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As concern over global warming intensifies, sequestration and storage of atmospheric CO_2 has become an important scientific and policy issue. Confusion persists, however, over interpretation of forest carbon (C) source-sink dynamics, in part because conclusions drawn depend on temporal and spatial scales of analysis (e.g. day-week scale vs. successional-scale), type of disturbance, and methodology (e.g. mass-based vs. flux-based). There is a need to resolve this confusion given that strategies for mitigating anthropogenic CO_2 emissions are based on estimates of forest C fluxes during various stages of succession, over which C fluxes and stores may change. Empirical study of changes in forest C stores can help to resolve this confusion by clarifying the C sources-sink dynamics of forests in space and time.

To better understand the impacts of disturbance on C source-sink dynamics, changes in C stores of an evergreen-dominated forest on the Wind River Ranger District in Southwestern Washington, U.S.A., were investigated along a 500-year chronosequence of 36 stands. Principle objectives were to evaluate 1) decomposition rates (*k*) of logs, stumps, and below-ground coarse roots, 2) net primary productivity (NPP) of dominant tree species' boles at the stand level, and 3) successional changes in net ecosystem productivity (NEP) for live trees and coarse woody debris (CWD), here called NEP_w.

In the case of decomposition, log and stump *k* values did not differ significantly within the two principle species studied, indicating substitution of log *k* values for stump *k* values in models of forest C budgets may be valid when stump decomposition data is lacking. Decomposition rates between species differed, with Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) decomposing more slowly ($k = 0.013$ yr^{-1}) relative to western hemlock (*Tsuga heterophylla* (Raf.) Sarg. ($k = 0.036$ yr^{-1}). This difference in *k* between species was observed for both above-ground stumps and logs as well as below-ground coarse roots. Given our mean *k* estimates and adjusting for regenerating stand age, these stands are losing C at a rate of 0.16-0.83 Mg C ha^{-1} yr^{-1} (assuming all CWD is *P. menziesii*) to 0.13-1.68 Mg C ha^{-1} yr^{-1} (assuming all CWD is *T. heterophylla*) from stumps, logs, and snags. Including coarse roots increases these losses to 0.28-1.25 Mg C ha^{-1} yr^{-1} and 0.30-2.53 Mg C ha^{-1} yr^{-1}, respectively. Based on these findings, if fragmentation of these decomposing C pools is ignored, and fragmented fractions have oxidized to CO_2, stands thought to be net C sinks could in reality be net C sources to the atmosphere.

Net primary production in tree boles (NPP_b) of regenerating stands (so called second-growth) ranged between 0.15-5.28 Mg C ha^{-1} yr^{-1}. NPP_b of 500-year old stands ranged between 1.3-3.9 Mg C ha^{-1} yr^{-1}, similar to NPP_b of boles in 20-25 year old second-growth. Mean radial increment widths from old-growth stands indicated that NPP_b of

these stands (neglecting mortality) can increase, decrease, or remain relatively constant. Based on 5-year increments for the previous fifteen years, the majority of old-growth stands sampled showed small increases in radial growth over time.

Timing of the transition from negative to positive of NEP_w ranged between 0 and 57 years after disturbance and depended strongly on live-tree growth rates as well as the fate of CWD and harvested wood. Estimated maximum and minimum NEP_w were 3.9 Mg C ha^{-1} yr^{-1} and –14.1 Mg C ha^{-1} yr^{-1}, respectively. Maximum mean C stores of 393 Mg C ha^{-1} were reached approximately 200 years after disturbance. At a rotation age of 80 years, regenerating stands stored approximately 50% as much C in woody biomass as a 500-year old primary forest, indicating conversion of older forests to plantations released C to the atmosphere. Given the high biomass of mature and old-growth stands relative to younger regenerating stands in the forest studied, landscape C stores in live wood would appear to be maximized in stands of older age classes.

Carbon Storage in a Pacific Northwest Conifer Forest Ecosystem: A Chronosequence Approach

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CONTRIBUTION OF AUTHORS

Dr. Mark E. Harmon guided design, execution, and analysis of this project and writing of each manuscript. Dr. Kermit Cromack, Jr. assisted with data collection and suggested improvements for each manuscript. Dr. Hua Chen oversaw coarse root sampling and analysis. Becky Fasth and Jay Sexton assisted with data collection from multiple C pools and data management.

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CHAPTER 1

INTRODUCTION

1.1 INTRODUCTION

Atmospheric carbon dioxide (CO_2) concentrations have increased from 316 ppmv in 1959 to 363 ppm_v in 1997 (Keeling and Whorf, 1998) and this trend is expected to continue due to burning of fossil fuels, conversion of forests to agriculture, and other anthropogenic changes in the biosphere (IPCC 2001). Increasing concentration of this gas has drawn attention because it belongs to a group of gases transparent to short-wave radiation but opaque to certain long wave radiation. Since long wave (infra-red) radiation is equivalent to heat, these gases, known as greenhouse gases (GHG), trap heat. Thus, as atmospheric concentrations of these gases increase, there is risk of altering radiative heat exchange between the planet and space. Potential changes in transport of heat between poles and equator may in turn alter atmospheric circulation patterns that drive climate, potentially redistributing energy responsible for precipitation patterns, as well as long-term weather cycles (Pierrehumbert 2000). How altered climate will affect the biosphere remains uncertain, but predictions include extinctions, range contractions, and/or range expansions of species across all phyla (Ford 1982, Kappelle et al 1999). Dollar costs associated with redistribution of climate and the biosphere are also unknown, though weather-related federal relief in the United States 1990-1997 totaled $12 billion

(Easterling et al 2000). Models predict a global mean temperature rise of 1-4° C (IPCC 1996) by 2100 in response to these heat balance changes, recently revised upward to 1.4-4.8° C (IPCC 2001).

Given the potential bio-geochemical consequences and costs of climate change, manipulation of world forests has been proposed as one means to mitigate atmospheric CO_2 enrichment (Marland 1988, Henderson and Dixon 1993, Iverson et al 1993). Discussion of forest C fluxes, however, has been confused by differences in methodology, pools and scale considered, and other factors. Estimates of temperate and boreal forest C fluxes, for example, have ranged between net C storage (Melillo et al. 1988, Johnson and Sharpe 1983) and net C release (Houghton et al 1983). In addition, only limited regional data may be available for global C flux models, resulting in local ecosystem parameters applied over planetary scales (Houghton et al 1983). There are also uncertainties still associated with estimates of CO_2 fluxes from forest components (Skole and Tucker 1993, Uhl and Kauffman 1990) and the planetary C budget does not yet balance (Dale et al. 1991). Further obscuring relevant climate signals are simultaneous atmospheric warming and cooling (Hartmann et al 1997), natural CO_2 flux variation (Bousquet et al 2000), long-term climatic and oceanic cycles (Kerr 2000), and mean global temperature increases stemming from non-CO_2 greenhouse gases (Hansen et al 2000). And, as pointed out by Schneider (2001), future climate predictions depend on baseline thresholds as well as modeling scenario probabilities. Aside from their scientific relevance, these complications and uncertainties also carry political significance. This is because apparently contrary findings could be used to discredit global change predictions and because policy responses to global warming, even when scientifically grounded, are value statements.

1.2 OBJECTIVES AND CHAPTER ARRANGEMENT

If forests are to be used to mitigate increasing atmospheric CO_2, it is essential to identify their biological C pools and understand how these pools function as C sources and sinks at appropriate scales, as well as reduce uncertainties in estimates of C pool mass and rates of growth and decomposition. Evergreen-dominated forests of the Pacific Northwest attain some of the highest C storage of any terrestrial ecosystem, with some mesic and coastal sites exceeding 1100 Mg C ha^{-1} in total stores (regional mean 671 Mg C ha^{-1}, Smithwick et al, accepted). The impacts of stand destroying disturbance, such as wildfire and clearcutting, on C flux and stores in these forests over time, however, are disputed.

To better understand these impacts, we pursued three objectives: 1) empirically derive estimates of log, stump, and below-ground coarse root decomposition (*k*) rates. This was accomplished by examining density and volume changes in these pools across stands of age 7-50 years (post-harvest); 2) empirically derive estimates of live tree bole net primary productivity (NPP) rates. This was accomplished by coring dominant tree species in 36 stands along a 400-600 year chronosequence; 3) investigate successional changes in net ecosystem productivity (NEP) following harvest of 400-600 year old trees by clearcut logging and wildfire. This was accomplished by measuring the stores of live and dead woody forest C pools along the chronosequence and combining this data with decomposition and growth rates to estimate maximum and minimum stand-level trajectories of NEP.

In Chapter 2, decomposition rates (*k*) for logs, stumps, and coarse roots, of Pacific Northwest conifer species are estimated along a chronosequence. While log *k* estimates exist for a range of forest types, decomposition of stumps and below-ground coarse root, both significant coarse wood debris (CWD) C pools, has been neglected with few exceptions (Fahey et al 1988, Fahay and Arthur 1994, Yavitt and Fahey 1982, Chen et al 2001). Since stump and coarse root mass is the second largest CWD pool generated by clearcutting, this work refines modeling of C storage by generating actual estimates of CO_2 flux from these major forest C pools. It also describes new estimates of log decomposition rates from four conifer species in a setting (clearcuts) that has not been examined before. This data also provides a context for interpreting estimates of NPP by describing what rates of CO_2 sequestration are needed to balance CO_2 loss from heterotrophic respiration.

Chapter 3 examines NPP dynamics over forest succession. By coring dominant tree species from each stand across their diameter distributions and analyzing radial increment, we consider NPP of tree boles at the stand level, which we call NPP_b. Its significance lies in examining how rates of NPP_b change in individual stands during succession and how the shape of an NPP_b curve generated by a chronosequence changes during succession. Since time series data existed for several stands in the region, we are also able to compare our results to NPP_b curves generated by times-series methods.

Chapter 4 examines stand-level NEP. In this preliminary analysis, live tree mass and CWD mass are combined with decomposition rates and growth rates to describe C storage in these components, which we call NEP_w, over forest succession following stand-destroying disturbance. The significance of this is that conclusions about whether forest stands function as sources or sinks of atmospheric CO_2 depend on whether NEP_w measurements are mass- or flux-based and whether these measurements are short-term (days-months) or long-term (over the succession process). Impacts on NEP_w are explored through a set of four hierarchical scenarios ranging between extremes of all coarse woody debris (CWD) removed from sites during harvest to all live trees killed by wildfire and decomposing *in situ*. While forest soils store an estimated 35% of total system C, other work indicates this C is released slowly relative to the time scale of forest disturbance and succession (Johnson and Curtis 2001). Thus, since a large fraction of non-soil forest C is stored in live boles and CWD (Smithwick et al, accepted), these components may largely govern forest C fluxes even though other C pools relevant to NEP exist in forest ecosystems and we focus on these stores.

Finally, the thesis concludes with Chapter 5, a short discussion of key findings and how forest management, changing climate, and politics may influence forest C storage policy and achieving C storage goals.

CHAPTER 2

A CHRONOSEQUENCE APPROACH TO CARBON FLUX FROM COARSE WOODY DEBRIS: *IN SITU* DECOMPOSITION IN A PACIFIC NORTHWEST CONIFER FOREST ECOSYSTEM

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2.1 ABSTRACT

Forest manipulation can release C stored in forests to the atmosphere by reorganizing CWD pools, but the degree to which these releases shift a stand's carbon (C) source or sink status is difficult to assess without knowing specific *in situ* decomposition rate constants (*k*). In this study, *k* of above-ground logs and stumps and sub-surface coarse roots were assessed by volume-density change methods along a 70-year chronosequence of previously clearcut stands on the Wind River Ranger District, Washington, U.S.A. Principle species sampled were *Tsuga heterophylla* (Raf.) Sarg. (logs, stumps, roots) and *Pseudotsuga menziesii* (Mirb.) Franco (logs, stumps, roots). Wood and bark tissue densities were weighted by sample fraction, adjusted for fragmentation, then regressed to examine *k* differences between stumps, logs, coarse roots, and species. No significant differences between stump and log *k* values were found within species, but *P. menziesii* decomposed more slowly ($k = 0.017$ yr^{-1}) relative to *T. heterophylla* ($k = 0.036$ yr^{-1}). This species pattern was the same for above-ground vs. below-ground *k* values. Small diameter *P. menziesii* roots (3-8 cm) decomposed faster ($k = 0.014$ yr^{-1}) than large (3-8 cm) diameter roots ($k = 0.008$ yr^{-1}), a pattern echoed by *T. heterophylla* roots (1-3 cm: $k = 0.023$ yr^{-1}; 3-8 cm: $k = 0.017$ yr^{-1}). Given our mean *k* estimates, stands studied are losing C at a rate of 0.4 -1.1 Mg C ha^{-1} yr^{-1} (assuming all CWD is *P. menziesii*) to 0.4 – 1.4 Mg C ha^{-1} yr^{-1} (assuming all CWD is *T. heterophylla*) from stumps, logs, and snags. Including coarse roots increases these losses to 0.8 - 2.2 and 0.6 - 3.6 Mg C ha^{-1} yr^{-1}, respectively. The key finding that log and stump *k* values did not differ significantly within the two principle species studied suggests substitution of log *k* values for stump *k* values in models of forest C budgets may be valid when stump decomposition data is lacking.

Key words: Carbon storage; coarse woody debris; decomposition rate; fragmentation; *k*; logs; stumps; coarse roots.

2.2 INTRODUCTION

Increased greenhouse gas (GHG) concentrations may shift atmospheric heat balances, triggering complex climatic and biosphere changes (Korner 1996, Wohl et al 2000) and potentially costing billions of dollars (Changnon and Easterling 2000, Kremen et al 2000). Predicted increases in global mean temperatures during the next century may result principally from atmospheric enrichment of one of these gases, CO_2, due to its abundance relative to other GHGs, its exchange between biological, atmospheric, and geochemical storage pools, and anthropogenic effects on the mass and rate of exchange between C stores (IPCC 2001). Terrestrial carbon (C) storage is therefore under study as a means to offset these increases (DeLucia et al 1999, Schulze et al 2000). Understanding terrestrial C storage is particularly relevant in regions implicated as large CO_2 sinks (~1.4-1.7 Pg C yr^{-1}), such as North America (Fan et al 1998) and the Neotropics (Grace et al 1995, Phillips et al 1998), in order to set reasonable C sequestration policies (e.g. Schulze et al 2000, Schneider 2001).

Wood stores atmospheric C sequestered photosynthetically until released back to the atmosphere as CO_2 through decomposition (Swift 1979, Harmon et al 1986). Time since disturbance, growth and decomposition rate, mortality, and other factors thus control these stores (Laurance et al 1997, 1998, Harmon 2001) and consequently net loss or gain of stand-level C. Processes altering these relationships, such as increasing rates of transfer of live wood stores to CWD stores (e.g. forest acreage reductions, forest product extraction, wildfire (Grantham 1974, Pong and Henely 1985)) may thus convert stands acting as C sinks or stands in C balance relative to the atmosphere to C sources (Houghton et al 1983, Harmon et al 1996). Conversion of old-growth forests to short-rotation forests and other purposes has released an estimated 1.5 $\times 10^9$-1.8 $\times 10^9$ Mg C from Pacific Northwest forests during the last century (Harmon et al 1996a). While this conversion may proceed at the stand level, when summed at landscape scales C storage is reduced because mean forest age and C storage has declined (Harmon 2001).

Global forest C stores roughly equal current atmospheric C stores (Dixon et al 1994). Given that approximately half of these C stores occur as live trees and CWD, and that live C stores eventually become detrital C stores, the consequences of inappropriate assumptions about growth and decomposition rates are not trivial and could conceivably bias the C source or C sink classification of forest stands. In addition, uncertainties still associated with estimates of CO_2 fluxes from forests related to total forest area cleared, decomposition rates of each CWD component, pre- vs. post-harvest CWD loads, and magnitude of CWD fragmentation over time (Uhl and Kauffman 1990, Skole and Tucker 1993) can obscure the actual C source or C sink status of a stand. Coarse woody debris stores, for example, are highly variable and related to successional stage (Lofroth 1998, Spies et al 1988), forest type (Harmon et al 1986, Spetich et al 1999), disturbance type and interval (Eyre and Longwood 1951, Spetich et al 1999), decomposition rates (Scheffer 1949, Brown et al 1996), and changes in harvest practices over time (Gibbons 1918, Harmon et al 1996a). On- vs. off-site fates of CWD compound these uncertainties (Cramer 1974, O'Connell 1997). If these uncertainties are not resolved, managing forests for increased C storage could be misguided and issued C credits could be revoked.

One major component needed to reduce uncertainties in predictions of forest-atmosphere CO_2 exchange is estimates of forest CWD C stores. Pre- and post-disturbance CWD masses based on direct measurement and allometric relationships

(Gholz et al 1979, Whittaker and Woodwell 1968) have been reported from tropical (Lang and Knight 1979, O'Connell 1997), temperate (Sollins 1982, Tinker and Knight 2000), and boreal (Hofgaard 1993, Krankina et al 1999) forests. Given these data, the three principle CWD pools left after disturbance are logs, stumps or snags, and coarse roots.

Since a major source of stumps and coarse roots now decomposing on the landscape were generated by clearcutting old-growth forest (e.g. large trees), estimates of stump, root mass, and entailing C fluxes may be best based on C stores in old-growth stands. Given a mean old-growth bole mass of 319 Mg C ha^{-1} (Janisch and Harmon, accepted), stump mass as 5% of bole mass, and coarse roots as 20% of bole mass, these two pools would add on average 79 Mg C ha^{-1} to stand CWD mass assuming these CWD pools originate from clearcutting.

Aside from data on stores, modeling CWD C flux from forests also requires species-specific *in situ* decomposition rate constants (*k*) of each component. Towards this end, temperate, tropical, and boreal log decomposition has received considerable attention (Mackensen and Bauhus 1999). Stump (Heal et al 1983) and coarse root (Yavitt and Fahey 1982, Chen and Harmon 2001) *k* values, however, remain scarce so stump *k* is often inferred from logs. Until tested, however, the appropriateness of these substitutions is open to question.

This study posed two principle questions: 1) at what rates do stumps, logs, and sub-surface coarse roots decompose, and 2) do decomposition rates differ between these three components. To address these questions, CWD from western hemlock (*Tsuga heterophylla* (Raf.) Sarg. (logs, stumps, roots)), Douglas fir (*Pseudotsuga menziesii*

(Mirb.) Franco (logs, stumps, roots)), western red cedar (*Thuja plicata* Donn ex D. Don (logs)), *Abies* sp. (likely *amabilis* Dougl. ex Forbes (Pacific silver fir)) (logs), and an unknown species (stumps) was sampled along a chronosequence of previously clearcut stands.

2.3 STUDY REGION

Data was collected from forest stands within the USFS Wind River Ranger District, approximately 20 km from the Columbia River Gorge in southwest Washington State. Since this study was part of an integrated project already in progress at the T.T. Munger Research Natural Area (RNA), stand selection was confined to an approximately 10 km x 10 km region centered on the RNA (45° 49' N, 121° 58' W). Regional elevation ranges between approximately 335 m to 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 annual precipitation recorded at the Wind River Ranger Station (1936-1972) is 250 cm yr^{-1} (Franklin and DeBell 1988), with less than 10% falling between June and September (Franklin and DeBell 1988). Mean annual RNA temperature is 8.7 °C (Wind River Canopy Crane data). Based on ring counts from stumps and trees inside or adjacent to the RNA, most old-growth forests in the Wind River region originated approximately 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 c.1490

(Franklin and Waring 1979). Dominant RNA vegetation is coniferous and transitional between *T. heterophylla* and *A. amabilis* (Pacific silver fir) zones (Franklin and Dyrness 1973). Study region tree species include *A. amabilis*, *Abies grandis* (Dougl. ex D. Don) Lindl. (grand fir), *Abies procera* Rehd. (noble fir), *T. plicata*, *Taxus brevifolia* Nutt. (Pacific yew), and *Pinus monticola* Dougl. ex D. Don (western white pine), with *P. menziesii* and *T. heterophylla* generally dominating. *Cornus nuttallii* Audubon (Pacific dogwood), *Acer macrophyllum* Pursh (big leaf maple), *Alnus rubra* Bong. (red alder), and other deciduous tree species exist as minor components in many stands. Shrub species include *Berberis nervosa* Pursh (Oregon grape), *Gaultheria shallon* (salal), *Acer circinatum* Pursh (vine maple), *Ceanothus sp.* (California lilac), *Vaccinium parvifolium* Smith (red huckleberry), and *Vaccinium membranaceum* Dougl. ex Hook (big huckleberry). Harvested stands regenerated by combinations of replanting and natural seeding.

2.4 METHODS

2.4.1 Stand Selection

Stands are defined here as forested USDA Forest Service harvest units. Initial lists of candidate stands were derived from district maps compiled from GIS layers (Gifford Pinchot Vegetation Database, Rev. 1.1) identifying stands regenerating from commercial clearcutting. Remaining selection criteria were then applied to these lists. Candidate stands were grouped into decadal age classes (1940-1949, 1950-1959, etc.) with stand age based on harvest date. Final stand selection criteria were:

- Elevation: Stands used lie within an elevation range of approximately 360 m and 730

m. The lower elevation limit is the valley floor. The upper elevation limit was selected to avoid the transition zone from *Pseudotsuga sp.*-dominated forest to *Abies sp.*-dominated forest.

- Size: Preference was given to stands at least 400 m per side (200 meter transect plus 100 m perimeter buffers) because estimation of CWD *k* values was a sub-objective of a larger project investigating net ecosystem productivity (NEP) (Janisch and Harmon, in review). Stand dimensions were estimated from scaled USFS orthophotos.
- Presence of cut logs: Changing definitions of marketable wood diameter and quality over time resulted in nearly complete log removal from some stands (Harmon et al 1996). These sites were avoided unless other sites with logs were not available.

After initial selection, additional stands were added to produce a final chronosequence with age gaps no larger than five years (years 1993-1945). Age limits (1993-1945) were determined by clearcutting history on the district and stands available within the elevation band. An additional cluster of stands, clearcut in 1928 following fire, were added to extend log and stump sampling. Estimates of decomposition rates were drawn from this sequence. Fifty stumps and 41 logs (total) were sampled from stands age 7, 16, 22, 26, 31, 34, 45, 50, and 71 years post-harvest. Coarse roots were sampled from 41 stumps from stands age 0, 3, 7, 16, 22, 40, and 50 years.

2.4.2 Stump and Log Selection

Logs were defined as downed dead tree boles with at least one cut end. A cut upper surface indicating commercial harvest of the tree bole distinguished stumps from snags. To reduce edge effects on decomposition rates and avoid perimeter slash, landings, and multiple age cohorts resulting from road building, sampling was restricted to stumps and logs 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 (age 400-600 years) forest that occurred on the district c. 1940 (Anonymous 1951). To avoid snags fallen by saw during harvest and left *in situ*, stumps and logs judged to have had heart rot at harvest, friable heartwood, woodpecker holes, or other indications of advanced decomposition (Harmon et al 1999) atypical of the sampling cohort were not used. Living stumps and stumps showing tissue growth over the cut stump surface were not used. Sampled logs and stumps were identified to species from bark, wood, and growth characteristics. Logs and stumps originating post-harvest through mortality and thinning were screened out by size and decomposition class and not sampled.

2.4.3 Stump Sampling

Since cut wood surfaces provide entry points for decomposition organisms (e.g. Meredith 1973, Harmon and Sexton 1996), the top 20-30 cm of each stump was removed by chainsaw and discarded to minimize sampling of this zone with elevated decomposition. Each stump was then assessed for sections best representative of overall decomposition and fragmentation. Three cuts, two vertical (pith to cambium (or bark layer)) and a single horizontal (through the disc of the stump), were made by chainsaw to remove a single, 30-40° (bark surface curvature) pie-shaped wedge of each stump. Wedge volumes were calculated from thickness, pith to outer bark radii, and bark or sapwood arc length. Shells of bark or branch stubs, often persistent until late decomposition phases, were used to estimate green (live) radius in cases where fragmentation had reduced sapwood volume (Harmon and Sexton 1996). After obtaining each total wedge weight, bark and wood tissues were separated and weighed. 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. Representative bark samples of approximately equal mass were also collected when available. All tissues were weighed, field wet, to the nearest 0.5 g on portable scales. Samples were packed in sealed plastic bags, transported back to the lab within 48 hours, and dried at 55 ºC in a forced air electric oven to constant mass.

2.4.4 Log Sampling

Selection of representative logs was as for stumps. Zones of advanced decomposition associated with cutting, 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 were collected from logs with diameters less than twice the working chain saw bar length (75 cm). Disc volumes were calculated as cylinders from thickness, diameter, and outer bark or wood circumference, adjusting for fragmented or missing sapwood as above. Logs > 1.5 m diameter were sampled by removing a wedge (see stump sampling above). Log tissue sub-sampling and sample processing was as for stumps.

2.4.5 Root Sampling

A second sub-set of stumps was selected to sample coarse root density. Selection was restricted to the same cohort population outlined above with 2 -5 stumps selected from each species at each stand. Living stumps were not sampled. Methods followed those of Chen et al (2001). Two dominant roots from each stump were excavated distally, stump butt to root tip, by hand shovel during summer 1999. After excavation, complete (wood + bark) 10-20 cm long sections of root were removed by saw. Total number of root samples per stump varied between 3 and 12. Root sections were then sorted into small (1-5 cm) and large (5-15 cm) classes based on average diameter. Average diameter and longitudinal length of each section was calculated as the mean of three measurements of each dimension. Root bark was sampled by visually estimating bark cover and collecting all bark from each section. Bark from highly decomposed roots was not always fully recovered during excavation but this was not expected to strongly influence decomposition rates (Chen et al 2001). Root measurements were repeated after samples were stripped of bark to determine wood dimensions. Samples were then returned to the lab and dried at 65° C to constant mass. The volume of each root section was calculated as a cylinder

$$\text{(Equation 2-1) } V = \pi * \frac{(D^2 * L)}{4},$$

where V equals volume, D equals average diameter, and L equals average longitudinal length. Bark volume was calculated as the difference between whole root (wood + bark) volume and root wood volume, with adjustment for large pockets of resin (Chen et al 2001).

2.4.6 Density

For all samples dry mass fraction was determined as dry sub-sample mass divided by wet sub-sample mass. For logs and stumps, total disc or wedge dry mass equaled the product of total wet (field) mass and dry mass fraction. To account for differences in tissue k values (Harmon and 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 weighted bulk density for each stump or log. A second weighting was applied when two samples were collected from logs to adjust for intra-log taper and density variation (Harmon and Sexton 1996). Bark, wood, and resin core densities of each individual root sample were calculated as the oven dry weight divided by its green volume. Reported densities reflect weighting each component of whole roots as a proportion of total volume. To adjust for fragmentation, estimated volumes of missing parts were added to existing volumes. Methods generally followed those described by Healy and Swift (1971), Yoneda (1975), Swift et al (1976), and Harmon et al (1999).

2.4.7 Data Analysis

Main and interaction effects of species, position, and stand age on density were evaluated in a multiple linear regression model, where species was an indicator variable, density was calculated raw density or its natural log transformation of each sample, stand age was years since clearcutting, and position was an indicator variable distinguishing stumps from logs. Due to small sample size, decomposition rates were calculated for each *Abies* sp. (n=2) and *T. plicata* (n=1) log as (Olson 1963):

$$\text{(Equation 2-2): } k = \frac{-\left[\ln\left[\,(D_0)/(D_t)\right]\,\right]}{t}.$$

Live sample mass was calculated for each tissue as the product of estimated tissue volume and harvest tissue density, assumed to be green and sound (free of decay). Assigned green wood densities of *T. plicata* and *Abies* sp. wood tissue and *Abies* sp. bark were 0.310 g/cm^3, 0.417 g/cm^3, and 0.50 g/cm3, respectively (e.g. USDA Handbook of

Wood 1972, Harmon 1992). *T. plicata* bark was not sampled. Equation 2-2 was also used to explore effects of fragmentation on *k* values using *P. menziesii* ($D_0 = 0.45$ Mg m^{-3}) and *T. heterophylla* ($D_0 = 0.42$ Mg m^{-3}) green wood densities.

Decomposition rate constants for the remaining 88 stump and log data points were derived from fitting a single-exponential statistical model (Olsen 1963, Means et al 1985, Foster and Lang 1982) of the form

$$\text{(Equation 2-3)}\ D_t = D_0\,(e^{-kt})$$

by species (NONLIN procedure, SAS v. 8 statistical software, SAS Institute 1999), where D_t equals density at time t, D_0 equals green wood density, and *k* equals an empirically-derived decomposition constant. Root *k* values were also determined by regression of Equation 2-3 on root density.

2.5 RESULTS

2.5.1 Stumps and logs

Both linear regression model fitting (-0.0109, SE: 0.0024, $p<0.001$ back transform) and automated model selection (stepwise: F=12.19, $p<0.001$, $C_{(p)}=5.567$, R-squared = 0.229) indicated stand age and species were the only significant main effects on stump and log density. There were no significant differences between log and stump density within species (*P. menziesii*: -0.101 Mg m^{-3}, SE: 0.100, p = 0.316; *T. heterophylla*: -0.035 Mg m^{-3}, SE: 0.140, p = 0.805) therefore stump and log data were combined by species. Only stumps were sampled from the unknown species.

Linear regression of log-transformed density against time (F=10.32, p=0.002, R^2= 0.232) indicated the intercept of *P. menziesii* (-0.939 (back transformed: 0.391 Mg m^{-3}), SE: 0.208, p=0.002) differed significantly from *T. heterophylla* and the unknown species. Intercepts of *T. heterophylla* (-1.283 (back transformed: 0.277 Mg m^{-3}), SE: 0.219 Mg m^{-3}) and the unknown species (-1.266 (back transformed: 0.281 Mg m^{-3}), SE: 0.107 were not significantly different (-0.0161, SE: 0.113, p=0.881) but because the unknown species may be a species mixture it was treated separately. Interaction between stand age and *T. heterophylla* was significant (-0.020, SE: 0.009, p = 0.031) but only at the expense of significance of individual variables. Regression of weighted individual *k* rates (stumps and log, *P. menziesii* and *T. heterophylla*) against log diameter at the sample point indicated a small but significant inverse effect of diameter (-0.0002 Mg m^{-3} m^{-1} yr^{-1}, SE: > 0.0001, p = 0.005).

Non-linear regression analysis predicted green wood densities of 0.348 Mg m^{-3} (SE: 0.034, n = 45, F=248.31, p<0.0001), 0.439 Mg m^{-3} (n = 25, F=132.63, p <0.0001) and 0.332 Mg m^{-3} (n=18, SE: 0.046, p<0.0001) for *P. menziesii*, *T. heterophylla*, and the unknown species, respectively (Figure 2-1). *P. menziesii* decomposed the slowest (*k* = 0.007 yr^{-1}, SE: 0.002) and *T. heterophylla* decomposed the fastest (*k* = 0.036 yr^{-1}, SE: 0.008,) (Table 2-1). The unknown species cluster was intermediate (*k* = 0.013 yr^{-1}, SE: 0.005, n = 18, F=112.82, p =<0.0001). A wood *k* value from the single *T. plicata* log was 0.013 yr^{-1}. Mean bark and wood *k* values for the first *Abies* sp. log were 0.004 yr^{-1} and 0.072 yr^{-1}, respectively. For the second, wood *k* was 0.069 yr^{-1}.

Given these data, 95% loss of *P. menziesii* C stores would require 426 years while a similar loss for *T. heterophylla* would occur in 83 years. When mean *P. menziesii* data was refit substituting green wood densities for Y_0 (Equation 2-3) since our intercept estimate was likely too low (see discussion), *k* increased to 0.013 yr^{-1} (SE: 0.001) or 230 years to 95% decomposition. The same procedure applied to *T. heterophylla* resulted in *k* declining to 0.033 yr^{-1} (SE: 0.004), equivalent to 95% decomposition in 90 years. To examine temporal variation in *k*, individual *k* values for each *P. menziesii* and *T. heterophylla* stump and log were calculated using current and green wood densities. Individual log *k* values ranged from 0.004-0.04 yr^{-1} (*P. menziesii*) and 0.002-0.05 yr^{-1} (*T. heterophylla*); stump *k* values ranged from 0.002- 0.03 yr^{-1} and 0.01- 0.09 yr^{-1}, respectively. In general, individual *k* values for both species start low, peak 22-26 years after harvest, then decline (Table 2-2). The general empirical trend in *k* values for above-ground stumps and logs was *Tsuga*>UNKN>*Pseudotsuga*.

2.5.2 Coarse Roots

Root *k* values varied significantly by size and species (Chen and Harmon 2001, Table 2-1). *P. menziesii* small diameter roots (1-3 cm) decomposed faster (Y_0=0.51 Mg m^{-3}, *k*=0.014 yr^{-1}, SE: 0.005) than large diameter roots (Y_0= 0.40 Mg m^{-3}, *k*=0.008 yr^{-1}, SE: 0.002). *T. heterophylla* roots followed the same pattern (1-3 cm: Y_0=0.36 Mg m^{-3}, *k*=0.023 yr^{-1}, SE: 0.004; 3-8 cm: Y_0=0.33 Mg m^{-3}, *k*=0.017 yr^{-1}, SE: 0.003). *P. menziesii* 1-3 cm and 3-5 cm roots thus decomposed 1.08 times and 0.62 times as fast as surface wood of the same species. The pattern for *T. heterophylla* was 0.64 times and 0.47 times as fast. Thus, root *k* values were more similar between species (*T. heterophylla*: *P. menziesii* ratios 0.61 (1-3 cm), 0.47 (3-5 cm)) than above-ground *k* values (ratio 5.14).

Table 2-1: Coefficients of single-exponential regressions used to estimate decomposition rate constants for above-ground stumps and logs and below-ground roots along a chronosequence of clearcut stands at Wind River, Washington. Standard errors are in parentheses.

C store	Species	Diameter (cm)	Regression Coefficients[a]			
			Y_0	*k*	R^2	N
Stumps and Logs[b]						
	P. menziesii		0.348 (0.034)	0.007 (0.002) 0.017[d]		45
	T. heterophylla		0.439 (0.048)	0.036 (0.008)		25
	unknown		0.332 (0.046)	0.013 (0.005)		18
Roots[c]						
	P. menziesii	1-3	0.51	0.014 (0.005)	0.56	19
		3-8	0.40	0.008 (0.002)	0.77	21
	T. heterophylla	1-3	0.36	0.023 (0.004)	0.73	9
		3-8	0.33	0.017 (0.003)	0.31	21

[a] Regressions were of the form $Y_t=Y_0e^{-kt}$ where Y_t was density t years after clearcutting, Y_0 was initial density, and *k* is the decomposition rate constant.

[b] each data point represents the weighted mean of bark and wood samples from an individual stump or log

[c] each data point represents the mean of 4-12 samples

[d] from mean of individual stump and log *k*

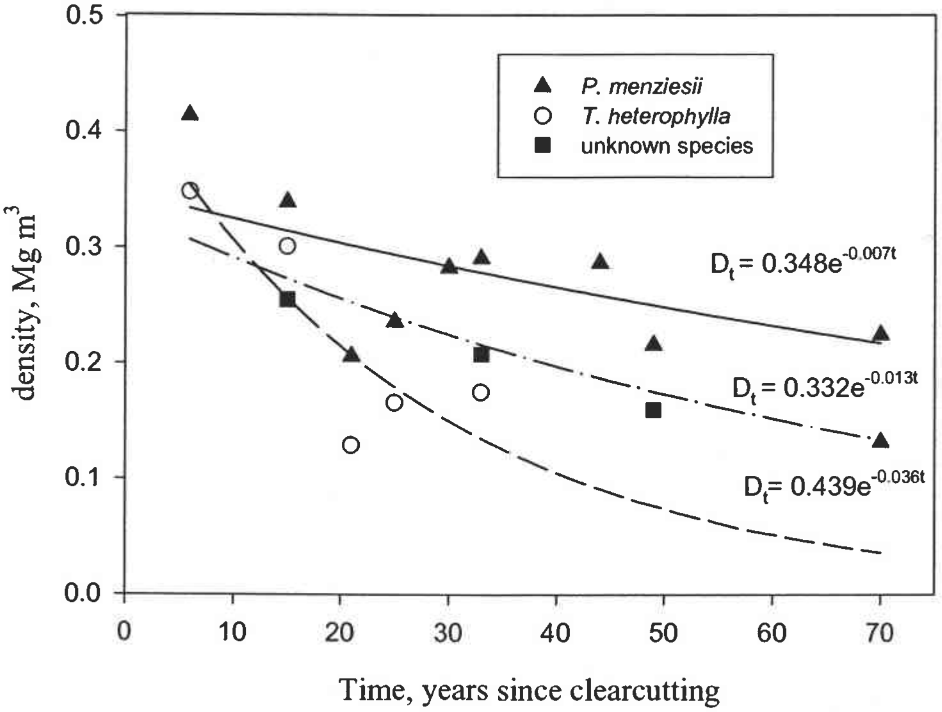

Figure 2-1: Decomposition trajectories based on non-linear regression parameter estimates shown against species mean and wood density in each stand. Data from above-ground stumps and logs along a chronosequence of conifer stands regenerating after clearcutting and fire at Wind River, Washington.

Table 2-2: Range of individual stump and log decomposition rates[a] based on bulk densities *t* years after clearcutting and green wood densities of 0.45 Mg m^{-3} (*P. menziesii*) and 0.42 Mg m^{-3} (*T. heterophylla*) at Wind River, WA.

	Range of Decomposition Rate (*k*)		
stand age (years)	*P. menziesii*	*T. heterophylla*	N
7	0.011-0.017	0.003-0.160	2, 9
16	0.011-0.031	0.002-0.056	5, 5
22	0.033-0.041	0.056-0.062	4, 2
26	0.026	0.026-0.058	1, 7
31	0.009-0.033	0.025-0.032	7, 2
34	0.013	----	1
45	0.004-0.021	----	10
50	0.005-0.025	----	6
71	0.004-0.020	----	9

[a] calculated as $-k=\{\ln(Y_t)/\ln(Y_0))/t\}$ where Y_t was density t years after clearcutting, Y_0 was initial density, and *k* is the decomposition rate constant.

2.6 DISCUSSION

2.6.1 Model and Intercepts

Linear, exponential, and logarithmic functions have all been applied to time series and chronosequence decomposition data sets (e.g. Means et al 1985, Sinsabaugh et al 1992) and at times have fit equally well within the same regional forest type (Lambert et al 1980, Graham and Cromack 1982). Equality of fit among different models, however, rather than being contradictory, may instead result from the multi-stage, long-term nature of woody decomposition (Fahey et al 1991, Harmon et al 1996). If, for example, a short-duration study examined a rapid and relatively constant phase of mass loss, linear models with high *k* rates might be inferred (e.g. O'Connell 1987), but these would inflate C flux when extrapolated over time. Conversely, simple exponential models, where *k* is constant, may adequately describe total change in C stores but mask temporal variation in *k* (e.g. initial lags, intermediate rapid mass loss, long recalcitrant phase). Underlying temporal variation in *k*, as suggested by an apparent spike in *k* 10-30 years after clearcutting (Figure 2-2), may be better addressed by vector-decomposition analysis (Harmon et al 2000).

Both linear and non-linear regression has been used to describe decomposition over time. In our case, linear regression intercepts were 13% below published green wood densities for *P. menziesii* (0.390 Mg m^{-3} vs.0.45 Mg m^{-3}), 34% below those for *T. heterophylla* (0.277 Mg m^{-3} vs. 0.42 Mg m^{-3}), and well below the generally accepted 10% coefficient of variation in green wood density (USDA Handbook of Wood 1972). The *T. heterophylla* intercept (0.439 Mg m^{-3}) derived from non-linear regression (Equation 2-3) agreed with literature values, but the *P. menziesii* intercept (0.348 Mg m^{-3}) fell well below two standard deviations away from the accepted green-wood density, suggesting our estimate is too low for this species. A second line of evidence against the intercept is a virtual lack of data for this species 1-10 years after harvest so that CWD pieces that had more time to decompose, and thus had lower density, were more influential in the regression. A third line of evidence is that mean *k* calculated for individual stumps and logs is higher by a factor of two (-0.017 $\mathrm{yr^{-1}}$). Thus in all subsequent calculations this higher value is used. Given the 23% differences between accepted and predicted green wood densities, use of the initial model could result in underestimates of C efflux from CWD. For example, given 100 $\mathrm{m^3\ ha^{-1}}$ of green starting material, using a density of 0.348 $\mathrm{Mg\ m^{-3}}$ instead of 0.45 $\mathrm{Mg\ m^{-3}}$ would underestimate initial C stores by 5.1 $\mathrm{Mg\ ha^{-1}}$ and C flux by 2.9 $\mathrm{Mg\ ha^{-1}}$ 50 years after disturbance.

2.6.2 Decomposition Rates

Several thorough reviews of log decomposition exist (Harmon et al 1986, Mackensen and Bauhus 1999, Chambers et al 2000). Relative to these, Wind River *P. menziesii* decomposed slower than Eastern temperate hardwood (Toole 1965, Harmon 1982 ($k = 0.08\text{-}0.18\ \mathrm{yr^{-1}}$), MacMillan 1988 ($k = 0.0189\text{-}0.0452$)), tropical species (e.g. $k = 0.461\ \mathrm{yr^{-1}}$, Lang and Knight 1979; $k = 0.03\text{-}0.172\ \mathrm{yr^{-1}}$, Harmon et al 1995), and eastern conifer species (Harmon 1982 ($k = 0.04\ \mathrm{yr^{-1}}$), Foster and Lang 1982 ($k = 0.01\text{-}0.03\ \mathrm{yr^{-1}}$), Alban and Pastor 1993 (0.04-0.05 $\mathrm{yr^{-1}}$)). Our *P. menziesii* *k* value was higher than that reported by Sollins et al (0.010 $\mathrm{yr^{-1}}$, 1987) for several species and stand ages in Pacific Northwest forests. Our estimate of 0.007 $\mathrm{yr^{-1}}$ was similar to that reported by Means et al (0.0063-0.007 $\mathrm{yr^{-1}}$, 1985) but these data neglect fragmentation and likely thus underestimate *k*. Other work reported *k* values intermediate to species' rates found here

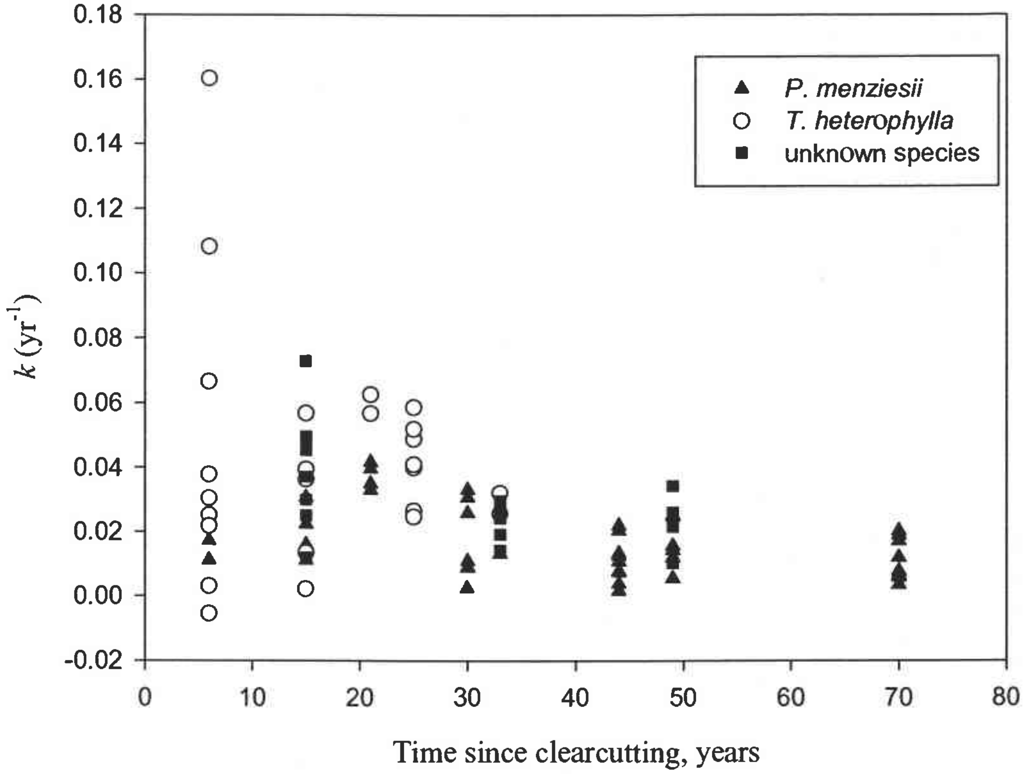

Fig 2-2: Decomposition constant (*k*) estimated for each stump and log sampled at Wind River, Washington. Estimated *k* calculated from Eq. 2, green wood densities for each species (USDA Wood Handbook), and empirical density estimates. Density of *P. menziesii* (0.45 Mg m^3) was used for the unknown species.

(0.028 yr^{-1} (Sollins 1982 (indirect methods)); 0.029 yr^{-1} (Spies et al 1988 (chrono-sequence-mass loss))). The derived *k* rate for *T. heterophylla* logs and stumps appears above average relative to other chronosequence-based estimates for this species (0.01-0.03 yr^{-1} (~8-15 years), Erickson et al 1985; 0.016 yr^{-1}, Sollins et al 1987; 0.008-0.023 yr^{-1} (35 years), Graham and Cromack 1982; 0.012 yr^{-1} (38 years), Grier 1978) and *Tsuga canadensis* L. ($k = 0.021 yr^{-1}$, Tyrell and Crow 1994). Published estimates of *Abies* species ranged from 0.029 yr^{-1}(*A. balsamea*, Lambert et al 1980) to 0.049 yr^{-1}(*A. concolor*, Harmon et al 1987), the same order of magnitude as Wind River *Abies* sp. Refitting the data using a *P. menziesii* green wood density of 0.45 Mg m^{-3} doubled the *k* rate but changed little relative to the above studies.

Our key finding indicated no significant difference between log and stump *k*-rates within the two principle conifer species studied. This suggests that C fluxes from stumps based on substitution of log *k* values for stump *k* values in forest C flux models may be reasonable. Since C flux models including stumps must already assume this equivalence, increased confidence in existing predictions would be gained and uncertainty related to missing C sinks could thus be reduced. Given the current lack of simultaneous stump and log decomposition studies, and general lack of stump data, however, generality of this result is unknown. Until needed studies are performed, use might be made of log *k* values, which are much more complete, as well as relative consistency of *k* reported within genera (Harmon et al 1999) in evaluating this result. Stump *k* values reported for the Asian softwoods *Larix olgensis* Henry and *Pinus koraiensis* Siebold et Zucc ($k =$ 0.01-0.05 yr^{-1}, Heal et al 1983), for example, are consistent with *k* for logs of *Pinus* sp. (k = 0.01-0.04 yr^{-1}, Mackensen and Bauhus 1999). Even this tactic is severely limited, however, because study of CWD decomposition has generally overlooked stumps. Exceptions include Odum (1970), who reported mean percent annual mass loss for stumps of the Puerto Rican species *Dacryodes excelsa* Vahl (10.5%), *Manilkara bidentata* (A. DC.) Chev. (8.3%), *Didymopanax morototoni* (Abul.) Decne. and Planch. (9.1%), *Drypetes glauca* Vahl (6.0%), and *Duggena hirsuta* (Jacq.) Britt. ex Britt. and Wilson (24.5%) over 1-3 years, as well as a mean log decomposition rate of 0.074 g C m^{-2} day^{-1} (species not reported). Other reported *k* values for stumps include *Pinus sylvestris* L. (~ $k = 0.06$ yr^{-1}, Sierota 1997) and *Picea* sp. (~ $k = 0.08$ yr^{-1}, Käärik and Rennerfelt 1957). Also, if distance from soil imposes a moisture gradient on decomposition, upper sections of tall stump may behave like snags.

A second key finding was that stump/log and coarse root decomposition rates differ enough to call substitutions of log *k* for root *k* into question even within the same species. Our results indicate stump biomass should be separated from root biomass and treated as on separate decomposition trajectories. Since coarse roots mass is approximately 4x stump mass in a clearcut, the consequences of biasing root decomposition rates, and thus C efflux, are not trivial. Stump height should be considered as a final refinement of C flux from harvested stands since stump height continues to decline (Harmon et al 1996). Since stumps grade into coarse roots, root *k* may be appropriate for stumps cut nearly flush with the soil surface.

P. menziesii coarse roots decomposed slower than many other species reported (Berg 1984, Camiré et al 1991, k=0.04-0.09 yr^{-1}, Fahey et al 1988, Fahey and Arthur 1994, k =0.02-0.06 yr^{-1},Yavitt and Fahey 1982 (k=0.042 yr^{-1}, Chen et al 2001), echoing patterns between species in above-ground CWD. Differences in decomposition resistance within the same region has been attributed in part to wood chemistry (Scheffer and Cowling 1966) but variation exists between species, as well as between and within trees of the same species (Rudman and Da Costa 1958, Englerth and Scheffer 1954). As with scale-related model effects on *k* discussed above, this variation may explain reports of small roots decomposing faster than large roots (Yavitt and Fahey 1982). Relative to surface CWD in this study, 1-3 cm *P. menziesii* coarse roots decomposed more slowly, consistent with sub-surface conditions favoring rapid fungal colonization and growth (e.g. Griffin 1977, Käärik 1974). Coarse roots, in contrast, decomposed more slowly. However, when revised upward to the mean value of $k = 0.017$ yr^{-1} (discussed above), logs and stumps decomposed slightly faster than 1-3 cm roots (0.014 yr$^{-1)}$. Relative to 3-8 cm roots, decomposition doubled. This is the pattern also observed in *T. heterophylla*. There may be several explanations for these observed patterns. For example, high rainfall much of the year in these forests may lead to soil saturation, where soil moisture exceeds percentages favoring growth of soil decomposer organisms. Thus, optimal conditions for wood decomposition might fluctuate seasonally between sub-surface and surface contact. That logs and stumps 50+ cm in diameter decomposed faster than wood of diameter 16x smaller also appear contrary to expected results from diameter-*k* rate relationship. Since these relationships appear to hold across sub-surface diameter classes, this is another line of evidence pointing towards other limits on decomposition.

2.6.3 Clearcuts vs. Closed-Canopy Forest

Despite widespread clearcutting of boreal, temperate, and tropical forests, and the high CWD loads it generates, few studies address CWD decomposition in clearcuts vs. intact forests. Further, *k* values from fine woody debris (FWD) in clearcuts, also limited

(Abbott an Crossley 1982, Barber and Van Lear 1984, Erickson et al 1985, Edmonds et al 1986, Mattson et al 1987), cannot yet be generalized since diameter-*k* value relationships remain unresolved. Thus, until behavior of CWD in clearcuts is clarified, the overall C source-sink magnitude or length of the C-source phase of clearcuts stands remains open to question. If forests are managed to increase C stores, then addressing this issue is key since levels of C efflux from stands will influence decisions about forest age-class structure at landscape scales.

Compared to a well-studied old-growth forest (T.T. Munger Research Natural Area (RNA)) within 10 km of our study sites, our *k* value for *P. menziesii* logs ($-0.017\ yr^{-1}$) from clearcuts is similar to rates of old-growth log ($k = -0.014\ yr^{-1}$) and snag ($k = -0.021\ yr^{-1}$) decomposition of the same species inside the RNA, which is still forested (Harmon et al, in preparation). Since RNA *k* values were derived from a time series, which is generally more precise than a chronosequence, these data indicate decomposition of CWD in both clearcuts and old-growth forests may proceed at similar rates. Other work from Olympic National Park, WA, indicated respiration from CWD in clearcuts was strongly seasonal but annual means did not significantly differ from adjacent old-growth forest (Marra and Edmonds 1996). Comparison of our *k* values from CWD in clearcuts by species to other regional studies of decomposition under intact canopies (e.g. Spies et al 1988 ($k = -0.029\ yr^{-1}$), Sollins 1982 ($k = -0.028\ yr^{-1}$)) is somewhat impaired as these studies covered a species mixture. However, our mean *k* for *P. menziesii* and *T. heterophylla* was $-0.026\ yr^{-1}$, very similar to the above mean values. It is also possible that *k* estimates from the T.T. Munger RNA may change if this time series is still young since CWD decomposition is long and non-linear. Thus, while evidence appears to point toward CWD in clearcuts and under intact forests decomposing at similar average annual rates, the question may not yet be fully answered. Wood originating from clearcutting also becomes a hybrid of open- and closed-canopy environments as the stand ages so any comparisons with old-growth *k* should be carefully defined due to the long-term nature of CWD decomposition

However, if old-growth forests store more C than the shorter rotation forests replacing them, differences in CWD *k* between old-growth and clearcuts are somewhat irrelevant. This is because if, for example, decomposition of wood at rates A and rate B eventually produce pools of recalcitrant material of similar mass, then absolute changes in C stores may be more relevant to forest C management than flux rates. The ultimate fate of CWD is important because flux-based methods of C gain and loss can lead to opposite conclusions depending on scale of analysis (Janisch and Harmon, submitted).

2.6.4 Diameter-*k* rate Relationships

While mean *k* values for all components examined were of similar magnitude, above vs. below-ground *k* values differ and these differences appear correlated in part with diameter. Inverse diameter-*k* value correlations have been widely reported for logs and branches (Harris et al 1972, Fogel and Cromack 1977, Foster and Lang 1982, Brown et al. 1996, Stone et al 1998, O'Connell 1997, Chambers et al 2000), but exceptions exist (e.g. Graham 1982, Harmon, 1982, Erickson et al 1985, MacMillan 1988, Marra and Edmonds 1996). More recently Mackesen and Bauhus (1999) reported log diameter explained approximately 60% of the variation in data compiled from nine *P. menziesii* and *T. heterophylla* log decomposition studies. Yet when viewed independently, some of these studies conflicted on whether *k*-diameter relationships existed, suggesting inferences about CWD decomposition may be sensitive to sample size or study length. This may explain why suggestive positive density-diameter correlations found here for age classes 6, 21, 33, 44, 49, and 70 years were reversed in age classes 15, 25, and 30 years. Independent work indicating inverse diameter-*k* rate trends across different types of woody detritus, such as branches (Edmonds et al 1986), small-diameter hardwoods (Mattson et al 1987, Harmon et al 1995), and tree roots (Chen et al 2000) also imply diameter effects are real. Further, branches and boles form a diameter continuum, with branches appearing to decompose faster relative to boles within a species. Thus, unless branch wood and bole wood differ in chemistry and density, inverse *k*-diameter patterns might be expected for logs. If true, this would finally bring harmony between woody detritus decomposition and predictions based on declining surface-volume ratios (Abbott and Crossley 1982, Harmon et al 1986) or increasing proportions of recalcitrant tissues (Hillis 1977, Harmon et al 1995). If *k*-diameter relationships are real, use of diameter based- rather than branch / log-based classes in the literature could reduce confusion since, for example, branches on older trees may exceed bole diameter of younger trees.

2.6.5 Fragmentation

Inclusion of fragmented or oxidized wood tissues departs from standard methods for estimating *k*, which frequently either neglect fragmentation and complete oxidation (Healey and Swift 1971; Christensen 1984), or solely couple density changes with CWD respiration (Mackensen and Bauhus 1999). When quantified, however, fragmentation contributes significantly to mass loss (Lambert et al 1980, Graham 1982). In our case, fragmentation was negligible since the oldest stumps and logs sampled appeared just to be entering the sapwood sloughing stage. When CWD has fragmented, however, and the fragments have oxidized, neglecting this process could translate into significant overestimation of density and underestimation of *k*. If, for example, all sapwood from stumps and logs in the 6-year old stand had been oxidized and these losses were ignored, (assuming sapwood/heartwood ratio of 0.1324 for tree diameters >0.3 m (FSL data base)), C fluxes would be underestimated by 7.24 Mg C ha^{-1} (mean), potentially enough to reverse conclusions about stands acting as C sinks. Since the sapwood's fate lies between extremes of fully fragmented but still present and fully oxidized to CO_2, calculating potential losses based on sapwood-heartwood ratios could improve estimations of limits on detrital C fluxes following stand harvesting.

2.6.6 Scale

Three lines of evidence indicate scale influences conclusions drawn about decomposition of CWD. First, vector analysis (Harmon et al 2000) indicates CWD *k* varies with stage of decomposition. Sampling which does not span the full life of CWD can thus be biased high or low. Second, combining data from several studies appeared to clarify diameter-*k* relationships (Mackesen and Bauhus 1999) obscure at the level of individual studies. If diameter influences on *k* are small, broad data sets may be needed to reveal them. Third, flux-based measurements indicate rates of C flux from CWD in clearcuts are influenced by duration and seasonality. Thus, consideration of seasonal C fluxes from CWD by flux-based measurements, if short term, may improve comparison to mass-based methods, providing independent estimates of C fluxes.

2.6.7 Implications for C Sources and Sinks

To fulfill larger objectives, CWD mass (logs, stumps, snags) weighted by decomposition class was estimated in stands sampled in this study (Janisch and Harmon, in review). Given our mean *k* values applied to the mass of these stores (Table 2-3), these stands are currently losing C at a rate of 0.4 – 1.1 Mg C ha^{-1} yr^{-1} (assuming all CWD is *P. menziesii*) to 0.4 – 1.4 Mg C ha^{-1} yr^{-1} (assuming all CWD is *T. heterophylla*) from stumps, logs, and snags (losses adjusted for regenerating stand age). When coarse roots are assumed equal to 20% of bole mass, these fluxes increase to 0.8 - 2.2 Mg C ha^{-1} yr^{-1} and 0.6 - 3.6 Mg C ha^{-1} yr^{-1}. Coarse root mass has been estimated at > 200 Mg ha^{-1} in old-growth conifer forests of the Pacific Northwest (Ehrenfeld et al 1997, Nadelhoffer and Raich 1992, Vogt et al 1986, 1991) but this value seems high given mean regional old-growth bole C stores of 296 Mg C ha^{-1} (Smithwick et al (in review)). Even these ~2-fold differences, however, underscore the importance of knowing both species-specific *k* values and partitioning CWD between above- and below-ground stores when modeling decomposition. None the less, C flux calculations based on the fastest and slowest species *k* of the region harvested improve understanding of C stores that may be lost following disturbance by describing the rapidity and magnitude of C pulses from the stand due to decomposition. These calculations are important because, while many net primary productivity (NPP) estimates for forest trees exist (e.g. Kajimoto et al 1999, Sundarapandian et al 1999, Hansen et al 2000), it is difficult to assess how stands function as C sources or sinks without estimates of detrital CO_2 efflux. By revealing what range of NPP fluxes are needed just to counter efflux from CWD, estimates of fluxes from such CWD pools provide context for interpreting NPP. Since *P. menziesii* dominated many of these stands prior to harvest, true fluxes are likely closer to the lower range.

Also relevant is how changing climate will affect *k* values. These effects may be weighted toward recently generated CWD since material lingering into advanced stages of decomposition is principally recalcitrant with a very low *k* (Harmon et al 1999). Unless climate change is expected to mobilize these recalcitrant stores, energy might be focused in stands recently disturbed. Ideal sites for these sorts of studies now exist in the form of stands that have been cut twice (so called third-growth) since CWD from the first rotation may still persist. CWD from both disturbances could thus be simultaneously examined.

Table 2-3: Estimated annual C flux from stumps, logs, and snags in a chronosequence stands previously clearcut. From coniferous stands dominated prior to harvest by *P. menziesii* and *T. heterophylla* at Wind River, Washington.

stand age, years since clearcutting	total CWD stores [a], Mg C ha^{-1}	losses per year[b], k=0.017[c], Mg C ha^{-1} yr^{-1}	losses per year[b], k=0.036[d], Mg C ha^{-1} yr^{-1}
6	113.76	0.90	2.01
11	100.19	0.79	1.77
14	125.58	0.99	2.22
16	82.01	0.65	1.45
17	61.76	0.49	1.09
22	125.35	0.99	2.21
23	52.99	0.42	0.94
26	45.18	0.36	0.79
30	64.66	0.51	1.14
31	102.36	0.81	1.81
34	49.85	0.40	0.88
35	90.51	0.72	1.60
36	132.40	1.05	2.34
39	67.23	0.53	1.19
41	96.79	0.77	1.71
44	61.59	0.49	1.09
45	84.91	0.67	1.50
49	43.46	0.69	0.77

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

[b] assuming wood is 50% carbon

[c] all CWD treated as *P. menziesii*

[d] all CWD treated as *T. heterophylla*

2.7 IMPROVING DECOMPOSITION ESTIMATES

Species, substrate, aspect, microclimate, and other factors affect CWD *k* values (Abbott and Crossley 1982, Harmon and Sexton 1996). While plot-level slope, aspect, diameter, and elevation data were collected to meet larger project objectives (Janisch and Harmon, in review), sampling was insufficiently systematic to test effects of these variables. However, other factors such as disturbance that, for example, cause stands of similar aspect to drift apart, may change decomposition environments. This in part may explain why understanding decomposition patterns has at times proved elusive.

Since this work was observational, between-stand variation was also not explored, though as much variation may exist within as between logs at individual sites(e.g. Harmon and Sexton 1996). Contributions to the variance term of these factors is thus unknown but may be significant features of low reported R^2 values. Despite this, however, we report values consistent with other regional studies incorporating some of this variation. This may indicate decomposition, while influenced by many factors, still proceeds within certain limits within a species—e.g. even under ideal conditions a *k* of 0.05 yr^{-1} for *P. menziesi*i might be unreasonable.

Scatter plots of stumps not identifiable to species fell between and overlapped both *P. menziesii* and *T. heterophylla* clusters, possibly representing a mixture of these species, a third thin-barked species such as *A. amabilis*, or more complex combinations. If this cluster is in reality a mixture of *P. menziesii* and *T. heterophylla*, reassignment to appropriate species would likely reduce mean *T. heterophylla k* and increase mean *P. menziesii k*.

Since our estimated *T. heterophylla* green wood density falls near the accepted value and using our derived *k* rate, Equation 2-2 may adequately capture decomposition parameters when samples from all decomposition classes are used. Thus, adding class 1 *P. menziesii* samples, lacking in this study, might improve data fit for this species.

Finally, key to determining chronosequence-based *k* values is accurate aging of sampled CWD. Grafted *P. radiata* roots, for example, have survived years after removal of tree boles (Yavitt and Fahey 1982), and root chronosequences have been criticized for this reason. It is thus possible that the independent variable, time, is not precisely known, because stand age is incorrect or the assumptions that trees were living when felled and died when cut were not met. However, harvest dates given by USDA Forest Service stand history records were cross-checked by increment cores so if this error exists it is likely <4 years. As decomposition proceeds, judging whether stumps and logs were cut live or were felled snags does becomes more difficult, however. This is because later stages of decomposition are protracted. Thus, during these long phases all CWD regardless of origin tends to converge in character. Seven logs from the oldest two stands were suspected of being snags when cut. If these trees had been dead for many years, lower densities relative to other samples from the same age class might be expected and thus treating them as originating during stand harvest could inflate our *k* estimates. Few calculated individual *k* values appeared extreme, however, so the leverage of this group appears weak.

2.7 MANAGEMENT IMPLICATIONS AND CONCLUSIONS

Log and stump *k* values were similar within species, suggesting these values might be interchanged. If modeling C efflux from CWD is an objective, this result has utility since log *k* values and C stores are far more completely known than corresponding stump *k* and stores. Knowing that logs and coarse roots *k* values differ is valuable for similar reasons relating to bias in estimates of C fluxes from CWD. While *k* values of stumps and logs appear similar, however, further study outside the coastal conifer zone of western North America is needed before results can be generalized. As of 1999, over 60% of CWD decomposition studies had been conducted in the Pacific Northwest (U.S.A) and British Columbia (Canada). Of these, approximately one third focused on *P. menziesii* (Mackensen and Bauhus 1999). It is also clear that since *k* varies by species, species composition on a landscape will affect C storage.

When considered against the substantial C mass in forest CWD (Harmon et al 1990) and estimated 80 % (454 Pg) of terrestrial C stored as forest biomass (Dixon et al 1994), lack of stump, coarse root, and in some cases log, *k* and C store data point toward sources of uncertainty in C flux models. Since we sampled only CWD originating from old-growth trees, more focus on *k*-diameter relationships would be useful since old-growth log *k* values may be inappropriate for the relatively smaller CWD from harvested second-growth forest. In addition, the magnitude of *k* values found here remind us that CWD left *in situ* can persist through several short (e.g. 50-80 year) rotations. Carbon flux estimates for multiple-rotation forests should thus reflect these multiple CWD cohorts.

Research on species-specific *in situ* decomposition rates should continue. This is because C flux from forest detritus is rate sensitive and small variations in *k* values may determine whether forest stands are classified as C sources or sinks, particularly if forest C influx and efflux are nearly balanced. Thus improved accuracy and precision in forest productivity data calls for similar improvement in CWD data if we are to judge the C source-sink status of forests.

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CHAPTER 3

NET PRIMARY PRODUCTIVITY OF TREE BOLES IN A PACIFIC NORTHWEST CONIFER FOREST ECOSYSTEM: A CHRONOSEQUENCE APPROACH

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3.1 ABSTRACT

Net primary productivity of tree boles (NPP_b) was assessed by reconstructing 5-year increments from cores collected along a 500-year chronosequence of stands on the Wind River Ranger District, Washington, U.S.A. Principle species sampled were *Tsuga heterophylla* (Raf.) Sarg. and *Pseudotsuga menziesii* (Mirb.), the dominants in this forest in terms of biomass. Using cluster analysis and Monte Carlo methods, biomass five-years previously of these stands was estimated and compared to current biomass based on current diameter breast height (DBH).

NPP_b of regenerating stands (i.e. second-growth) ranged between 0.15-5.28 Mg C ha^{-1} yr^{-1}. Early in succession (0-10 years) NPP_b was low but rose rapidly, peaking 25-30 years after clearcutting. Between 30-45 years after stand initiation, NPP_b appeared to level off or decline slightly. NPP_b of 500-year old stands ranged between 1.3-3.9 Mg C ha^{-1} yr^{-1}. Mean NPP_b of the nine old-growth stands (2.7 Mg C ha^{-1} yr^{-1}) was lower than mean NPP_b of 30-50 year-old stands (4.1 Mg C ha^{-1} yr^{-1}) but similar to that in 15-25 year old (2.3 Mg C ha^{-1} yr^{-1}) and 65-150 year-old stands (3.0 Mg C ha^{-1} yr^{-1}).

Based on 5-year increments for the previous fifteen years, the majority of old-growth stands sampled showed small increases in radial growth rate over time. While NPP_b was lower in mature and old-growth stands relative to younger regenerating stands in the forest studied, the higher biomass of these stands indicates that landscape C stores in live wood may still to be maximized in older age classes.

Key Words: Biomass, Douglas fir, increment, net primary productivity, NPP, old growth, Wind River

3.2 INTRODUCTION

Since forests sequester carbon (C) photosynthetically and may persist for centuries, manipulating these ecosystems to help mitigate increasing atmospheric CO_2, a greenhouse gas (GHG) implicated in global warming (IPCC 1996), has been proposed (Henderson and Dixon 1993, Iverson et al 1993, Marland 2000). Net ecosystem productivity (NPP), along with allocation from production and heterotrophic respiration, is an important part of understanding how forests sequester C since net C storage results from a balance between these simultaneous C losses and gains. In addition, NPP is a useful index relating productivity between ecosystems, ranging from 0.05 Mg C ha^{-1} yr^{-1} (deserts and tundra) to 20 Mg C ha^{-1} yr^{-1} (mangrove swamps and intertidal zones, Larcher 1975). This variation stems from biological, chemical, and physical differences, such as species composition, climate, and soil, (e.g. Bollinger et al 1991, Raich et al 1997, Gough et al 2000) as well as temporal variation, such as ecosystem maturity (e.g. Turner and Long 1975). Thus, coupling an understanding of why NPP varies within systems with an understanding of where C stores are allocated can help predict when and where ecosystems such as forests will release or absorb atmospheric C.

Available data indicate NPP varies with stand age, peaking early in succession, then declining (Turner and Long 1975, Ryan et al 1997, Acker et al 2000, Acker et al, accepted), but these patterns are still not well know as time-series studies of NPP extending beyond a few decades are rare. Whether this decline stems from reduced leaf area, changes in enzymatic activity, changes in hydraulic conductance, or other mechanisms is still unknown (Ryan et al 1997), but the answer is also relevant to the discussion of C sequestration and future forest management. This is because radial increment generally decreases with tree age while tree diameter increases with age, tying NPP both to radial increment and tree volume over time. Thus, NPP of large-diameter, late-successional trees with narrow growth increments, for example, could rival that of small-diameter, early-successional trees with much wider growth increments due to differences in tree volume. Thus, consideration of which age class structure on the landscape would store more C might be better illuminated.

Time series-based methods of determining NPP are generally more accurate than chronosequences (e.g. Grier 1978, Harmon and Sexton 1996) since growth, ingrowth, and mortality of individual trees can be tracked over the study interval (Clark et al 2001). Existing forest time series, however, have rarely followed stand development for more than several decades. Thus, whether NPP of forest stands continues to decline, levels off, or increases in later successional stages is still an open question (Ryan et al 1997). Given this scientific interest, as well as growing policy interest in use of forests to sequester increasing atmospheric CO_2 (IPCC 2001), a need exists for both more long-term data and methods that reveal long-term patterns in stand NPP within a few years rather than decades or centuries. A possible short-term method would be to examine the growth records inside trees using increment cores. In addition to successional change, this could also reveal responses of forests to increasing atmospheric CO_2 and climatic variation.

In this study, NPP of tree boles, which we call NPP_b, was examined using 36 stands along a chronosequence ranging from 7 years (post-clearcutting) to approximately 500 years (post-stand-destroying fire or other disturbance) in age. Growth of trees was measured from tree cores and used to estimate NPP_b over the past five years. We had three principle objectives: a) examine how rates of NPP_b change with stand age across the chronosequence, b) determine how radial increment width has changed within individual stands over time, and c) compare age-related rise and decline of NPP_b documented by time-series based methods to those from the chronosequence we examined.

3.3 STUDY REGION

Data were collected from forest stands within the USFS Wind River Ranger District, approximately 20 km from the Columbia River Gorge in southwest Washington State. Since this study was part of an integrated project already in progress at the T.T. Munger Research Natural Area (RNA), stand selection was confined to an approximately 10 km x 10 km region centered on the RNA (45° 49' N, 121° 58' W). Regional elevation ranges between approximately 335 m to 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 annual precipitation recorded at the Wind River Ranger Station (1936-1972) is 250 cm yr^{-1} (Franklin and DeBell 1988), with less than 10% falling between June and September (Franklin and DeBell 1988). Mean annual RNA 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 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 c.1490 (Franklin and Waring 1979). Dominant RNA vegetation is coniferous and transitional between *T. heterophylla* and *A. amabilis* (Pacific silver fir) zones (Franklin and Dyrness 1973). Study region tree species include *A. amabilis*, *Abies grandis* (Dougl. ex D. Don) Lindl. (grand fir), *Abies procera* Rehd. (noble fir), *T. plicata*, *Taxus brevifolia* Nutt. (Pacific yew), and *Pinus monticola* Dougl. ex D. Don (western white pine), with *P. menziesii* and *T. heterophylla* generally dominating. *Cornus nuttallii* Audubon (Pacific dogwood), *Acer macrophyllum* Pursh (big leaf maple), *Alnus rubra* Bong. (red alder), and other deciduous tree species exist as minor components in many stands. Shrub species include *Berberis nervosa* Pursh (Oregon grape), *Gaultheria shallon* (salal), *Acer circinatum* Pursh (vine maple), *Ceanothus sp.* (California lilac), *Vaccinium parvifolium* Smith (red huckleberry), and *Vaccinium membranaceum* Dougl. ex Hook (big huckleberry). Harvested stands regenerated by combinations of replanting and natural seeding.

3.4 METHODS

3.4.1 Stand Selection

Stands are defined here as forested USDA Forest Service harvest units. Stands ranged in age from five years to 400-600 years and fit into three general "groups": a) commercially clear-cut (19 stands, age 5-50 years post-harvest), b) stands destroyed by wildfire (9 stands, age 75-150 years, some salvaged logged), and c) unlogged primary forest (9 stands, age 400-600 years). These groupings are artifacts of available stand ages and are used only for ease of discussion. Initial lists of candidate stands were derived from district GIS layers compiled from harvest dates (Gifford Pinchot Vegetation Database, Rev. 1.1). The second tier of stand selection was based on five selection criteria:

- Age: Stands harvested c.post-1940 where grouped into decadal age classes (1940-1949, 1950-1959, etc to present) with stand age based on harvest date. At least three stands were selected from each decade to produce the chronosequence.
- Aspect: To attempt to capture the range of site productivity due to aspect, one stand each of roughly North, South, and Flat (valley floor) aspect were selected in each decade.
- Elevation: Stands used lie between approximately 360 m and 730 m in elevation. The lower elevation limit is the valley floor. The upper elevation limit was selected to avoid the transition zone from *Pseudotsuga sp.*-dominated forest to *Abies sp.*-dominated forest.
- Size: Preference was given to stands large enough to contain a 200 meter transect with a perimeter buffer of 100 meters (stands at least 400 m side). Stand dimensions were estimated from scaled USFS orthophotos.
- Stand canopy homogeneity: USFS orthophotos of candidate stands were examined to screen for interior swamps, experimental plantings, and other large features that could interfere with plot placement.

After initial selection, additional Group 1 stands were added to produce a final chronosequence with age gaps no larger than five years over the 1945-1993 period. The lower age limit (1945) for Group 1 stands was chosen because full-scale clearcutting began on the district c. 1940. The upper age limit (1993) was determined by available harvested stand ages. Stands age 70, 110, and 150 years post-disturbance (Group 2) were available age classes added to partially fill the 400+ year gap between Group 1 and

Group 3 stands. Primary forest stands were available fragments on the district. Slope and aspect of sampled stands range from 0-37° and 2-355°, respectively.

3.4.2 Transect Design

All stands were sampled for live trees and CWD using plots along a transect. Transect bearings generally followed the long axis of each stand but vary due to stand shape and area. With the exception of one two-plot transect, each transect consisted of three circular plots separated by 50-100 m, plot center-to-enter distance. To reduce edge effects (Chen and Franklin 1992, Hughes and Bechtel 1997, Mesquita et al 1999) outer plot radii were separated from stand boundaries by 50-100 m buffers. Variation in plot number, plot-to-plot distances, and buffer widths, was due to constraints of 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. A sample zone of radius 12.6 m surrounded each point, providing sample area equal to 0.05 ha for live tree biomass. For old-growth stands, plot area was doubled (0.1 ha, radius 17.8 m) because trees in these stands were more widely spaced. Plot radii were measured by calibrated Sonin ® and meter tape.

3.4.3 Tree Selection

During the 1998-1999 field seasons all species defined as trees (DBH>5cm) within each plot were tagged at breast height and described by vigor, crown ratio, and diameter breast height (DBH) to meet larger project objectives (Janisch and Harmon, accepted). Breast height was defined as 1.4 m above the soil surface on the upslope side of the trunk. Trees lying on the plot boundary were tagged if more than half of the bole was inside the plot. DBH was measured to the nearest 0.1 cm just above the aluminum tag using metric diameter tapes. Representative individual trees of the dominant species in each plot where selected for increment coring from the DBH distribution. Two small- (DBH near the lower limit), midsize- (DBH near the species plot mean), and large- (DBH near the upper limit) diameter trees (six trees total) were then selected from the diameter distribution of each of the two most dominant species on each plot. As less than ten species were frequently inventoried on our plots, assignment of dominance was generally straightforward. All species were treated as co-dominant when individual counts were approximately equal, as was sometimes the case in old-growth stands. To assess growth of less abundant tree species, western yew (*Taxus brevifolia* Nutt.), western red cedar (*Thuja plicata* Donn ex D. Don), red alder (*Alnus rubra* Bong) and Pacific dogwood (*Cornus nuttallii* Audubon) trees of representative DBH were also selected and cored when present.

3.4.4 Coring and Core Processing

All 139 plots were revisited during the 1999 field season and cored using 5.1 mm ID increment borers. Cores were stored in labeled plastic straws and each day's set was dried at 55 ° C for 48 hours at the field station in a forced-air electric oven to stop fungal rot. At the end of the field season all cores were oven dried an additional two weeks prior to mounting. Cores were then mounted in grooved wooden trays and sanded to enhance ring boundaries. Ring widths were read, outer ring inward, in five-year increments to the nearest 0.001 mm using a dissecting microscope and mobile stage. Core breaks were subtracted out.

3.4.5 Mean Increment

Cluster analysis (Proc Cluster, SAS v. 8) was applied to the 5-year increments from all stands. This was done because the mean stand-level increment width and its variance differed by stand age. This procedure, which resulted in five clusters of ages 6-29 years, 30-49 years, 70-88 years, 154 years, 500 years (old-growth), simplified analysis by statistically grouping stands of similar mean increment and variance. Mean and standard deviation were calculated as pooled values for all species (e.g. a single mean and standard deviation for each cluster) in each of clusters 1-4. This simplification was applied since few species other than *P. menziesii* and *T. heterophylla* were encountered in second-growth stands sampled. Since old-growth increment means varied widely within species by stand (cluster 5), such simplification was not possible and separate means and standard deviations calculated at the species level in each old-growth stand.

3.4.6 Monte Carlo Estimates

Calculated means and standard deviations were then combined with DBH data for all tagged trees (*n*=3,854) in a Monte Carlo method. to predict DBH 5,10, and 16 years prior. DBH data was first adjusted by subtracting out twice the estimated bark thickness of each tree. Bark thickness coefficients were estimated by regression of bark-wood dendrology data for dominant species within the study region (TV009, FSDB, Oregon State University). A Monte Carlo method based on random number generation and cluster means and standard deviations (Table 3-1) was then run to produce estimates of 5-year increment for each tagged live tree. This method was repeated 20 times for each stand. Two times the resultant increment estimate was then subtracted from the current wood diameter of each tagged tree. Using bark coefficients described above, bark was then restored to each new wood diameter and this data set became our estimate of live tree DBH five years previously, here after referred to as DBH2. DBH2 was then converted directly to bole wood mass and bark mass using species-specific BIOPAK allometric regression equations that were based on both regional (Central Cascades) and specific forests (Means et al 1994). These totals were then averaged by plot and converted to Mg C ha^{-1}, yielding 20 estimates of biomass five years previously for each stand. Stand-level means and standard deviations were then calculated from the 20 biomass calculations for each stand. Current biomass, based on DBH, was also calculated for each stand. Boles were assumed to be sound (free of rot) and solid (without hollows). Data were slope corrected at the plot level by calculating a correction factor (cf) as:

$$\text{(Equation 3-1)} \quad cf = 1/(\cos(\operatorname{atan}(slope/100))),$$

where slope = degrees.

3.4.7 NPP_b

Change in bole biomass over five years was calculated as DBH minus mean DBH2. Mean annual biomass changes refer to this difference divided by five. Values are adjusted to C mass assuming bark and wood is 50% C (Swift et al 1979) and reported as Mg C ha^{-1} yr^{-1}. NPP_b for 154 year-old stands was calculated analogously, but was based on actual successive DBH measurements (1994 and 1999 time-series data, FSL data base, Oregon State University; Acker, personal communication) rather than reconstructed tree diameters from 5 years previously. Mortality was neglected in all stands, but this error is expected to be <5 % for a 5-year period given rates of tree death from conifer forests in the general region of study (Acker et al, accepted). Ingrowth was neglected for similar reasons.

Table 3-1: Summary of Monte Carlo method parameters used to estimate biomass of stands 5-years before present along a chronosequence on the Wind River Ranger District, Washington.

cluster age range, years	number of stands	mean 5-year increment, cm	standard deviation, cm
6-29	10	2.1122	0.8114
30-49	9	1.0511	0.6572
70-88	6	0.6237	0.4128
154	2	0.5729	0.2967
500	9	0.115-0.783[a]	0.021-0.805[a]

[a] varies by species and by stand

3.5 RESULTS

NPP_b of second-growth stands ranged between 0.15-5.28 Mg C ha^{-1} yr^{-1} (Table 3-2). NPP_b was lowest early in succession (0-10 years) but rose rapidly, peaking 20-30 years after clearcutting (Figure 3-1). Between 30-45 years, NPP_b appeared to level off or decline, though this trend may be due to differences in stand productivities. NPP_b appeared to increase slowly between 65-150 years after disturbance, from a mean of 2.9 Mg C ha^{-1} yr^{-1} to 4.2 Mg C ha^{-1} yr^{-1}. NPP_b of the 500-year old stands ranged between 1.3-3.9 Mg C ha^{-1} yr^{-1}, similar to those rates found in 20-25 year old second-growth. Mean NPP_b of 500-year old stands (2.7 Mg C ha^{-1} yr^{-1}, Figure 3-2) was somewhat lower than mean NPP_b of 30-50 year-old stands (4.1 Mg C ha^{-1} yr^{-1}) and 65-150 year-old stands (3.0 Mg C ha^{-1} yr^{-1}).

Temporal trends were also apparent in standard deviations of the twenty Monte Carlo calculations per stand (Table 3-1). Standard deviations, smallest early in succession, increase to 2.3 Mg C ha^{-1} yr^{-1} 30-50 years after clearcutting, then declined slightly between ages 65-150 years (2.0 Mg C ha^{-1} yr^{-1}). Mean standard deviation of old-growth stands was 1.9 Mg C ha^{-1} yr^{-1}.

Based on 5-year radial increment of all stands, *Abies procera* Rehd. grew the fastest, followed by *P. menziesii* and *T. heterophylla* (Figure 3-3). Mean stand-level *P. menziesii* increment declined rapidly early in succession, then remained relatively constant for stand > 50 years in age. (Figure 3-4). In contrast *T. heterophylla* showed a U-shaped increment pattern, starting high, declining, then increasing back to early successional levels in old-growth stands. Mean radial increment widths for second-growth 30-49 years in age, those stands in which all cored trees were old enough to record 15 years of growth at DBH (three 5-year increments), all declined over time for individual stands (i.e. the oldest increment was widest). This pattern, also seen in 70 and 88 year old stands, was less pronounced in 154 year-old stands, with either the second (6-10 years before present) or the third (11-15 years before present) increment being widest.

Data from the two increments immediately preceding the outer increment (6-15) years before present), which are complete for stands age 20 and older, indicate mean stand-level radial increment is declining in stands <500 years old (Figure 3-5, data for *P. menziesii* shown). This is consistent with the idea that diameter growth declines as trees age. In contrast, growth across these DBH increments in the old-growth stands show a mixture of patterns (Figure 3-6, data for *P. menziesii* shown), with five stands showing increases in DBH increment, two showing relatively no change, and two showing slight declines in increment width. It should also be pointed out that across the old-growth stands DBH increments are narrow and the changes in growth small.

Table 3-2: Bole mass and net primary productivity of individual second-growth and old-growth stands at Wind River, Washington.

Stand age, years	mean bole mass, 1999[a], Mg C ha^{-1}	mean bole mass, 1994[b], Mg C ha^{-1}	bole mass SD[b], 1994, Mg C ha^{-1}	Mean NPP$_b$ of boles, Mg C ha^{-1} yr^{-1}	2SD
6	1.1	0.3	0.46	0.2	0.04
10	3.2	0.4	0.07	0.6	0.03
13	8.1	2.2	0.19	1.2	0.08
15	1.7	0.3	0.05	0.3	0.02
19	26.4	10.3	0.41	3.2	0.16
21	22.2	9.4	0.37	2.6	0.14
22	12.8	4.1	0.31	1.7	0.12
25	34.9	17.6	0.68	3.5	0.27
29	33.0	16.5	0.89	3.3	0.36
30	63.5	50.4	1.08	2.6	0.44
33	55.9	41.5	0.85	2.9	0.34
34	58.9	46.6	1.21	2.5	0.49
35	143.3	116.8	1.42	5.3	0.57
38	90.6	71.3	1.14	3.9	0.46
40	141.9	118.5	1.28	4.7	0.51
43	60.5	47.1	0.96	2.7	0.39
44	93.5	71.7	0.87	4.4	0.35
49	82.7	61.0	1.32	3.7	0.53
70	132[c]	118[c]	1.04[c]	2.8[c]	0.42[c]
88	163[c]	145[c]	1.20[c]	3.6[c]	0.48[c]
154	289[c]	268[c]	0.65[c]	4.2[c]	0.26[c]
500	270[c]	257[c]	0.95[c]	2.7[c]	0.38[c]

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[a] calculated from actual DBH measurements

[b] calculated from Monte Carlo results, based on 20 runs

[c] average of multiple stands

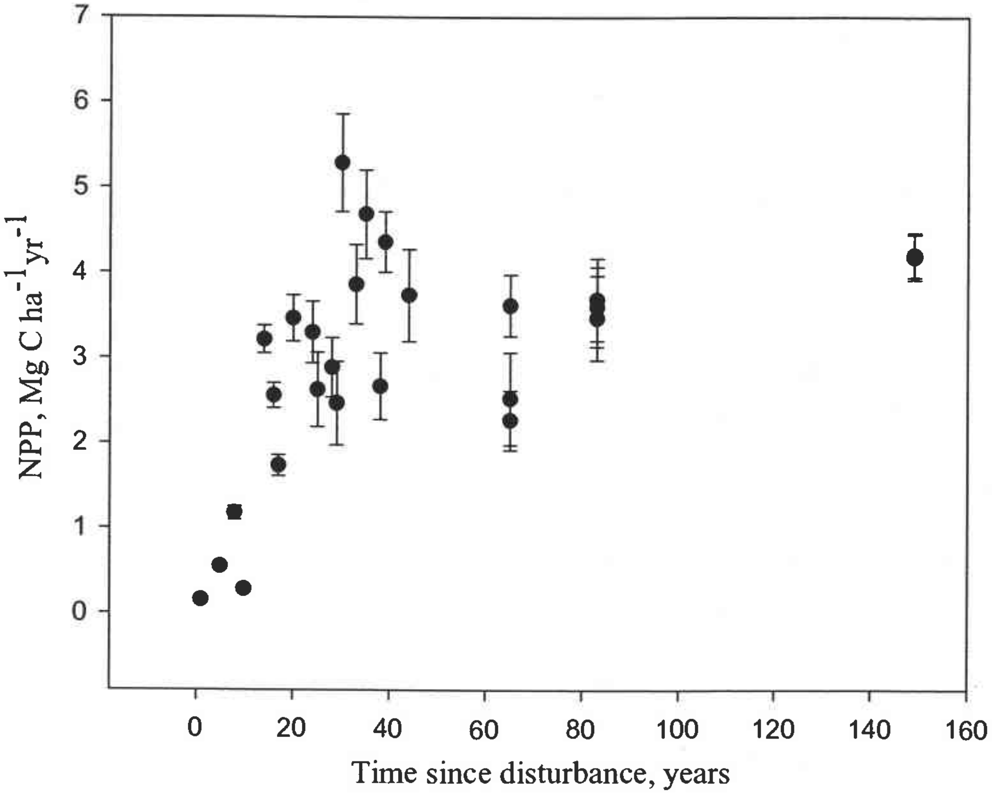

Figure 3-1: NPP$_b$ of individual second-growth conifer forest stands on the Wind River Ranger District, Washington. Data represent differences between 1999 biomass determined by DBH and the mean of 20 Monte Carlo runs, scaled to annual values and C content, +-2SDs.

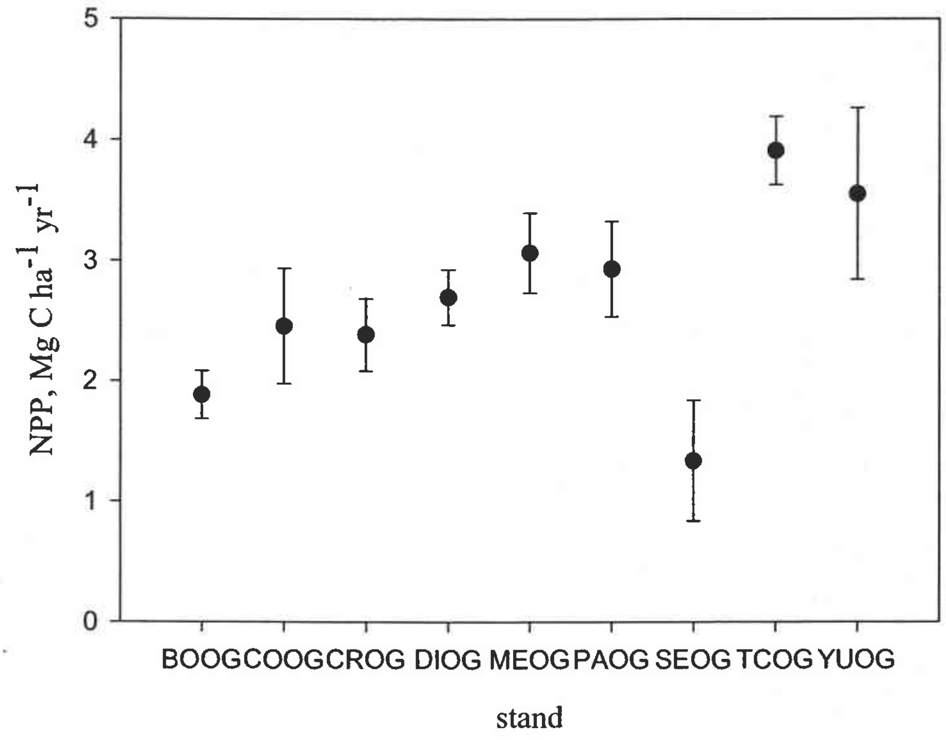

Figure 3-2: NPP$_b$ of individual 500-year old conifer forest stands on the Wind River Ranger District, Washington. Data represent differences between 1999 biomass determined by DBH and the mean of 20 Monte Carlo simulations, scaled to annual values and C content, +- 2 SD.

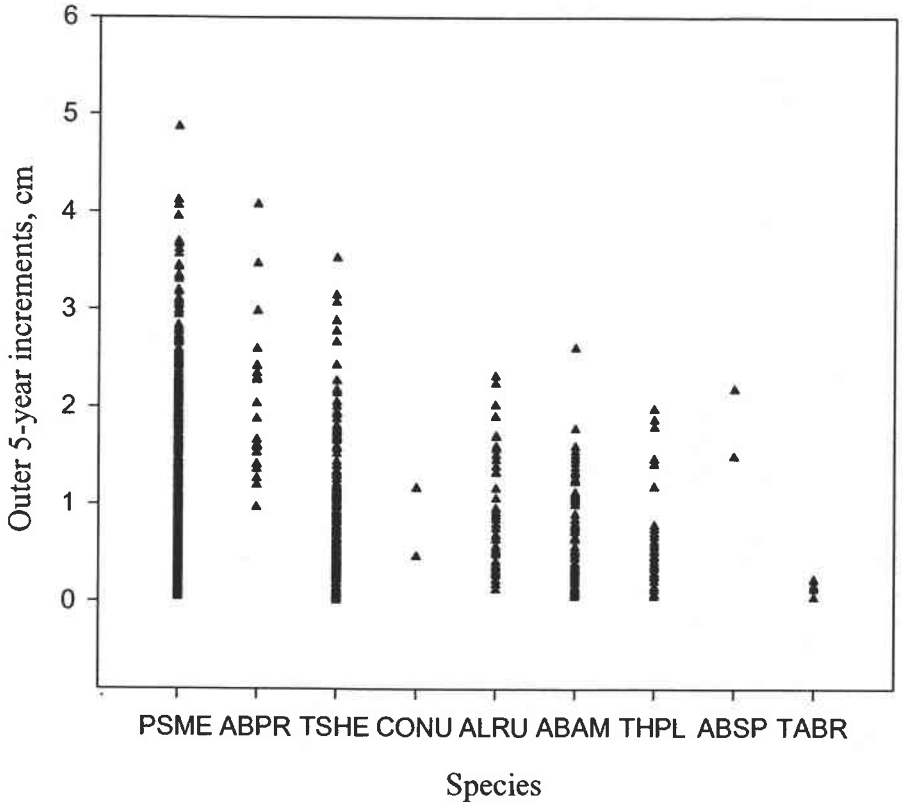

Figure 3-3: Distribution of DBH increment in the last 5 years of growth for major tree species of all stands sampled. Data from Wind River, Washington.

3.6 DISCUSSION

Since the 154-year old stands were part of the Douglas Fir Growth and Yield study, we were able to compare our results to actual DBH data from a time series. These data account for mortality and ingrowth and thus provide an index to check our estimate of NPP_b and stand biomass. Based on actual DBH, biomass of the two 154-year old stands in 1994 was 275 Mg C ha^{-1} and 280 Mg C ha^{-1}. Estimates given by the Monte Carlo runs gave a biomass of 261 Mg C ha^{-1} and 275 Mg C ha^{-1}, respectively. This underestimated the observed time series-based biomass for these two stands over the same period by more than two standard deviations (261 Mg ha^{-1} and 275 Mg ha^{-1}, respectively), a difference that could be due to tree mortality over the five year period. Comparison of mean DBH from actual measurements to those from our Monte Carlo calculations indicate this method systematically underestimated DBH five years before the current measurement--e.g. 32.5 cm vs. 30.8 cm, 47.4 cm vs. 44.7 cm. Based on 1999 and 1994 DBH measurements, annual NPP_b of these stands was 1.5 Mg C ha^{-1} yr^{-1} and 3.3 Mg C ha^{-1} yr^{-1}, well below our estimates of 4.1 Mg C ha^{-1} yr^{-1} and 4.2 Mg C ha^{-1} yr^{-1}. When our estimates were adjusted for stand mortality and ingrowth using the available time-series data, results were mixed, with NPP_b declining to 1.1 Mg C ha^{-1} yr^{-1} and 4.0 Mg C ha^{-1} yr^{-1}, respectively. Thus these differences may be due to how cored trees in the 154-year old stands were selected (discussed below).

NPP_b for mature stands at the H.J. Andrews Experimental Forest (dominated by *P. menziesii, T. heterophylla*, and *Castanopsis chrysophylla* (Dougl.) A. DC., approximately 150 km south), was also lower than our estimate (2.4 Mg C ha^{-1} yr^{-1}, Acker et al, accepted). This was also true of estimated NPP_b for the Wind River T.T.

Munger Research Natural Area (1.22 Mg C ha^{-1} yr^{-1}, Harmon et al, in preparation) and other old-growth plots in the region (1.1 Mg C ha^{-1} yr^{-1}, Bible 2001). The temporal trend described at the H. J. Andrews, however, which summarized 10-15 years of time-series data on watersheds age 29, ~100, and ~400 years, was similar to that along our wind River chronosequence, with NPP increasing on the young watershed but otherwise relatively constant. Thus, while NPP_b of forests at both Wind River and the H.J. Andrews show similar patterns over time, our estimate appears too high. Given adjustment for mortality and ingrowth produced mixed results, the cause of this difference between time series coring-based methods is still uncertain. One possible but unlikely source of error is use of bark-wood ratios inappropriate for these stands, which are relatively productive river terraces. Sampling of non-representative trees and low number of trees cored ($n = 6$ per stand) may also be influencing the result. If the latter is the principle source of error, NPP_b estimates from other age stands sampled, both younger and old-growth, may be closer to the true stand NPP_b value since more trees were cored (at least 18 trees per stand).

As is shown in Figure 3-4 for *P. menziesii*, mean increment width declined early in succession, leveling off around 50-years post-clearcutting at roughly 0.4 cm yr^{-1}. Declining increment does not require NPP_b to decline, however, since DBH increases as trees age even if radial increment declines. Thus, NPP_b may remain constant or continue to increase due to tree geometry. Similarly, while NPP could be positive or increasing in older forest, stand-level NEP could be near zero. Given the C source to sink dynamics during secondary forest succession, maximum NPP_b may actually occur when NEP of a stand is most negative (Janisch and Harmon, accepted).

Interpreted against increasing mean DBH over time, and given our finding that NPP_b of old-growth stands was similar to 65-100 year old age classes, these temporal changes in DBH increment may point to benefits of using large trees in older forests to store C. This is because while increments are widest in rapidly growing young forest and heart rot may be negligible, if these young forests are replacing forests of high biomass, such as old-growth, and replacement released CO_2 by generating CWD, then apparent gains in C storage from the young forest are in reality paying off a CO_2 debt, which may reach 200 Mg C ha^{-1} in losses immediately following clearcutting (Janisch and Harmon, accepted). Conversely, incorporating reductions to bole C storage, such as heart rot, would help clarify forest C storage policy for older stands. However, if, biomass of older forests (and thus C storage) is higher relative to young regenerating forests, (Table 3-2), and these C stores can be maintained even by narrow growth increments, then potentially more C could be stored both at stand (Janisch and Harmon, accepted) and landscape levels in older forest (Harmon 2001).

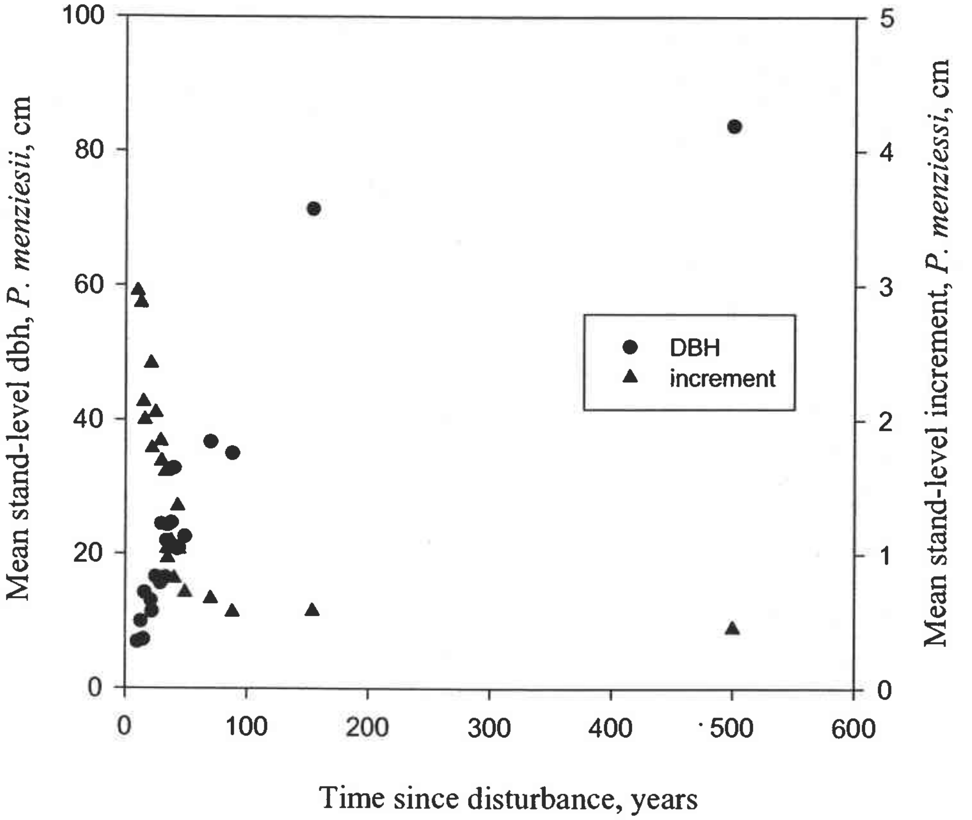

Figure 3-4: Relationship between mean DBH and mean increment (first five years before present) of *P. menziesii*. Data from a chronosequence of confier dominated stands at Wind River, Washington.

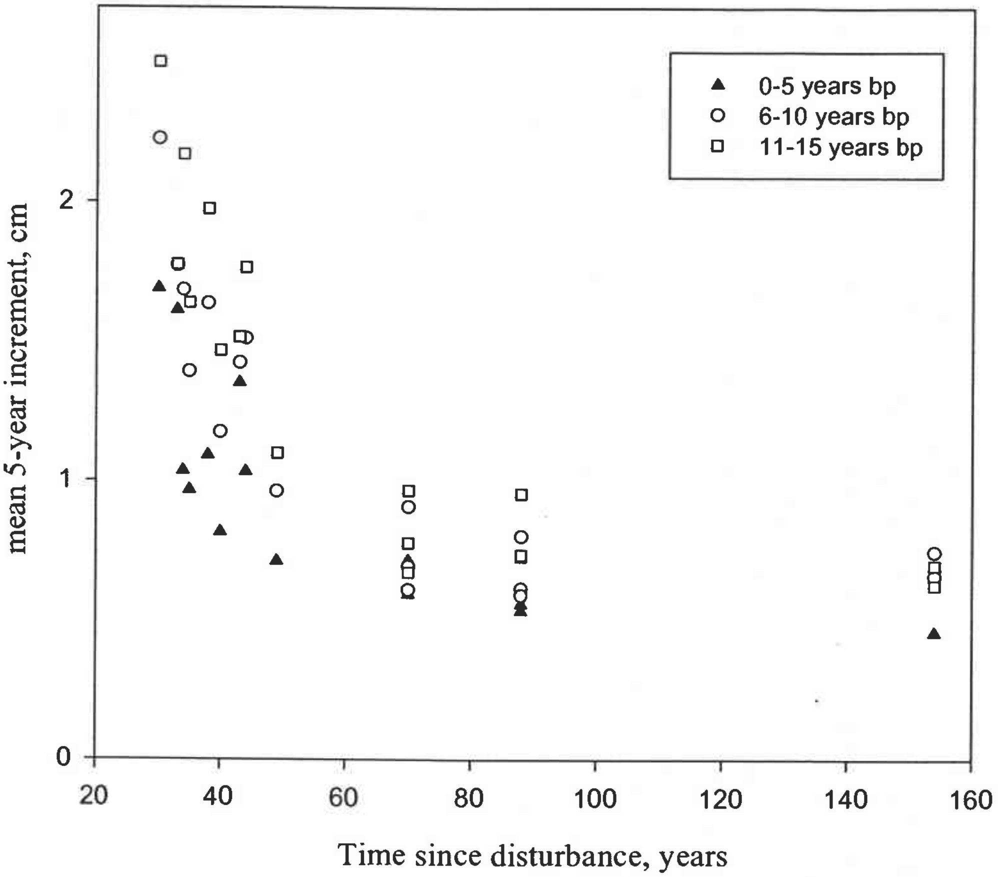

Figure 3-5: Radial increment width of second-growth stands > 30 years of age showing decline in mean increment width of individual stands over time. Each stand's current age on the X-axis is used for all of its increments for clarity. Data from a chronosequence of conifer-dominated stands at Wind River, Washington.

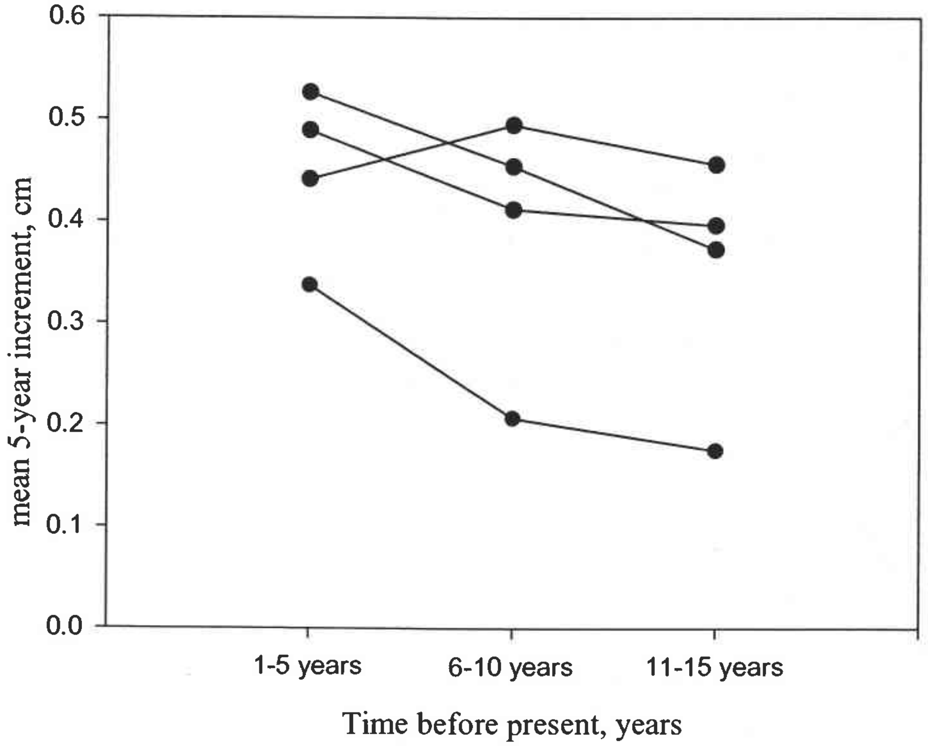

Figure 3-6: Radial increment of four old-growth stands. Points are mean 5-year radial increment widths, all species, for the 15-year period before the present. Data from a chronosequence of conifer-dominated stands at Wind River, Washington.

3.7 METHODOLOGICAL LIMITATIONS

The coring-based methods we used to infer NPP_b have several methodological limits, the consequences of which vary in their effect on NPP_b. Such calculations do not, for instance, easily account for mortality or ingrowth. Though biases introduced into NPP_b by failing to account for these two processes can be small (Clark et al 2001). controlling such biases is particularly relevant if such estimates are used in larger-scale analyses. Given the longevity of the conifer species studied, which dominate these stands, and estimates of mortality rates from the region (Acker et al, accepted), however, neglecting mortality and ingrowth over a single 5-year increment in this region may be reasonable, provided the cored sub-set of trees reflect a stand's true diameter distribution. Estimates of ingrowth and mortality rates might be used to establish sampling interval length to minimize bias in cases where NPP_b is needed but must be derived by coring since time-series data does not exist.

No adjustment for heart rot was applied to our NPP_b estimates. While assuming boles to be sound (rot free) is probably inappropriate given that heart rot may occupy >30% of old-growth *T. heterophylla* 'live' volume (Boyce and Wagg 1953, Goheen et al 1981), these losses may be of little consequence to NPP_b. This is because decomposition must either invade the shell of new wood produced during successive stand measurements or reduce tree photosynthetic rates to affect NPP_b. Heart rot would, in contrast, affect estimates of change in stand biomass (Δ biomass), since decomposing tissues in living trees would be converted to CO_2. Thus, Δ biomass could decline while NPP_b remained constant or increased over the same interval, pointing out the difference between NPP_b and Δ biomass, which have sometimes been used interchangeably. NEP could be strongly affected, however, since an additional heterotrophic term describing C losses from heart rot must be taken into account, as well as transfers of biomass between 'live' and detrital stores.

Soil, aspect, and other factors influence stand productivity and thus radial increment (Bradshaw 1969, Perry 1994). Incorporation of these variables in a regression analysis may thus account for some of the observed between-stand variation. In addition, since an objective of this analysis was to core trees across the diameter distribution in each plot, this likely contributes to the relatively wide confidence intervals around NPP_b estimates, especially those from stands of later successional ages. Accuracy might also be gained by using the mean and standard deviation of each stand rather than cluster parameters, though given the statistical clustering these gains may be small, as well as relevant only to second-growth stands in this analysis.

A bark/wood ratio from *T. heterophylla* was substituted for *A. rubra*, *C. nuttallii*, *Acer macrophylla*, and other hardwoods since data for these species was not readily available. Substitution of *A. amabilis* for all *Abies* sp. and *T. plicata* for *T. brevifolia* was done for the same reason. Given observed bark thickness of these species, these substitutions seem reasonable in the absence of species-specific data. However, both under- and over-estimation biases in biomass and NPP_b are possible as a result. However, since these species were rarely encountered, with often < 10 individuals of each in the data set (*A. rubra* was more numerous), error associated with such substitutions is likely small.

Generally trees were cored on the uphill sides, but because various crews worked on the project this is not fully verifiably and was probably not consistently followed. Cores thus represent a mixture of tension and compression wood, which can affect ring width, with the bias likely toward tension wood. The effect of a tension wood bias, which may have narrower rings than compression wood would be to underestimate NPP_b.

Since our work included many different successional ages, continued monitoring of these stands over time as well as addition of newly regenerating, 150-500 year-old, and 500+ year-old stands may provide useful inferences about responses of Pacific Northwest forests to climate change or CO_2 fertilization. Re-coring similar subsets of trees when our full plots are remeasured in 2003 will also show whether stand-level NPP_b calculated from relatively few cores is reasonable, since full plot and sub-set values could be compared.

Perhaps more significant, however, is that while inferring NPP_b from tree cores has its weaknesses, when applied along a chronosequence as done here it is also potentially very powerful. This is because upon remeasurement the entire chronosequence becomes a chronosequence-time series hybrid from which two independent estimates of NPP_b (one neglecting mortality, one not) can be compared.

3.8 MANAGEMENT IMPLICATIONS AND CONCLUSIONS

The successional pattern of rapid increase followed by decline of NPP_b in our data is consistent with reported time-series patterns for conifer forests in the Pacific Northwest (Turner and Long 1975, Acker et al 2000, Acker et al, accepted). Peak NPP_b of second-growth stands was within the range reported by Keyes and Grier (1981), where a range of low (2.5 Mg C ha^{-1} yr^{-1}) to high (5 Mg C ha^{-1} yr^{-1}) productivity *P.*

menziesii sites were considered. Productivity of old-growth stands was approximately half that of peak productivity of second-growth stands in the same region, indicating significant NPP_b despite narrow growth rings in old-growth stands. This result is similar to that reported from 36 years of monitoring an old-growth P. menziesii-T. heterophylla stand at the T.T. Munger RNA (DeBell and Franklin 1987).

Given the high biomass of mature and old-growth stands relative to younger stands, landscape C stores in live wood would be maximized by stands of these age classes. In the case of coniferous old-growth, however, little productive, mesic, or low-elevation forest remains in the region so the radial increments of late successional trees on such sites is not well known. Low-elevation old-growth that persists to the present, such as the T.T. Munger RNA, was likely passed over in part due to low productivity. Thus, low or declining NPP_b rates often observed in old-growth could reflect measurement of stands that had never grown well rather than the range of rates of which these old forests are capable. Regional conifers can apparently grow to large size on these productive sites, however. There are, for example, *T. plicata* stumps on a river terrace not far from the RNA > 5 m, DBH, but this size may be due to age (e.g. escaping fire in a wet environment) rather than rapid growth. We have also found old-growth *P. menziesii* at Wind River with ring widths similar to 65-100 year old forest and sapwood thicknesses exceeding 6 cm, somewhat higher than general opinion might indicate. Recent work showing released or fertilized old-growth trees may begin increasing their growth increments relative to pre-release or pre-fertilization (Poage, 2000), further indicates old-growth trees may be potentially more productive than previously thought.

Finally, while net ecosystem productivity (NEP) rather than NPP may be more relevant to future forest management if maximizing forest C storage becomes a policy objective, the role of NPP is not diminished. This is because direct measurement of stand C gains and losses can be used to evaluate both flux-based estimates of C store changes (e.g. Moncrieff et al 1997, Constantin et al 1999) and predictions of climatic change models.

3.9 ACKNOWLEDGEMENTS

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CHAPTER 4

SUCCESSIONAL CHANGES IN LIVE AND DEAD WOOD CARBON STORES: IMPLICATIONS FOR NET ECOSYSTEM PRODUCTIVITY

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4.1 ABSTRACT

If forests are to be used in CO_2 mitigation projects, it is essential to understand and quantify the impacts of disturbances on 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 over secondary succession using 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 Mg C ha^{-1} $year^{-1}$ and –14.1 Mg C ha^{-1} $year^{-1}$, respectively. Maximum live and total wood C stores of 319 Mg C ha^{-1} and 393 Mg C ha^{-1}, respectively, were reached approximately 200 years after disturbance. Decomposition rates (*k*) of CWD ranged between 0.013-0.043 $year^{-1}$ for individual stands. It took regenerating stands 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 as remaining nearby old-growth forests (predominant age 500 years), indicating conversion of the latter forests to younger managed forests results in a significant net release of C to the atmosphere.

Key words: Biomass accumulation; carbon sequestration; coarse woody debris; CWD; disturbance; negative to positive; NEP; net ecosystem productivity.

4.2 INTRODUCTION

As atmospheric CO_2 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) (Marland 2000, Iverson et al 1993). Opinion on this strategy (Schlamadinger and Marland 1998, Schulze et al 2000), as well as the role of CO_2 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 effects on forest growth and decomposition (Rogers et al 1993, Korner 1996) further point toward uncertainties in the future C storage capacity of forests.

If forests are to be used to manipulate atmospheric CO_2, 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. NEP, 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

$$\text{(Equation 4-1) } NEP=dC/dt.$$

When NEP is negative, the ecosystem of interest is a CO_2 source relative to the atmosphere. When it is positive, the system is a CO_2 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 levels off during stand maturation, and finally stabilizes or declines in late-successional phases. For the CWD component, chronosequence studies in wave-regenerated *Abies balsamae* (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 (a) 1996) 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, in press) 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 (NEP negative) associated with decomposition of dead wood both 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). Using 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 clearcutting.

While Pacific Northwest forest soils store an estimated 35% of total system C (Smithwick et al, accepted), this C is released slowly relative to the time scale of forest disturbance and succession (Johnson and Curtis 2001). Thus, since a large fraction of non-soil forest C is stored in live boles and CWD (Smithwick et al, accepted), 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 and the above 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 clearcutting and if so for how long, and 4) can these dynamics be used to place extreme positive and negative limits on NEP. 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.

4.3 STUDY REGION

Data was collected from forest stands within the U.S. Forest Service Wind River Ranger District, approximately 20 km from the Columbia River Gorge in southwest Washington State. Since this study was part of an integrated project already in progress at the T.T. Munger Research Natural Area (RNA), stand selection was confined to an approximately 10 km x 10 km region centered on the RNA (45° 49' N, 121° 58' W). Elevation ranges between approximately 335 meters to 1200 meters. 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 annual 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 RNA temperature is 8.7 °C (Wind River Canopy Crane data). Based on ring counts from stumps and tree cores collected inside or adjacent to the RNA, these forests originated approximately 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 c.1490 (Franklin and Waring 1979). Vegetation of the study region is dominated by *P. menziesii-Tsuga heterophylla* (Raf.) Sarg. forest. RNA 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*, *Acer circinatum* Pursh, *Ceanothus sp.*, *Vaccinium parvifolium* Smith , and *Vaccinium membranaceum* Dougl. ex Hook.

4.4 METHODS

4.4.1 Stand Selection

This study was observational with no true replication. *Stands* were defined here as forested sites used as harvest units by the U.S. Forest Service. Stands ranged in age from five years to 400-600 years and formed three general groups: (1) clearcut, regenerating stands age 5-50 years post-harvest, (2) 75-150 years 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:

- 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.

- Aspect: To represent the range of site productivity, one stand each of northerly, southerly, and flat (valley floor) aspect were selected in each decade.
- Elevation: Stands used lie roughly between 760 m 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.
- Size: Preference was given to stands large enough to contain a 200 meter transect and 100 m edge buffers (at least 400 m per side). Stand dimensions were estimated from scaled USFS orthophotos.
- Stand canopy homogeneity: USFS orthophotos of candidate stands were examined for interior swamps, experimental plantings, and other features interfering with plot placement.
- 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, Conway 1982, Pool 1950), and total non-merchantable mass of CWD (slash) have changed over time (Harmon et al 1996, 1996a). Old-growth stands may thus provide an estimate of pre-clearcut 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 five years for the first fifty years of stand development (1945-1993). Three more stands were then added between harvest dates 1960 and 1970 because an initial analysis predicted NEP switched from negative to positive in this age range. The upper age limit (1945) for Group 1 stands was chosen because full-scale clearcutting began in the district c. 1940. The lower age limit (1993) was determined by available harvested 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, 9, and 9 stands respectively in Groups 1, 2, and 3. Old-growth stands represented remaining tracts of 400-600 year-old forest in the district.

4.4.2 Transect Design

All stands were sampled for live trees and CWD using 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 m and 17.8 m surrounded each point, providing sample areas equal to 0.05 ha for live tree and 0.1 ha for CWD biomass. Plot radii were measured by calibrated Sonin ® and meter tape.

4.4.3 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. DBH was measured to the nearest 0.1cm just above the aluminum tag using commercial metric D tapes. 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):

(Equation 2-2): $cf= 1/(\cos(\operatorname{atan}(slope/100)))$,

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

4.4.4 Coarse Woody Detritus

Three principle forms of above-ground 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 diameter at breast height. 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. CWD mass of unknown species or genus was calculated using *P. menziesii* densities. Logs, stumps, and snags entering the CWD pool from the regenerating stand through mortality and thinning (hereafter referred to as *de novae* CWD) were separated from pre- and post-clearcutting 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 0.1m by 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 et al 1996). Stump hollow volumes were calculated as above and subtracted out. Snag volumes were calculated as frustums of cones using 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

(Equation 4-3) Initial CWD mass = (legacy CWD volume) x (0.45 Mg m^{-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 clearcutting 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 1996). Slope correction of CWD mass was as for live trees.

4.4.5 Model

A Chapman-Richards function (Equation 4-3) was fit to data describing biomass accumulation in tree boles following stand initiation (Richards 1959) as

(Equation 4-4): $L_t = L_{max} (1 - e^{-k_L t})^{r_L}$

where L_{max} is maximum (asymptotic) live tree biomass, L_t is live tree biomass at time t, k_L is an empirically derived growth constant, and r_L is a shaping parameter. Mean live tree parameters (L_0, k_L, r_L) were estimated by fitting PROC NLIN, SAS® v. 7, to the set of 36 mean stand-level live tree mass (Mg ha^{-1}) estimates using Equation 4-4. 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 using a negative exponential function (Kira and Shidei 1967)

(Equation 4-5): $D_t = D_0 (e^{k_D t})$

where D_t is CWD mass at time t after clearcutting, 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 fitting PROC NLIN to Equation 4-5 using 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

(Equation 4-6): $k = -\ln[(\text{legacy CWD mass})/(\text{initial CWD mass})]/\text{time}$

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

Accumulating *de novae* CWD mass was also modeled using a Chapman-Richards function. *De novae* parameters (N_{max}, k_N, r_N) were estimated by fitting PROC NLIN to Equation 4-4 using *de novae* 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 (SAS 1999). Total CWD mass was calculated as

(Equation 4-7): $TD_t = D_t + N_t$,

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

4.4.6 NEP$_w$

NEP$_w$ was then calculated by difference as the sum of live and CWD stores (Equation 4-8)

(Equation 4-8): $\text{NEP}_w = \Delta L + \Delta D = (L_{(t+1)} - L_t) + (TD_{(t+1)} - TD_t)$.

and presented as mean, upper extreme, and lower extreme for four scenarios (Table 1, Figures. 4-8). In Scenario 1, all on-site CWD is assumed removed by clearcutting (CWD mass = 0) and off-site decomposition is ignored. While 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 clearcutting 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, while 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 are assumed 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 PROC NLIN (Table 1) into Equation 4-8. 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 novae* CWD parameters were the same in all scenarios because CWD accumulations was modeled as converging on mean old-growth CWD stores.

Table 4-1: Parameters used to fit NEP$_w$ curves. In each case, curves are calculated as mean live C stores+ mean CWD stores+ mean *de novae* C stores, upper live C stores+upper CWD C stores + mean *de novae* C stores, and lower live C stores + lower CWD C stores + mean *de novae* C stores.

process	case	definition	mean			upper limit			lower limit		
			L_{max}	k_L	r_L	L_{max}	k_L	r_L	L_{max}	k_L	r_L
growth	1--4	the range of current old-growth live tree C stores. The same in all cases.	319	-0.017	2.09	451.5	-0.017	2.09	184.5	-0.017	2.09
			D_0	k_d		D_0	k_d		D_0	k_d	
decomposition	1	all legacy CWD removed by logging. Live tree and *de novae* C stores accumulate	0			0			0		
	2	the range of calculated initial CWD C stores	76	-0.025		118.5	-0.025		42	-0.025	
	3	the range of current old-growth CWD C stores	74	-0.025		160.5	-0.025		32	-0.025	
	4	all live trees killed by catastrophic fire and move into on-site CWD C stores. Limits are high killed live+high CWD and low killed live+low CWD C stores	393.5	-0.025		612	-0.025		216.5	-0.025	
			N_{max}	k_N	r_N						
de novae	1--4	the same in all cases	74.3	-0.025	11.13						

4.5 RESULTS

Live tree stores ranged from 184.5 Mg C ha^{-1} to 451.5 Mg C ha^{-1} (mean: 315.4 Mg C ha^{-1}, *SE:* 30.8) 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 Mg C ha^{-1}, F=183.68, p<0.0001, *SE:* 16.40). The fitted growth parameter (k_L) was 0.017 year^{-1} (*SE:* 0.005), indicating that maximum live tree C stores were reached in approximately 200 years. The fitted shaping parameter (r_L) was 2.09 (*SE:* 0.72).

Mean initial CWD mass in Group 1 stands was 76 Mg C ha^{-1} (range: 42 – 119 Mg C ha^{-1}, *SE:* 7.4, n =19) and not significantly different from mean CWD mass in old-growth stands in 1998 (mean: 74 Mg C ha^{-1}, range: 32 - 160 Mg C ha^{-1}, *SE:* 12.7, 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 3) was not significant either by linear (time = -1.03, t = -1.16, p = 0.26, *SE:* 0.88) or quadratic (time = -0.02, t = -1.04, p = 0.312, *SE:* 0.02) regression of mass against time. The fitted Group 1 legacy CWD C storage (D_0) was 55 Mg C ha^{-1} (F=81.11, p<0.000, *SE:* 9.58, Figure 3).

Legacy CWD C stores declined with increasing stand age across Group 1 with a fitted mean decomposition rate (k_d) of 0.010 year^{-1} (n=18, *SE:* 0.006) (see Figure 2 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 (Sollins 1982, Janisch et al (b), in preparation). NEP$_w$ was based on mean decomposition rate of individual stands because of this. Mean fitted asymptotic *de novae* mass (N_0), accumulation rate (k_N), and shaping parameter (r_N) were 74 Mg C ha^{-1} (*F*=50.73, *p*<0.001, *SE:* 6.65), 0.025 year^{-1} (*SE:* 0.013), and 11.13 (*SE:* 14.31) respectively (Figure 4). Regression of 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 Mg C ha^{-1} CWD per 1 Mg C ha^{-1} live tree mass, $n = 9$, $t = 1.41$, $p = 0.200$, *SE:* 0.14).

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 novae* CWD). This is 193 Mg C ha^{-1} below old-growth levels (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} year^{-1} were reached approximately 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 removed and ignored, stands functioned as net sinks of CO_2 from the atmosphere from year 0 (Figure 5). In Scenario 2 (Figure 6), where CWD loads are reorganized by clearcutting, stands functioned as CO_2 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 CO_2 sinks. When an old-growth stand was assumed killed by fire and decomposed *in situ* (Scenario 4), the transition took 50-56 years (Figure 8). NEP 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.

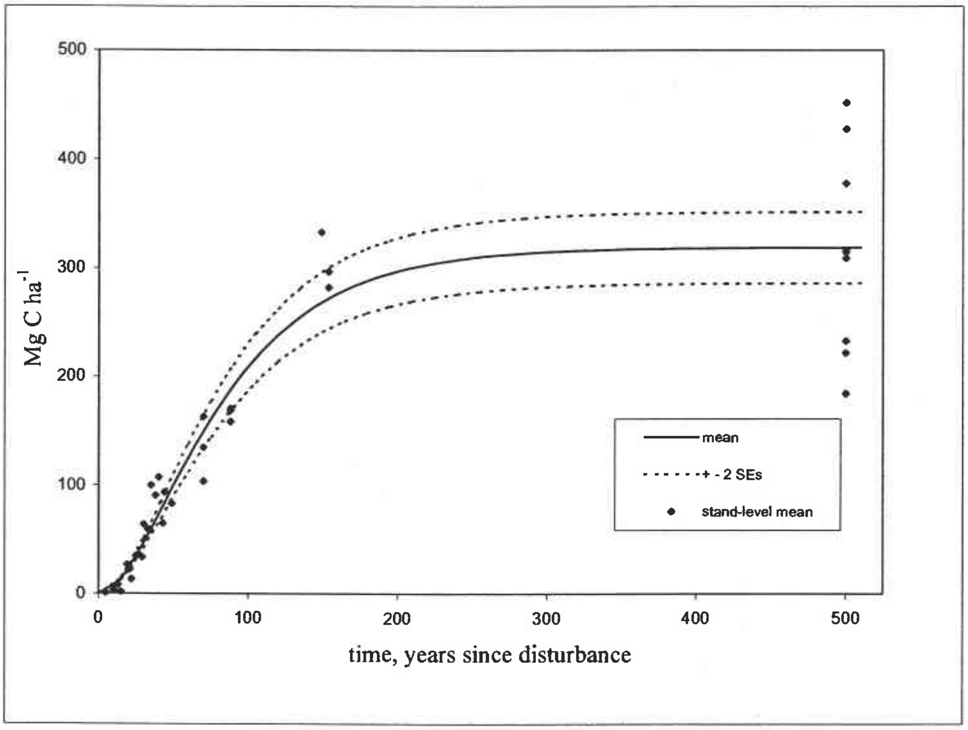

Figure 4-1: Live tree bole C stores along a 500-year chronosequence of 36 *Pseudotsuga-Tsuga* dominated forest stands at Wind River, Washington. The x-axis is years since disturbance, or age of the stand. The y-axis is live bole C stores in each stand. Data were fit using a Chapman Richards function where all parameters were allowed to vary.

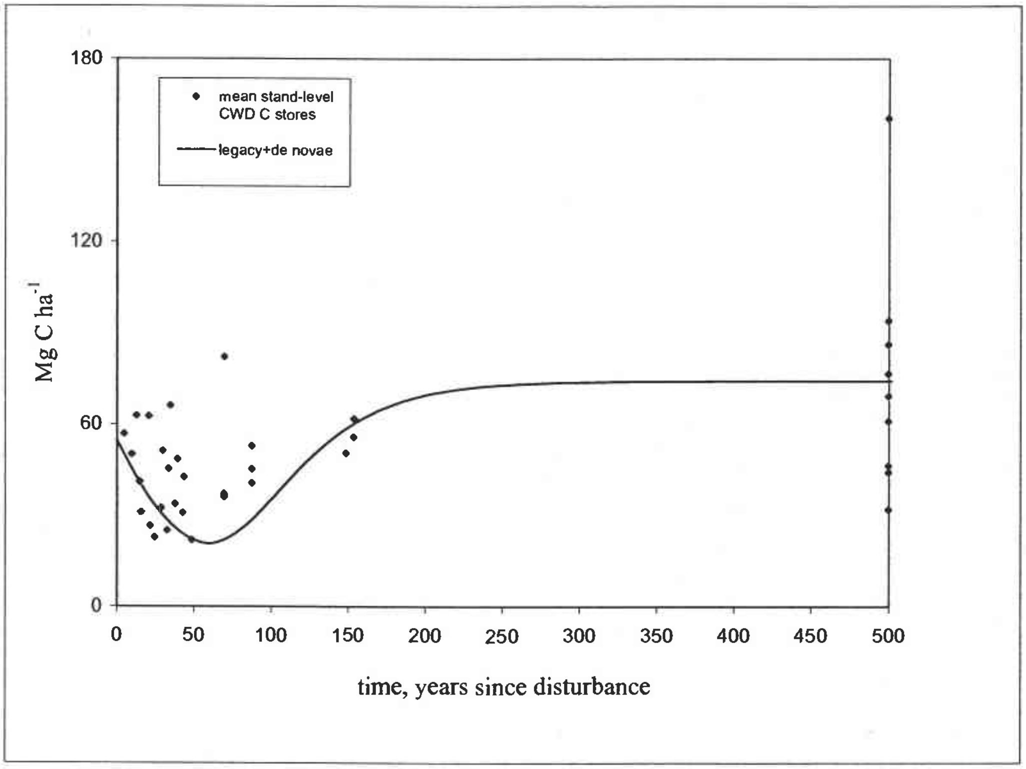

Figure 4-2: Total CWD C stores along a 500-year chronosequence of 36 *Pseudotsuga-Tsuga* dominated forest stands at Wind River, Washington. Curve represents the sum of two separate functions: decline in legacy CWD C stores after clearcutting due to decomposition (y=De-kt) and accumulation of *de novae* CWD following stand regeneration (Chapman-Richards function). The x-axis is years since disturbance, or age of the stand. The y-axis is CWD C stores in each stand.

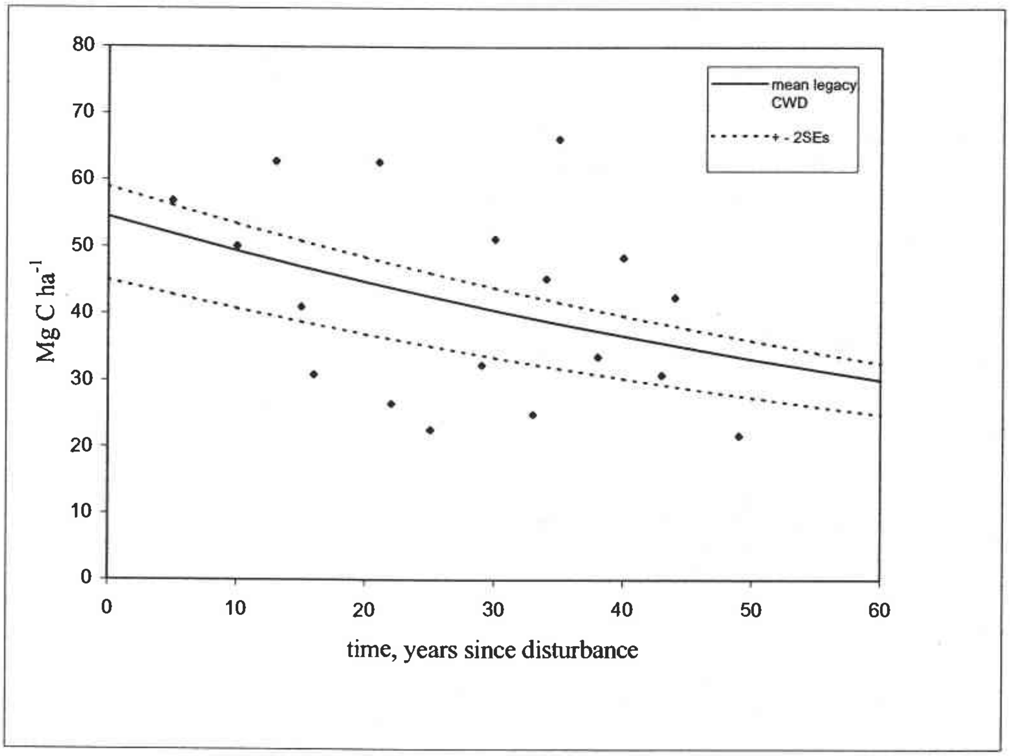

Figure 4-3: Change in estimated initial CWD C stores (stands <60 years old (Group 1)) using a simple exponential decomposition model ($y=De^{-kt}$). The weak time bias in mass of CWD C left on site after clearcutting indicated was not statistically significant. The x-axis is years since disturbance, or age of the stand. The y-axis is estimated initial CWD C stores in each stand. Data from *Pseudotsuga-Tsuga* dominated second-growth stands at Wind River, Washington.

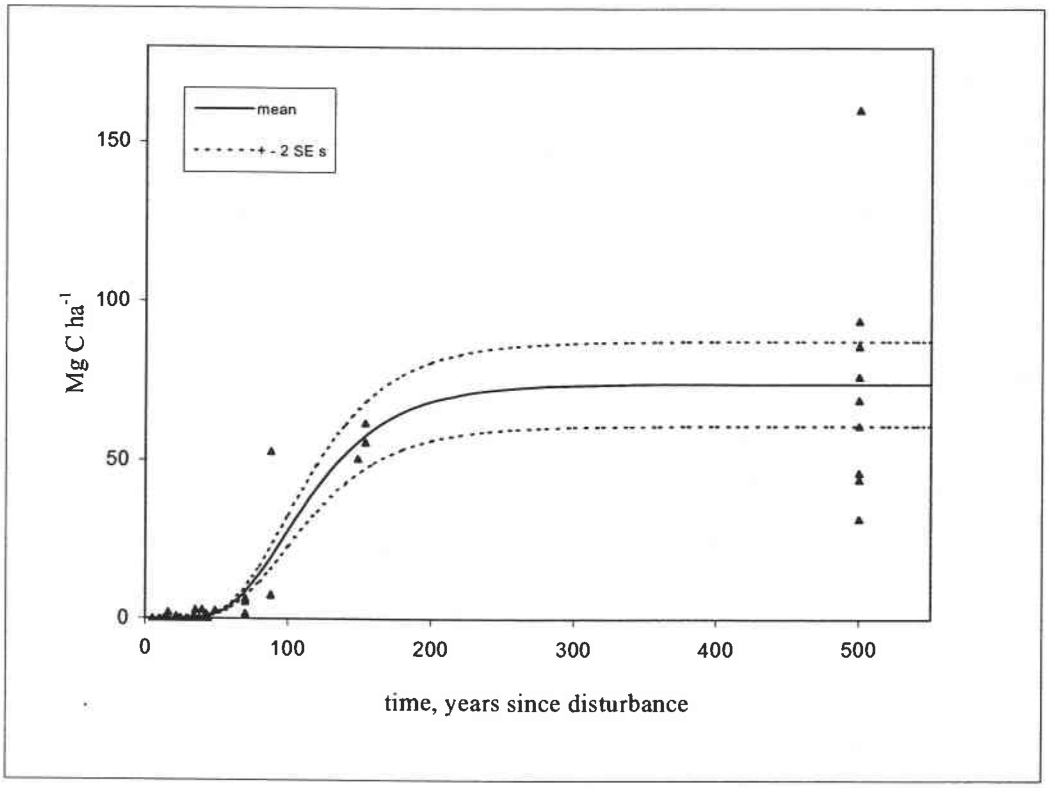

Figure 4-4: Change in *de novae* CWD C stores along a 500-year chronosequence of *Pseudotsuga-Tsuga* dominated stands at Wind River, Washington. Data was fit using a Chapman-Richards function. Mean old-growth CWD C mass was used as an asymptotic mass in the model. The x-axis is years since disturbance,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

4.6 DISCUSSION

4.6.1 Regional Live Wood and CWD

Mean live bole C stores in old-growth stands (319 Mg C ha^{-1}) was consistent with estimates from the Wind River RNA (302 Mg C ha^{-1}, Harmon et al, in review), the H. J. Andrews Experimental Forest (295-585 Mg C ha^{-1}, Grier and Logan 1977), and the regional mean of 296 Mg C ha^{-1} (Smithwick et al, accepted), but higher than other regional coniferous forests (158 Mg C ha^{-1} (*Tsuga mertensiana*, 225 year, Boone et al 1988), 222.5 Mg C ha^{-1} (*A. amabilis*, 180 years, Grier et al 1981), 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 (127 Mg C ha^{-1}, Means et al 1992; 29.5-325.8 Mg C ha^{-1}, Grier and Logan 1977; 95.5 Mg C ha^{-1}, Harmon et al (in review)) and coastal British Columbia *T. plicata*-dominated old-growth forests (182 Mg C ha^{-1}, Keenan et al 1993). Relative to 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, the protracted regeneration of existing old-growth stands (Tappeiner et al 1997) may increase variability when all old-growth stands are the same age. Some of the increased variation with forest age may have been related to the small plot area used to sample old-growth stands; while sufficient for young stands, it may have been too small for older forests.

4.6.2 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 1996). This suggests that differences in initial CWD masses maybe 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 more study is warranted.

Lack of significant difference between initial Group 1 CWD loads and old-growth CWD mass does not, however, mean CWD was not affected by disturbance. Initial CWD mass in harvested stands, for instance, included stumps, and by excluding them mean Group 1 CWD stores decline 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 in 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} (Group 1) vs. 67-281 Mg C ha^{-1} old-growth). This suggests clearcutting both reduces initial CWD loads relative to old-growth stands and reduces variability in CWD loads between harvested stands.

4.6.3 Live Biomass Accumulation

While studies of aggrading live tree biomass appear to support some models of stand development (Siren 1957, Zackrisson et al 1996), since 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 (Spies, personal communication) years while time-series data in old-growth forests suggests biomass remains relatively constant (Franklin and DeBell 1988). Our data indicate regrowth biomass approximates that found in old-growth by approximately 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. Adding 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.

4.6.4 NEP_w and Initial Conditions

The influence of initial conditions on NEP_w was investigated through a hierarchical set of four scenarios. In general, NEP 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 oxidized or moved off-site during clearcutting, 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. Given, for example, pre-harvest C stores of 300 Mg 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 clearcut 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 clearcut. Unlike Scenario 2, however, the range of CWD stores in intact old-growth forest rather than the range of CWD stores left by clearcutting are used to model NEP_w. Since clearcutting 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. Relative to 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 since 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 decomposes *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 Mg C ha^{-1} year^{-1}), and the positive NEP_w phase is dampened (peaking at 1.79 Mg C ha^{-1} year^{-1}) relative to other scenarios. While its role 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 1996). 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 feel NEP could also be used in this context, provided conservation of mass is observed so that artificial C sinks are not created (e.g. NEP measured in stands is adjusted for C stores have moved off-site).

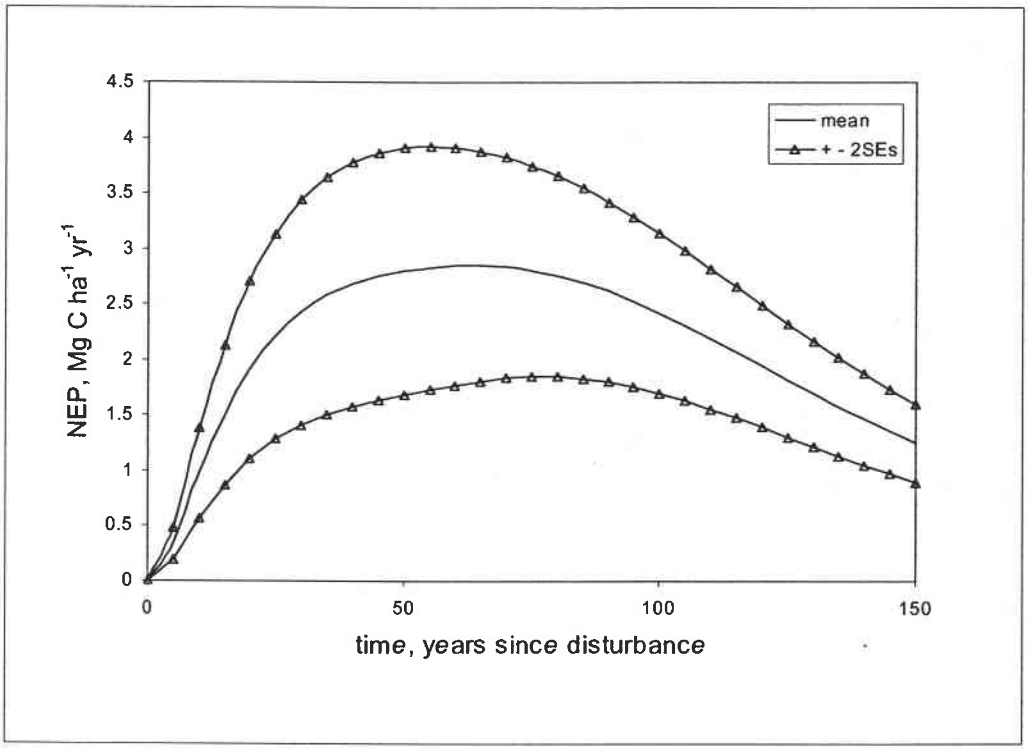

Figure. 4-5: Predicted NEPw dynamics over time (on site) during secondary succession. This scenario (1) shows live tree biomass accumulation (stand regeneration) assuming all CWD C stores are removed by logging and/or burning . Curves represent changes in NEP$_w$ based on mean growth rate derived from a Chapman-Richards function and mean asymptotic live tree mass +-2 SEs. Predicted NEPw values are based on data from a chronosequence of *Pseudotsuga-Tsuga* dominated stands at Wind River, Washington.

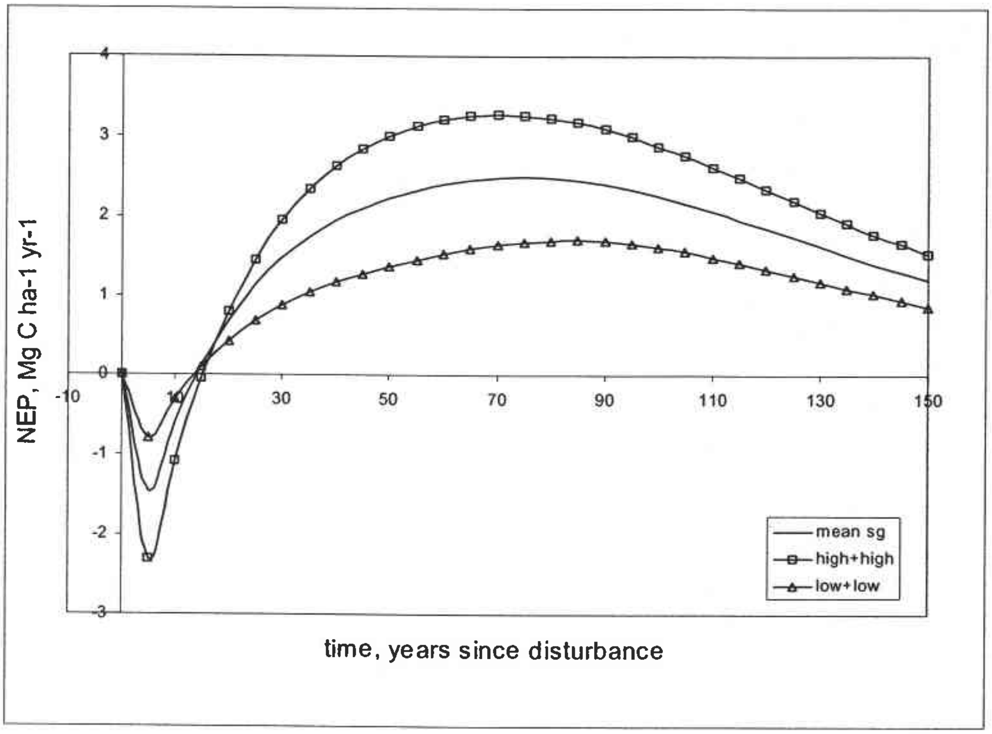

Figure 4-6: Predicted NEP_w dynamics over time (on site) during secondary succession when legacy CWD C stores were paired with live bole regeneration (Scenario 2). The solid curve describes NEP_w over succession based on mean legacy CWD C mass and mean asymptotic live bole mass. Dashed curves describe pairings of extremes of the ranges of live and CWD C stores. Totals include *de novae* CWD, but not stores removed from the site by clearcutting. Predicted NEP_w values are based on data from a chronosequence of *Pseudotsuga-Tsuga* dominated stands at Wind River, Washington.

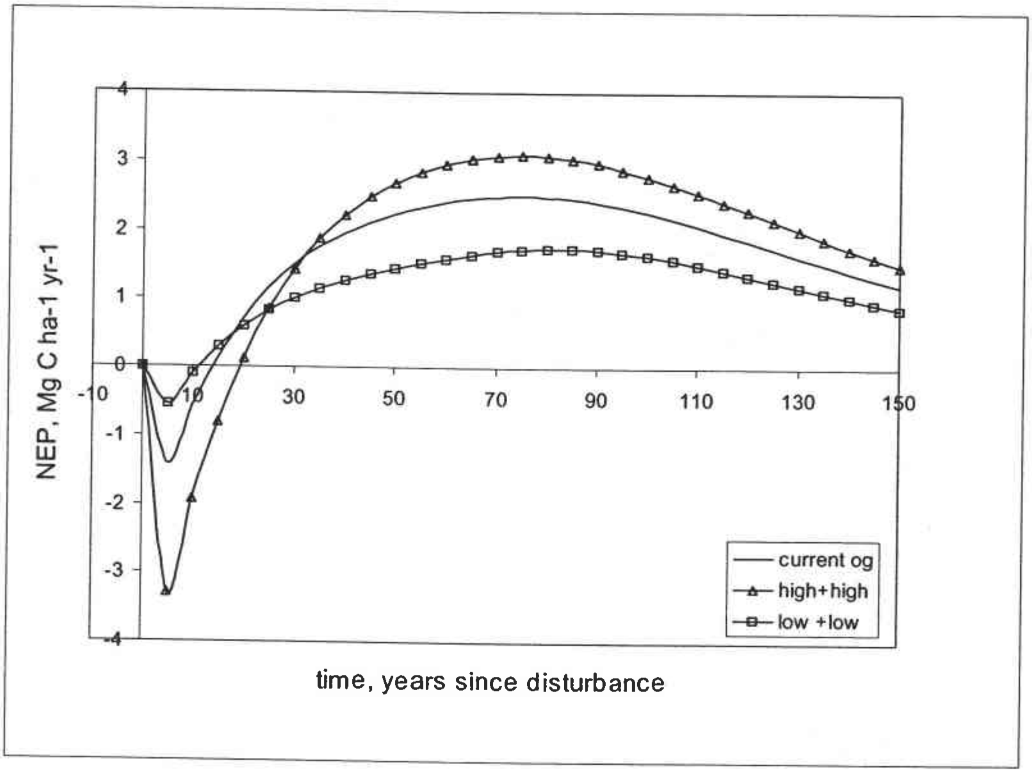

Figure 4-7: Predicted NEP_w dynamics over time (on site) during secondary succession for scenario when decomposition of old-growth CWD C stores are paired with live bole regeneration (Scenario 3). As with Scenario 2 (figure 6), the transition from negative to positive NEP_w occurred approximately 14 years after clearcutting. However, the curves, parings of means and extremes of the ranges of live and CWD old-growth C stores, show a wider range than scenario 2, indicating CWD stores are homogenized by clearcutting. C stores removed from the site by clearcutting are not included. Predicted NEP_w values are based on data from a chronosequence of *Pseudotsuga-Tsuga* dominated stands at Wind River, Washington.

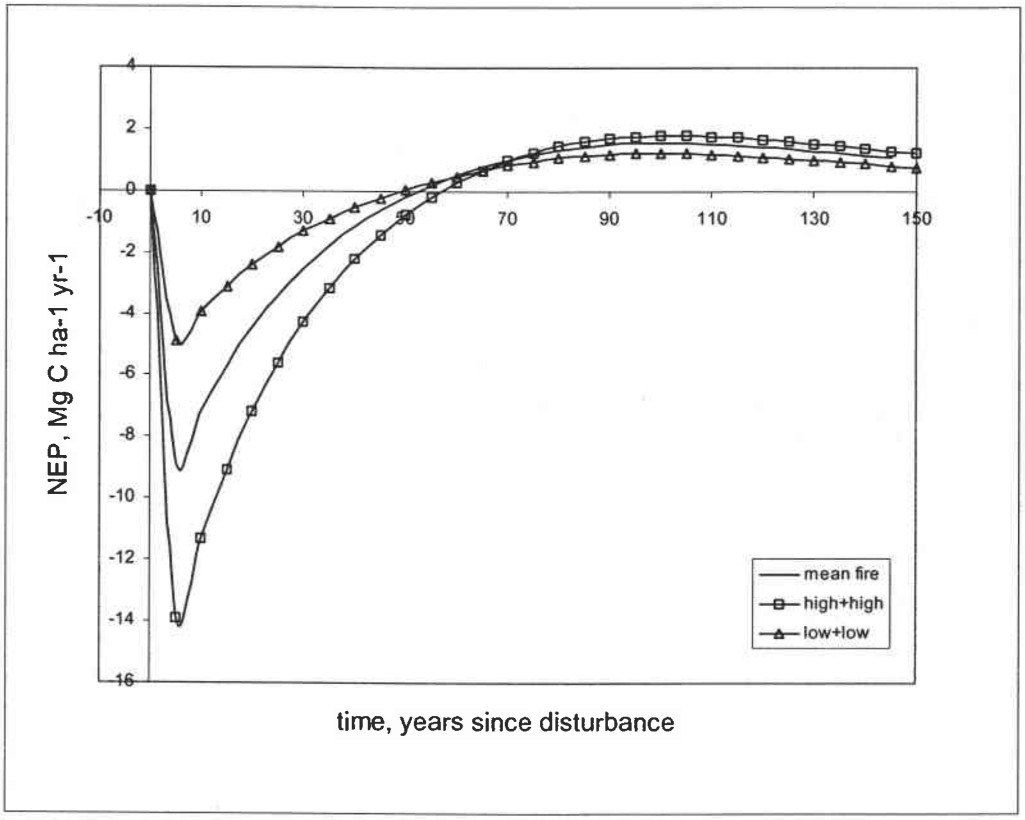

Figure 4-8: Predicted NEP_w dynamics over time (on site) during secondary succession for Scenario (4), in which all live trees in an old-growth stand are assumed killed by fire and allowed to decompose *in situ*. When these stores remained on site the transition from negative to positive NEP_w took approximate 50 years. As in other scenarios 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 at Wind River, Washington.

4.6.5 NEP$_w$ and Carbon Storage

The number of years NEP$_w$ is negative is somewhat irrelevant, however. This is 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 Mg C ha^{-1} was released and the mass of the replanted stand was trivial. Secondly, since 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 clearcutting. 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 vs. range of CWD). Scenario 4 upper C storage limits are approachable only by accumulating both *de nova* 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 they replace, must be included in assessing how forest management can mitigate increasing atmospheric CO_2. 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.

4.6.6 Improving NEP Estimates

Considering whole tree storage rather than just boles and bark would improve our NEP estimates, increasing the maximum NEP calculated by approximately one-third. Inclusion of herbaceous /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 – 8 Mg C ha^{-1} $year^{-1}$ for all scenarios.

Accumulations in forest floor litter might also add to the positive phase of NEP, whereas the fine sub-surface woody detritus pools would probably not as 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 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.

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

4.7 MANAGEMENT IMPLICATIONS AND CONCLUSIONS

Some publications considering forests as a means of atmospheric CO_2 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 CO_2 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 CO_2 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 results of these methods run contrary to flux-based estimates. While the legitimacy of flux tower and chamber-based measurement of NEP (e.g. Arneth et al 1998, Schmid et al 2000) are not disputed here, key events in a stand's history, such as during stand-destroying wildfire, may rapidly release high percentages of stored stand C. Since these events may span only days or weeks, very short relative to potential stand life spans of several centuries or longer, there is high probability 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 has 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 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 CO_2 debt that may persist for over 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 CO_2 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 replacing 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.

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CHAPTER 5

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

5.1 SUMMARY OF STUDY RESULTS

If forests are to be used to mitigate increasing atmospheric CO_2, it is essential to understand how these systems function as C sources and C sinks. This is because disturbance such as wildfire or clearcutting could release back to the atmosphere some C currently stored in forests. These release could be significant in regions such as the Pacific Northwest, for example, where total conifer forest C may exceed 1100 Mg C ha^{-1} (Smithwick et al 2001). The impacts of stand-destroying disturbance on C storage dynamics of forests during succession, however, are still disputed.

To better understand these impacts in Pacific Northwest conifer forests, we pursued three objectives on the Wind River Ranger District, Washington. First, we derived estimates of log, stump, and below-ground coarse root decomposition (k) rates. This was accomplished by examining density and volume changes in these pools across stands of age 7-50 years (post-harvest). Second, we derived estimates of live tree bole net primary productivity (NPP). This was accomplished by coring dominant tree species in 36 stands along a 400-600 year chronosequence. Third, we examined successional changes in net ecosystem productivity (NEP) in old-growth, as well as in regenerating second-growth following removal of 400-600 year old trees by clearcut logging and wildfire. This was accomplished by measuring live and dead woody forest

C pools along the chronosequence and combining this data with decomposition and growth rates in simple statistical models of live and dead wood accumulation and decomposition. Models were then used to predict changes in the woody component of NEP, which we call NEP_w, to estimate maximum and minimum stand-level trajectories of NEP.

In this study of several dominant Pacific Northwest conifer species, above-ground logs and stumps decomposed at similar rates within a species (P. menziesii: k= -0.013, T. heterophylla: *k*= -0.036). Relative to above ground logs and stumps, below-ground 3-8 cm coarse roots of the same species decomposed more slowly (*P. menziesii*; *k*= -0.008 yr^{-1}, *T. heterophylla*: *k*= -0.017 yr^{-1}). We also found that decomposition rates varied by species, with *T. heterophylla* CWD decomposing more rapidly than *P. menziesii* both above and below ground, indicating species composition affects C storage.

Substituting log decomposition rates (*k*) into C flux calculations when stump *k* are unknown may thus result in reasonable estimates of C flux from stumps in these forests. Substitution of log *k* values, however, are not appropriate for root decomposition even when of the same species since, given our results, assuming coarse root *k* approximated log *k* would overestimate C flux from roots to the atmosphere. Use of *P. menziesii* log *k* to estimate C flux from a coarse root store of 100 Mg C ha^{-1} , for instance, would overestimate the flux by 0.5 Mg C ha^{-1} yr^{-1} the first year after harvest. Since many stumps currently decomposing on the landscape resulted from clearing large-diameter old-growth trees, and coarse root mass is approximately 20% of total live bole mass, inappropriate *k* substitutions could lead to significant errors in flux estimates, potentially resulting in misclassification of C sources as C sinks.

Study of net primary productivity in tree boles of dominant conifer species (NPP_b) showed that NPP_b varied with successional stage, consistent with time series data from the same region (e.g. Acker et al, accepted). NPP_b rose rapidly early in succession, peaked 20-30 years after the stand-initiating disturbance, then declined to a relatively stable level 70-150 years after disturbance. Mean NPP_b of the nine old-growth stands (2.7 Mg C ha^{-1} yr^{-1}) was lower than mean NPP of 30-50 year-old stands (4.1 Mg C ha^{-1} yr^{-1}) but similar to 65-150 year-old stands (3.0 Mg C ha^{-1} yr^{-1}).

Mean stand-level radial increment width also indicated that NPP_b of old-growth stands (neglecting mortality) can increase, decrease, or remain relatively constant depending. Based on 5-year increments for the previous fifteen years, the majority of old-growth stands sampled showed small radial growth increases over time.

In the case of NEP_w, the transition from negative to positive occurred between 0 and 57 years after disturbance. The timing of this transition decreased as live-tree growth rates increased and increased as CWD remaining after disturbance increased. Maximum and minimum NEP_w for all scenarios were 3.9 Mg C ha^{-1} yr^{-1} and –14.1 Mg C ha^{-1} yr^{-1}, respectively. Maximum live and total wood C stores of 319 Mg C ha^{-1} and 393 Mg C ha^{-1}, respectively, were reached approximately 200 years after disturbance. Decomposition rates (*k*) of CWD ranged from 0.013-0.043 yr^{-1} for individual stands. At a rotation age of 80 years, regenerating stands stored approximately half the wood C as remaining nearby old-growth stands (predominant age 500 years), indicating conversion of the latter forests to younger managed forests results in a significant net release of C to the atmosphere.

While forest initiating conditions influence the number of years required to switch from negative to positive NEP, forest growth rates, and CWD decomposition rates, focusing strictly on this transition obscures large C debts (i.e. reductions to pre-disturbance stand C stores through conversion to CO_2 by heterotrophic respiration or fire) incurred by stand destroying disturbances. Our results indicate that the C source-sink status of forest stands must thus be defined at temporal scales reflecting succession. This is because large fractions of a stand's stored C can be rapidly lost in key short-term events during succession such as wildfire. Since these events may last only days or weeks, very short relative to potential stand life spans, there is high probability short-duration monitoring regardless of method will miss these rapid changes in C stores. Thus, while our results do not invalidate short-term measurements of NEP, relying on 'instantaneous' estimates to determine a stand's C source-C sink status may result in actual C sources being classified as C sinks.

Finally, if during succession stands do not regain their pre-disturbance C stores, then C has been lost from the system. This is particularly significant during conversion of old-growth forest to second-growth forest, but has often been obscured by the many fates of woody stores taken off-site during harvest. Use of pre-harvest C stores to set upper and lower limits on C flux from slash and forest products, as in Chapter 4, Scenarios 1and 4, may help clarify this.

5.2 MAXIMIZING AND PRESERVING *IN SITU* TERRESTRIAL C STORES

Since forests store the majority of relatively exchangeable C in live trees and CWD (Harmon et al 1986, Johnson and Curtis 2001), our data indicate stands where trees are large and where relatively high CWD loads can be maintained would represent one option for maximizing *in situ* C storage. Given the high biomass of mature and old-growth stands relative to younger stands indicated by our NEP_w results, landscape woody C stores would be maximized in Pacific Northwest forests by using stands of these successional phases. This result is significant since while CO_2 is only one many greenhouse gases, predicted increase in global mean temperatures prior to c. 2100 are eventually expected to result largely from atmospheric CO_2 enrichment (Hansen 2000, IPCC 2001). Thus, identifying major planetary C stores, and describing how these stores function as C sources and sinks of CO_2 over time is an essential component of climate change analysis.

If using ecosystems to sequester and store atmospheric C becomes public policy, interest will focus on those systems where maximum benefits are derived. Thus, with high biomass relative to many boreal, temperate, and tropical forests (Harmon et al 1986, Schlesinger 1991), low rates of woody decomposition (Graham and Cromack 1982, Chen et al 2001), and adequate land area to realize benefits, Pacific Northwest conifer forests offer many qualities relevant to achieving such goals.

Even treeless systems may store C, however. In grasslands, for example, where herbaceous matter accumulates but vegetation biomass in low (Chadwick et al 1994), soil C may be key to accumulating photosynthetically sequestered atmospheric C. This pool can store significant amounts of C, averaging 35% of total system C in Pacific Northwest forests (Smithwick et al, accepted) and thought to hold roughly 1,200-1,500 Pg of terrestrial C globally (Eswaran et al 1993, Dixon et al 1994). Bicarbonate weathering of soil silicates and other processes that transfer soil C into long-term terrestrial storage (Chadwick et al 1994) might also be exploited to maximize C storage in such systems where soil C is a significant pool. Where other vegetation layers achieve high biomass relative to tree mass (e.g. Hobbie and Chapin 1998, Ringrose et al 1998), maximizing C storage may focus on relevant successional phases, vegetation components, or temporal dynamics. In all cases, however, maximizing C storage involves manipulation of system C pools, which in turn involves understanding how these pools function in space and time. Since climate also strongly influences biomass and productivity (Lambers et al 1998), both of which are relevant to attaining C storage goals, such goals will need to be adaptive, tracking climate-induced changes over time. This is because forecasted perturbations to ecosystems resulting from climatic change (IPCC 2001) may, for example, attenuate C storage in such pools as live trees and CWD. Under more extreme but related effects such as latitudinal or elevational range contraction (Davis 1986) and complex reorganization of forest structure and species composition (Rolin et al 2001, Wimberly and Spies 2001) C storage may shift to other pools.

While forest C storage might also be increased by intensive management (e.g. Johnsen 2001), fertilization, competition control, genetic selection, and other factors used to enhance tree growth (e.g. Makipaa et al 1998, Oechel et al 1994) must be evaluated to ensure that hidden C losses are not incurred. Carbon fluxes to the atmosphere resulting from fertilizer manufacture (either directly or indirectly through burning fossil fuels to generate electricity), for example, count against C sequestration gains resulting from these fertilizers (Marland and Marland 1992). This would hold even if sites of manufacture and application were widely separated in space and time.

More frequent logging may also damage adjacent forest, indirectly compromising these C stores (Nepstad et al 1999). In addition, it is unclear how much C storage would be gained from growing trees faster to marketable sizes if allometrics were preserved. This is because C pulses from stumps, roots, foliage, and other detrital pools would still be similar to those released from trees growing more slowly to similar diameter unless rates of decomposition also declined. Variations on this theme, such as storing C in coarse roots by balancing slow root decomposition against reduced rotation length, may need to be considered against diameter effects on *k*. As indicated here, smaller roots decomposed faster than larger roots. Thus, shorter rotations producing smaller trees with proportionately smaller and faster decomposing roots would affect C storage goals (Marland and Marland 1992). Conversely, root diameter-*k* relationships in species we studied may differ for other regions or species.

Maximum C storage capacity resulting from vegetation type, climate, disturbance regime, and other factors is also a theoretical number potentially very different from realizable C storage. Rapid growth rates of many tropical tree species and significant biomass of many tropical forests (Korner 1998, Clark et al 2001a), for example, favor use of such forests to sequester and store atmospheric C. It is estimated, however, fifty percent of the land area historically covered by tropical forests is in some stage of recovery from human-related disturbance (Jepma 1995) and deforestation rates remain high throughout the tropics (Barnes 1990, Puig 2001). Thus, many ecosystems of high C storage potential may be unsuitable unless complex social policy issues are addressed.

5.3 IMPLICATIONS FOR MANAGEMENT OF ECOSYSTEM C STORES

As indicated in earlier chapters, C storage in the woody components of forests results from a balance between atmospheric C sequestration and simultaneous heterotroph-mediated C release. Forest C storage is thus sensitive to factors driving this balance point towards a new equilibrium. In the Pacific Northwest, for example, converting older forests to short-rotation forests such that stand-level C storage declined relative to base-line stores (e.g. older forest), released an estimated 2 Pg of C (Harmon et al 1996), a result confirmed by our study of NEP_w. Thus, some components of policies aimed at preserving C in these forests may include stopping further harvest of old-growth and increasing the mean age of forests at landscape scales (Harmon 2001).

Soils, shrubs, and other C pools are no less vulnerable than tree boles and CWD to disturbances rebalancing system C sequestration and C loss, however. While some soil C may be exchanged slowly relative to successional processes (Johnson and Curtis 2001), over-grazing (Li et al 1997), declining rainfall and sulfur fertilization (Bailey et al 2001), or disruption of weathering processes that divert soil C into long-term storage (Chadwick et al 1994), could deplete these stores. Similarly, rapid growth- and decomposition-related cycling of C in tropical forests (e.g. Clark and Clark 1999) may be desirable C storage attributes, but lower biomass relative to Pacific Northwest forests (Schlesinger, 1991) could require storing C in multiple vegetation layers across wide areas to achieve similar goals. Rates of tropical deforestation (Trejo and Dirzo 2000, Li 1995) relative to regrowth and secondary forest biomass (Silver et al 2000), as well as erosion and productivity declines of old tropical soils that often follow (Islam et al

2001, Barbosa et al 2000), may further limit the range of suitable sites. In addition, interaction between forests and economies dependent on manufacture of wood products may lead to destructive positive feedback. As climate-related forest death (Urban et al 1993) released forest C stores back to the atmosphere, for example, pressure on any persisting remnant forests would increase in the form of misguided government polices, energy needs, and local resource needs (Stewart and Maine 1996), further eroding C stores. Thus, few ecosystem C stores are invulnerable to release, and interaction between complex social and natural drivers may lead to such releases. Since forests hold an estimated 80% of terrestrial above-ground C and occupy over 4 billion ha globally (Dixon et al 1994), however, these systems offer a relatively accessible, inexpensive, and low-technology way to sequester atmospheric CO_2 if some factors limiting C storage in forests can be resolved.

Since the mass of atmospheric C is thought to be of similar magnitude to that stored in the terrestrial biosphere (e.g. Berner and Lasaga 1989), appreciably reducing atmospheric C through forest manipulation will require application of C storage policies at large spatial scales. Data collected at the stand level, as in this study, can be used in predicting landscape C storage, but such a change in scale requires translating C storage and disturbance effects from the stand to the landscape, as has been recently described by Harmon (2001). Succession and stochastic variation in forests also point to how spatial and temporal scale affects C storage. For example, waves of tree mortality from adjacent clearcuts or insect epidemics could creep into old-growth stands preserved to conserve their high C stores. If these transfers of live trees in preserved old-growth stands to the CWD pool exceeded normal mortality rates, total system C stores could be eroded and thus decline from projected C storage goals. For this reason, considering both individual stands as well as surrounding matrix forest in harvest planning is essential when managing forest for C storage. Carbon sequestration accounting also cannot be considered in isolation from policies governing ecosystem management on the matrix of lands under private, state, and federal control. Eastern U.S. forests now recovering on abandoned agricultural land could be cut and converted back to agriculture or other uses, (Houghton and Hackler 2000) as national priorities change. Thus forests thought to contribute significantly toward current U.S. terrestrial C sinks, would be lost and cannot be viewed as permanent C reservoirs (Schimel et al 2000).

Using ecosystem C stores under the current climate to predict future stores can also be misleading since future stores will be influenced by future climate. There is, for example, no evidence that climate of the temperate zone has oscillated around a climatic mean during the last 20,000 years (Davis 1986). Thus, both rates of C accumulation or loss and absolute C storage outlined in our results may change over time. Forest C storage reference states against which these changes can be weighed must thus be defined. Otherwise, it will remain unclear whether regions currently absorbing C should count as sinks. This is because, due to the nature of NEP (Chapter 4), forest C sink phases are often preceded by C source phases, such that in reality regions with positive C flow (sink status) are still recovering from previously incurred C debts. At least in the case of forests existing prior to settlement, these reference conditions should be equivalent to old-growth C stores since C lost during disturbances such as logging is otherwise not counted and C sequestration will appear inflated. Thus, global-level analysis of C sources and C sinks indicating C sequestration in northern latitude temperate forests may be balancing C released by tropical deforestation (Jarvis and Dewar 1993, Trans 1993, Gifford 1994) may not reflect such stand-level mechanisms. Carbon sources and sinks indicated by such analyses may thus be misleading.

Finally, while C storage dynamics of ecosystem soils are still poorly known, soils underlie vegetation of many ecosystems and this connection makes them relevant to vegetation C management. This is because land use such as logging may mix soil organic and mineral horizons, potentially either liberating or burying C stored in the soil profile (Federer 1984, Johnson et al 1995) or creating more stable forms such as charcoal (Zackrisson et al 1996, Schmidt and Nyack 2000). Under other management, simultaneous increases and declines of C stores in various soil horizons point to linkages between soil C distribution and overlying vegetation (Hamburg 1984), yet potentially confuse whether C has been gained or lost. Recent work indicating at least some soil C is released slowly relative to the time scale of forest disturbance and succession (Johnson and Curtis 2001), but opinion is mixed (e.g. Davidson et al 2000, Giardina and Ryan 2000), and sequestration of C by deep-rooted South American grasses may account for some of the so called missing terrestrial C sink (Fisher et al 1994) further illustrates the continued relevance of soil C dynamics to C storage policy.

5.4 OTHER MITIGATION STRATEGIES

There are also alternatives to forests for sequestering and storing atmospheric C. Since CO_2 is highly soluble and world oceans already store approximately 38,000 times (Post et al 1990) the current atmospheric mass of CO_2, for example, further storage of atmospheric CO_2 in world oceans is being considered. As with manipulating forests to increase C storage, however, chemical and physical limits (e.g. CO_2 solubility dependence on temperature), as well as other factors restrict the mass of CO_2 that can be stored. Re-injection of CO_2 into the sea floor, for example, is already used to limit emission of CO_2 drawn out of strata from CH_4 wells (Herzog et al 2000), but requires porous rocks. Routing atmospheric CO_2 into deep ocean water is being considered (e.g. Marchetti 1977), but effects on marine life, both directly and through increased ocean water acidity, need further study to ensure CO_2 mitigation strategies are not more harmful to the biosphere than global warming (Herzog et al 2000). A variation, using surface water injection of CO_2 to remove atmospheric CO_2, requires more detailed study of ocean current to understand its effectiveness (Haugan and Drange 1992). Fertilization of iron-poor ocean waters to stimulate phytoplankton growth has also been proposed, but simulations indicate only modest reductions of atmospheric CO_2 after 100 years of such treatment (Peng and Broecker 1991). Wood could also be stored in landfills, under agricultural land, in deep lakes, or other relatively anoxic environments where decomposition is reduced (e.g. Micales and Skog 1997). There is public resistance to building or living on landfills, however, and excavation could release more C than is gained in wood burial by disturbing soil profiles by exposing C deep in the soil profile to oxidation and other surface processes that could return such C to the atmosphere. Thus, choice of CO_2 mitigation strategy is as much a question of cultural values and objectives as science.

Given the advantages and disadvantages of other C storage options, forest offer relatively obtainable, economical C sequestration that can be implemented on the existing land base. This strategy is still under discussion, however, as the C sequestration benefits predicted by some C storage models require very productive forests and highly efficient harvest methods (Marland and Marland 1992).

5.5 POLICY IMPLICATIONS

If increased frequency of extreme weather events, rising sea levels, extinctions, and other predictions resulting from increased atmospheric CO_2 concentrations are real, and mounting evidence suggests this is the case (Easterling et al 1997, Easterling et al 2000), the political and monetary value of sequestrating atmospheric C will increase since land area, fresh water supplies, food production, and other human interests may be threatened. Due to this increase in value, ever more refined estimates of both ecosystem C losses and C gains will be required because from these component system C source-sink status can be calculated.

Full and accurate accounting of global C fluxes, however, still does not indicate which policy to pursue. This is because answers to policy questions, even those with scientific underpinnings, reflect political and social values. It is hypothesized, for example, overfishing would stop if subsides were withdrawn since money-losing jobs would be abandoned (Fluharty 2000, Murawski 2000). Despite data consistent with stock declines due to overfishing (e.g. Lae 1997, Myers et al 1996), however, such practices continue. National interests have also slowed consensus on international issues such as global warming. November 2000 Kyoto Protocol negotiations, for example, collapsed largely due to United States insistence on credit for existing forest and soil C sinks, contrary to Kyoto goals of establishing new sinks to off-set emissions (Bolin 2000). Thus, depending on where value is assigned, destructive or short-sighted policies or national self-interests may prevail even when contrary evidence exists. This is particularly harmful when a single interest group is given full veto power.

While C credits offer a useful tool to encourage C sequestration, it is also possible unforeseen consequences may arise from this subsidy. Conversion of too much agricultural land to forest land, or conversion of other ecosystems to plantation-style forests, for example, could have the undesirable consequences of limiting food supplies or placing C management at odds with species conservation. If not addressed in the initial language of C policies, such trends may be difficult to reverse once initiated due to increasing landowner dependence on such subsidies and the perception that retraction of such policies are contrary to reducing global warming.

Success of policies designed to mitigate global warming also depend on cultural acceptance. Limits on CO_2 emissions called for by the Kyoto Protocol (i.e. 95% reduction of 1990 levels, Bolin 1998), for example, are viewed as a challenging target. Yet climate-change related benefits realized by achieving this goal may be modest (Wigley 1998) and CO_2 reductions 30 times larger may be needed to slow the pace of climatic warming (Malakoff 1997). Local users of ecosystems may also not view these systems as degraded, further complicating C storage efforts (Fearnside 1996). Uncertainties over C sources and C sinks, conflicting industry and environmental objectives, mixed public opinion or indifference, and increasing tension over property rights and public vs. private land-use benefits all threaten adoption of C policy management (Duinker 1996). If appreciable reduction of atmospheric C is to be achieved by manipulating ecosystems, there is a pressing need for global C policy so that coordinated large-scale action can begin. Otherwise, C negotiations will continue to founder over differences in North-South latitude responsibilities for C reductions, confusion over land use change accounting will persist, and erosion of ecosystems by an increasing human population will continue to reinforce C-related climatic effects.

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APPENDICES

APPENDIX 1

Map of Study Region

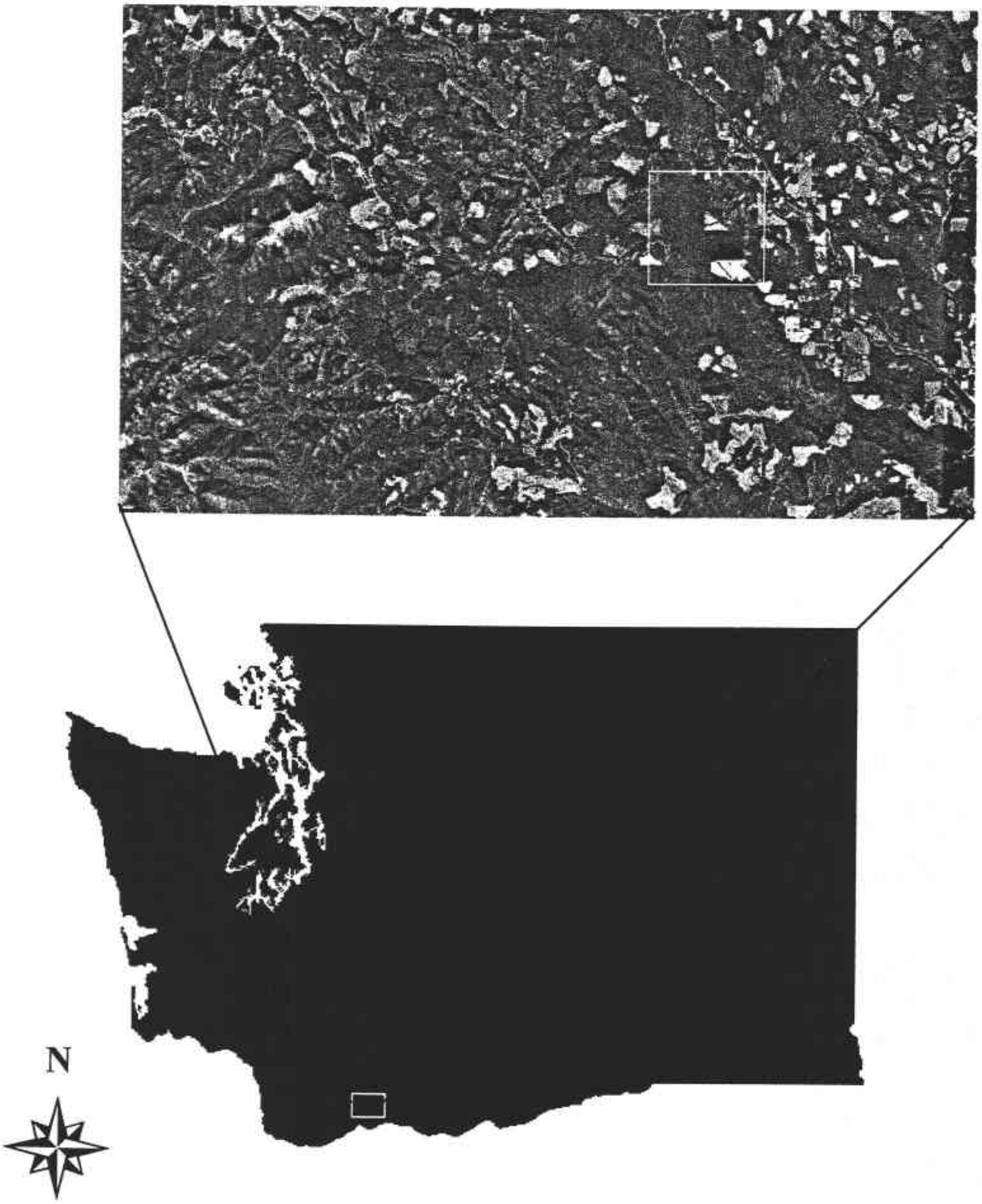

Figure 1-1: Study region in relation to Washington State, U.S.A. Magnified region shows distribution of clearcuts and T.T. Munger Research Natural Area (RNA) (inscribed in white box). The roughly circular region west of the RNA is the Wind River Experimental Forest, Trout Creek Division. Photo courtesy of U.S. Geological Service.

APPENDIX 2

Plot dimensions and sampling design.

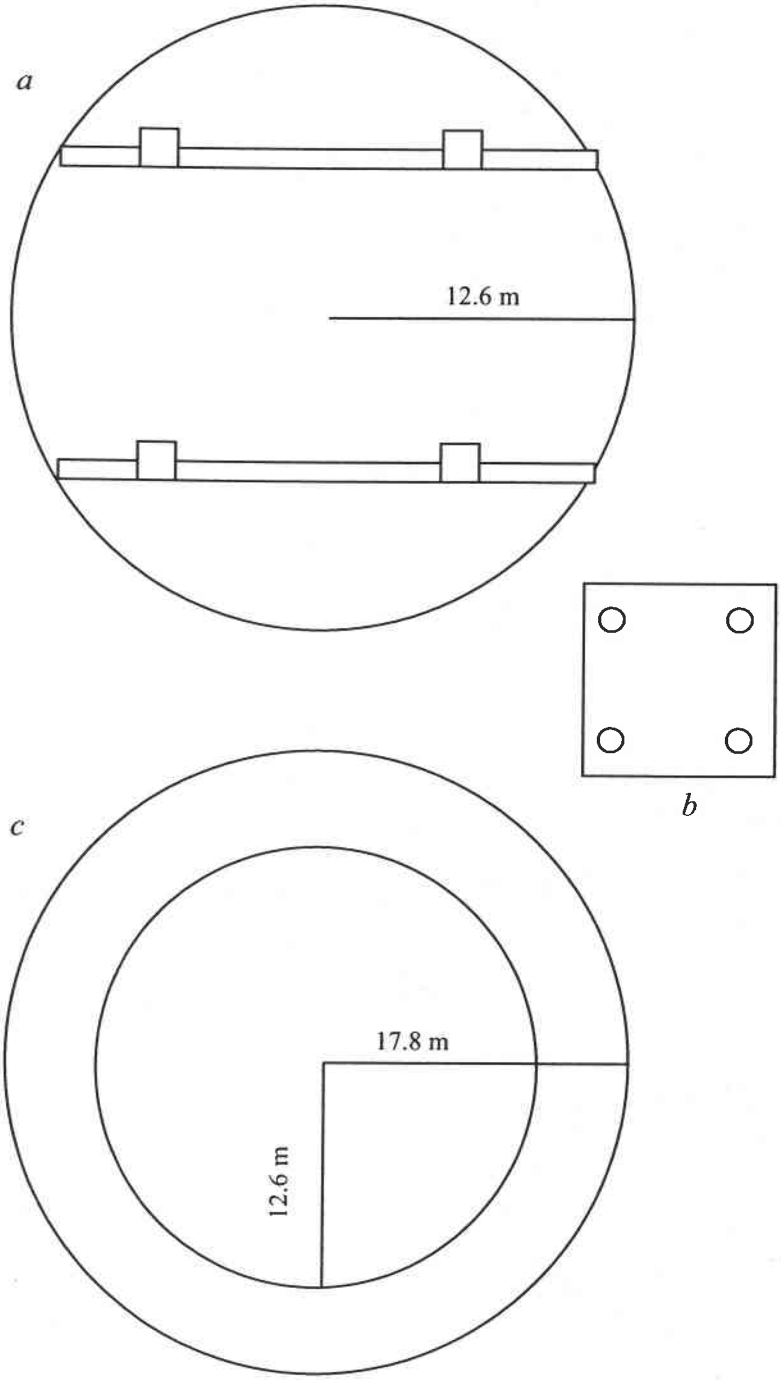

Figure 2-1: Spatial arrangement of sampling system: a) inner circle magnified to show belt transect used to inventory shrub stems and 1 m^2 quadrants used to inventory herbaceous species and fine wood debris, b) magnified 1 m^2 quadrant showing location of litter cores, c) full view of individual plot showing concentric live tree (radius=12.6 m, 0.05 ha) and CWD (radius=17.8 m, 0.1 ha) sample zones.