledgments

This research was sponsored by the U.S. Department of Energy (DOE), National Institute for Global Environmental Change (NIGEC), Western Regional Center for Global Environmental Change (WESGEC), University of California, Davis, under Grant DE-FC03-90ER61010. Other support was provided by the H.J. Andrews LTER Program (DEB 9632921). We thank Kermit Cromack for field assistance and comments, and Gody Spycher for processing data used in this article. Suggestions from Steve Acker, Christian Wirth and Rod Keenan greatly improved the paper. We thank Jay Sexton, Becky Fasth, Jenna Boyle, Julia Hyatt, the Wind River Canopy Crane staff, and many others for their contributions.

References

- Aber, J.D. and J.M. Melillo. 1991. Terrestrial ecosystems. Saunders College Publishing, Philadelphia, 429 p.
- Acker, S.A., P.A. Harcombe, M.E. Harmon and S.E. Greene. 2000. Biomass accumulation over the first 150 years in coastal Oregon *Picea-Tsuga* forest. *J. Veg. Sci.* 11:725–738.
- Anonymous. 1999. Wood handbook: Wood as an engineering material. USDA Forest Service, Forest Products Laboratory, Madison, WI, Gen. Tech. Rep. FPL-GTR-1134, 63 p.
- Arneeth, A., F.M. Kelliher, T.M. McSeveny and J.N. Byers. 1998. Net ecosystem productivity, net primary productivity and ecosystem C sequestration in a *Pinus radiata* plantation subject to soil water deficit. *Tree Physiol.* 18:785–793.
- Bible, K. 2001. Long-term patterns of Douglas-fir and western hemlock mortality in the western Cascades of Washington and Oregon. Ph.D. Diss., Univ. Washington, Seattle, WA, 85 p.
- Boone, R.D., P. Sollins and K. Cromack, Jr. 1988. Stand and soil changes along a mountain hemlock death and regrowth sequence. *Ecology* 69:714–722.
- Bormann, F.J. and G.E. Likens. 1979. Pattern and process in a forested ecosystem: Disturbance, development, and the steady state based on the Hubbard Brook ecosystem study. Springer-Verlag, Berlin, 253 p.
- Chen, J. and J.F. Franklin. 1992. Vegetation responses to edge environments in old-growth Douglas-fir forests. *Ecol. Appl.* 2: 387–396.
- Constantin, J., A. Grelle, A. Ibrom and K. Morgenstern. 1999. Flux partitioning between understorey and overstorey in a boreal spruce/pine forest determined by the eddy covariance method. *Agric. For. Meteorol.* 98/99:629–643.
- Conway, S. 1982. Logging practices: principles of timber harvesting systems. Miller Freeman Publications, San Francisco, 432 p.
- Davis, M.B. 1986. Climatic instability, time lags, and community disequilibrium. *In* Community Ecology. Eds. J. Diamond and T.J. Case. Harper and Row, New York, pp 269–284.
- DeBell, D.S. and J.F. Franklin. 1987. Old-growth Douglas-fir and western hemlock: A 36-year record of growth and mortality. *West. J. Appl. For.* 2:111–114.
- Eberhart, K.E. and P.M. Woodard. 1987. Distribution of residual vegetation associated with large fires in Alberta. *Can. J. For. Res.* 17:1207–1212.

- Fischlin, A. 1996. Conflicting objectives while maximizing carbon sequestration by forests. *In* Forest Ecosystems, Forest Management, and the Global Carbon Cycle. Eds. M.J. Apps and D.T. Price. Springer-Verlag, Berlin, pp 163–172.
- Foster, R.E. and A.T. Foster. 1951. Decay of western hemlock on the Queen Charlotte Islands, British Columbia. *Studies in forest pathology*. *Can. J. Bot.* 29:479–486.
- Franklin, J.F. and D.S. DeBell. 1988. Thirty-six years of tree population change in an old-growth *Pseudotsuga-Tsuga* forest. *Can. J. For. Res.* 18:633–639.
- Franklin, J.F. and C.T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA Forest Service Gen. Tech. Rep. PNW-8, 417 p.
- Franklin, J.F. and R.H. Waring. 1979. Distinctive features of northwestern coniferous forests: Development, structure, and function. *In* Forests: Fresh Perspectives from Ecosystem Analysis. Ed. R.H. Waring. Oregon State University Press, Corvallis, OR, pp 59–86.
- Franklin, J.F., F.C. Hall, C.T. Dyrness and C. Maser. 1972. Federal research natural areas in Oregon and Washington: a guidebook for scientists and educators. USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, OR, 498 p.
- Gibbons, W.H. 1918. Logging in the Douglas-fir region. USDA Forest Service Contribution Bull. 711, 8 p.
- Gifford, R.M. 1994. The global carbon cycle: A viewpoint on the missing sink. *Aust. J. Plant Physiol.* 63:351–356.
- Graham, R.L. and K. Cromack, Jr. 1982. Mass, nutrient content, and decay state of dead boles in rain forests of Olympic National Park. *Can. J. For. Res.* 12:511–521.
- Grier, C.C. 1978. A *Tsuga heterophylla*–*Picea sitchensis* ecosystem of coastal Oregon: Decomposition and nutrient balance of fallen logs. *Can. J. For. Res.* 8:198–206.
- Grier, C.C. and R.S. Logan. 1977. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: Biomass distribution and production budgets. *Ecol. Monogr.* 47:373–400.
- Grier, C.C. and J.G. McColl. 1971. Forest floor characteristics within a small plot in Douglas-fir in Western Washington. *Soil Sci. Soc. Am. Proc.* 35:988–991.
- Hanzlik, E.J., F.S. Fuller and E.C. Erickson. 1917. A study of breakage, defect, and waste in Douglas-fir. *Univ. Washington Forest Club Annual* V:32–39.
- Harmon, M.E. and J. Sexton. 1996. Guidelines for measurements of woody detritus in forest ecosystems. LTER Network Publication No 20. Univ. Washington, Seattle, WA, 91 p.
- Harmon, M.E., J.F. Franklin, F.J. Swanson, et al. 1986. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* 15: 133–302.
- Harmon, M.E., W.K. Ferrell and J.F. Franklin. 1990. Effects of carbon storage on conversion of old-growth forests to young forests. *Science* 247:699–702.
- Harmon, M.E., D.F. Whigham, J. Sexton and I. Olmsted. 1995. Decomposition and mass of woody detritus in the dry tropical forests of the Northeastern Yucatan Peninsula, Mexico. *Biotropica* 27: 305–316.
- Harmon, M.E., S.L. Garman and W.K. Ferrell. 1996a. Modeling historical patterns of tree utilization in the Pacific Northwest: Carbon sequestration implications. *Ecol. Appl.* 6:641–652.
- Harmon, M.E., J.M. Harmon, W.K. Ferrell and D. Brooks. 1996b. Modeling carbon stores in Oregon and Washington forest products: 1900–1992. *Clim. Change* 33:521–550.
- Hensen, J., M. Sato, R. Reudy, A. Lacis and V. Oinas. 2000. Global warming in the 21st century: An alternative scenario. *Proc. Natl. Acad. Sci.* 97:9875–9880.
- Hodgson, A.H. 1930. Logging waste in the Douglas-fir region. *Pacific Pulp and Paper Industry and West Coast Lumberman* 56: 6–13.
- Howard, J.O. 1981. Ratios for estimating logging residue in the Pacific Northwest. USDA Forest Service Research Paper PNW-288, 26 p.
- Iverson, L.R., S. Brown, A. Grainger, A. Prasad and D. Liu. 1993. Carbon sequestration in tropical Asia: An assessment of technically suitable forest lands using geographic information systems analysis. *Clim. Res.* 3:23–38.
- Jarvis, P.G. and R.C. Dewar. 1993. Forests in the global carbon balance: From stand to region. *In* Scaling Physiological Processes: Leaf to Globe. Eds. J.R. Ehleringer and C.B. Field. Academic Press, San Diego, pp 191–222.
- Johnson, D.W. and P.S. Curtis. 2001. Effects of forest management on soil C and N storage: Meta analysis. *For. Ecol. Manage.* 140: 227–238.
- Johnson, C.M., D.J. Zarin and A.H. Johnson. 2000. Post-disturbance above-ground biomass accumulation in global secondary forests. *Ecology* 81:1395–1401.
- Keenan, R.J., C.E. Prescott and J.P. Kimmins. 1993. Mass and nutrient content of woody debris and forest floor in western red cedar and western hemlock forests on northern Vancouver island. *Can. J. For. Res.* 23:1052–1059.
- Kira, T. and T. Shidei. 1967. Primary production and turnover of organic matter in different forest ecosystems of the western Pacific. *Jpn. J. Ecol.* 7:70–87.
- Körner, Ch. 1996. The response of complex multi-species systems to elevated CO₂. *In* Global Change and Terrestrial Ecosystems. Eds. B. Walker and W. Steffen. Cambridge University Press, Cambridge, pp 20–42.
- Krumlik, G.J. and J.P. Kimmins. 1976. Studies of biomass distribution and tree form in old virgin forests in the mountains of southern coastal British Columbia. *In* Forest Biomass Studies. Ed. H.E. Young. Univ. Maine, Orono, ME, pp 361–373.
- Kuersten, E. and P. Burschel. 1993. CO₂-mitigation by agroforestry. *Water Air Soil Pollut.* 70:533–544.
- Lang, G.E. 1985. Forest turnover and the dynamics of bole wood litter in sub-alpine balsam fir forest. *Can. J. For. Res.* 15:199–293.
- Marland, G. 2000. The future role of reforestation in reducing buildup of atmospheric CO₂. *In* The Carbon Cycle. Eds. T.M.L. Wigley and D.S. Schimel. Cambridge University Press, Cambridge, pp 190–198.
- Marland, G. and S. Marland. 1992. Should we store carbon in trees? *Water Air Soil Pollut.* 64:181–195.
- Matthews, R.W. 1992. Forests and arable energy crops in Britain: Can they help stop global warming? *In* Wood: Fuel for Thought. Ed. G.E. Richards. Proc. Conf. Energy Technology Support Unit, Harwell, U.K., pp 21–32.
- Matthews, R.W. 1994. Towards a methodology for the evaluation of the carbon budget of forests. *In* Carbon Balance of the World's Forested Ecosystems: Towards a Global Assessment. Ed. M. Kanninen. Proc. Workshop Intergovernmental Panel on Climate Change AFOS, Joensuu, Painatuskeskus, Helsinki, pp 105–114.
- Means, J.E., K. Cromack, Jr. and P.C. MacMillan. 1985. Comparison of decomposition models using wood density of Douglas-fir logs. *Can. J. For. Res.* 15:1092–1098.
- Means, J.E., P.C. MacMillan and K. Cromack, Jr. 1992. Biomass and nutrient content of Douglas-fir logs and other detrital pools in an old-growth forest, Oregon, USA. *Can. J. For. Res.* 22:1536–1546.
- Means, J.E., H.A. Hansen, G.J. Koerper, P.B. Alaback and M.W. Klopsch. 1994. Software for computing plant biomass—BIOPAK users guide. USDA Forest Service Gen. Tech. Rep. PNW-GTR-340, 184 p.

- Mesquita, R.C.P., P. Delamonica and W.F. Laurance. 1999. Effect of surrounding vegetation on edge-related tree mortality in Amazonian forest fragments. *Biol. Conserv.* 91:129–134.
- Moncrieff, J., R. Valentini, S. Greco, G. Seufert and P. Ciccioli. 1997. Trace gas exchange over terrestrial ecosystems: Methods and perspectives in micrometeorology. *J. Exp. Bot.* 48:1133–1142.
- Odum, E. 1969. The strategy of ecosystem development. *Science* 164:262–270.
- Pare, D. and Y. Bergeron. 1995. Above-ground biomass accumulation along a 230-year chronosequence in the southern portion of the Canadian boreal forest. *J. Ecol.* 83:1001–1007.
- Peet, R.K. 1981. Changes in biomass and production during secondary forest succession. *In* *Forest Succession: Concepts and Application*. Eds. D.C. West, H.H. Shugart and D.B. Botkin. Springer-Verlag, New York, pp 324–338.
- Pool, C.G. 1950. An analysis of falling and bucking. *Timberman* 51: 78–82.
- Richards, F. 1959. A flexible growth function for empirical use. *J. Exp. Bot.* 10:290–300.
- Rogers, H.H., G.B. Runion and S.V. Krupa. 1993. Plant responses to atmospheric CO₂ enrichment with emphasis on roots and the rhizosphere. *Environ. Pollut.* 83:155–189.
- Romme, W.H. 1982. Fire and landscape diversity in sub-alpine forest of Yellowstone National Park. *Ecol. Monogr.* 52:199–221.
- Schlamadinger, B. and G. Marland. 1996. Carbon implications of forest management strategies. *In* *Forest Ecosystems, Forest Management, and the Global Carbon Cycle*. Eds. M.J. Apps and D.T. Price. Springer-Verlag, Berlin, pp 217–232.
- Schlamadinger, B. and G. Marland. 1998. Substitution of wood from plantation forestry for wood from deforestation: Modeling the effects on carbon storage. *In* *Carbon Mitigation Potentials of Forestry and Wood Industry*. Eds. G.H. Kohlmaier, M. Weber and R. Houghton. Springer-Verlag, Berlin, pp 205–218.
- Schmid, H.P., F. Cropley, H.-B. Su, B. Offerle and C.S.B. Grimmond. 2000. Measurements of CO₂ and energy fluxes over a mixed hardwood forest in the mid-western United States. *Agric. For. Meteorol.* 103:357–374.
- Schulze, E.-D., C. Wirth and M. Heimann. 2000. Managing forests after Kyoto. *Science* 289:2058–2059.
- Shroeder, P. and L. Ladd. 1991. Slowing the increase of atmospheric carbon dioxide: A biological approach. *Clim. Change* 19:1431–1438.
- Siren, G. 1955. The development of spruce forest on raw humus sites in northern Finland and its ecology. *Acta For. Fenn.* 62:1–363.
- Smithwick, E.A.H., M.E. Harmon, S.M. Reimillard, S.A. Acker and J.F. Franklin. 2002. Potential upper bounds of carbon stores in forests of the Pacific Northwest. *Ecol. Appl.* In press.
- Sollins, P. 1982. Input and decay of coarse woody debris in coniferous stands in Western Oregon and Washington. *Can. J. For. Res.* 12:18–28.
- Sollins, P., S.P. Cline, T. Verhoeven, D. Sachs and G. Spycher. 1987. Patterns of log decay in old-growth Douglas-fir forest. *Can. J. For. Res.* 17:1585–1595.
- Spies, T.A., J.F. Franklin and T.B. Thomas. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. *Ecology* 69:1698–1702.
- Sturtevant, B.R., J.A. Bissonette, J.N. Long and D.W. Roberts. 1997. Coarse woody debris as a function of age, stand structure, and disturbance in boreal Newfoundland. *Ecol. Appl.* 7:702–712.
- Swift, M.J., O.W. Heal and J.M. Anderson. 1979. *Decomposition in terrestrial ecosystems*. University of California Press, Berkeley, CA, 372 p.
- Tappeiner, J.C., D. Huffman, D. Marshall, T.A. Spies and J.D. Bailey. 1997. Density, ages and growth rates in old-growth and young-growth forests in coastal Oregon. *Can. J. For. Res.* 27:638–648.
- Trans, P.P. 1993. Observational strategy for assessing the role of terrestrial ecosystems in the global carbon cycle: Scaling down to regional levels. *In* *Scaling Physiological Processes: Leaf to Globe*. Eds. J.R. Ehleringer and C.B. Field. Academic Press, San Diego, pp 179–190.
- Whittaker, R.H. and G.M. Woodwell. 1969. Structure, production, and diversity of the pine–oak forest at Brookhaven, New York. *J. Ecol.* 55:155–174.
- Wirth, C., E.-D. Schulze, B. Lühker, et al. 2002. Fire and site type effects on the long-term carbon and nitrogen balance in pristine Siberian Scots pine forests. *Plant Soil*. In press.
- Zackrisson, O., M.C. Nilsson and D.A. Wardle. 1996. Key ecological function of charcoal from wildfire in the boreal forest. *Oikos* 77: 10–19.