Available online at www.sciencedirect.com

SCIENCE DIRECT®

Forest Ecology and Management 209 (2005) 273–291

Forest Ecology and Management

www.elsevier.com/locate/foreco

Variability in net primary production and carbon storage in biomass across Oregon forests—an assessment integrating data from forest inventories, intensive sites, and remote sensing

S. Van Tuyl [a,*], B.E. Law [a], D.P. Turner [a], A.I. Gitelman [b]

[a] *Department of Forest Science, Oregon State University, Corvallis, OR 97331, USA*
[b] *Department of Statistics, Oregon State University, Corvallis, OR 97331, USA*

Received 16 September 2004; received in revised form 4 February 2005; accepted 4 February 2005

Abstract

We used a combination of data from USDA Forest Service inventories, intensive chronosequences, extensive sites, and satellite remote sensing, to estimate biomass and net primary production (NPP) for the forested region of western Oregon. The study area was divided into four ecoregions differing widely in climatic conditions and management regime. The forest age distributions (as derived from inventory data) differed by ecozone with fewer old stands in the Coast Range and the East Cascades, and a relatively uniform distribution of ages from 0 to 815 in the Cascade Mountains. Age distributions also differed by land ownership, with fewer old stands on non-federal lands than on national forest lands. Estimated biomass increased rapidly in early stand development and tended to stabilize after about 200 years. Peak biomass in the semi-arid East Cascades was about one-third that of the other ecoregions (median biomass at asymptote ~9 and ~25 kg C m^{-2}, respectively). The timing and magnitude of maximum net primary production also varied by ecoregion, with the high productivity Coast Range forests reaching a maximum NPP before 30 years of age (median ~1 kg C m^{-2} y^{-1}), and the low productivity East Cascades reaching a maximum NPP between 80 and 100 years (median ~0.3 kg C m^{-2} y^{-1}). Productivity was generally lower in older stands with the exception of the East Cascades ecoregion where, contrary to the paradigm of age-related decline in forest growth, the oldest stands had the highest NPP. The East Cascades also differed from the other ecoregions in that the proportion of NPP allocated belowground decreased rather than increased with stand age. This study demonstrates the value of combining data from intensive and extensive measurement sites for improved estimates of carbon stocks and fluxes as well as improved parameterization of process models used in scaling carbon flux over broad regions.

Keywords: Biomass; Net primary production; Forest inventory; Carbon storage; Carbon flux; Pacific Northwest

1. Introduction

Recent terrestrial carbon cycle research has aimed at improved estimates of carbon storage and fluxes,

---

* Corresponding author. Present address: USDA Forest Service, Northern Global Change Research Program, 11 Campus Boulevard, Suite 200, Newtown Square, PA 19073, USA. Tel.: +1 610 557 4073; fax: +1 610 557 4095.

E-mail address: svantuyl@fs.fed.us (S. Van Tuyl).

0378-1127/$ – see front matter © 2005 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2005.02.002

and deeper examination of variation across regions and continents. The inevitable trade-off between the intensity of measurements at a given site and the number of sites that can be studied means that both intensive and extensive measurements approaches are needed for regional analyses.

Forest inventories cover a range of conditions and disturbance regimes, and they tend to include measurements of many of the basic components needed to estimate biomass and net primary production (NPP). In the United State (US) and elsewhere, inventory data have been used for making estimates of biomass and productivity at various scales from regional (Brown et al., 1997, 1999; Jenkins et al., 2001) to continental (Turner et al., 1995; Ni et al., 2001). These estimates can potentially be improved by including data from research sites where more intensive measurement programs have been implemented. For example, belowground biomass is particularly difficult to quantify and is typically assumed to be a fixed fraction of aboveground biomass and productivity (e.g., Jenkins et al., 2001) or ignored (e.g., Ni et al., 2001) for lack of better information. Intensive measurement sites may be particularly useful if stratified across representative forest types and environmental conditions.

In this study, we used forest inventory data, supplementary data from 96 plots in different age classes and forest types, and remotely sensed leaf area index to estimate biomass and NPP in the forested region of western Oregon. We explored broad patterns of biomass and NPP associated with stand age, ecoregion, and type of land-ownership. Finally we estimated the uncertainty associated with assumptions made in our methodology.

2. Methods

2.1. Study area

The study region is a 120,000 km^2 area covering all of the state of Oregon west of the 120th meridian (Fig. 1). Sixty-one percent of the study area is forested land, and 60% of that is publicly owned versus 40% privately owned (Powell et al., 1993). The remainder is considered non-forest (alpine, rock, etc.), woodland, agricultural, or urban (Law et al., 2005).

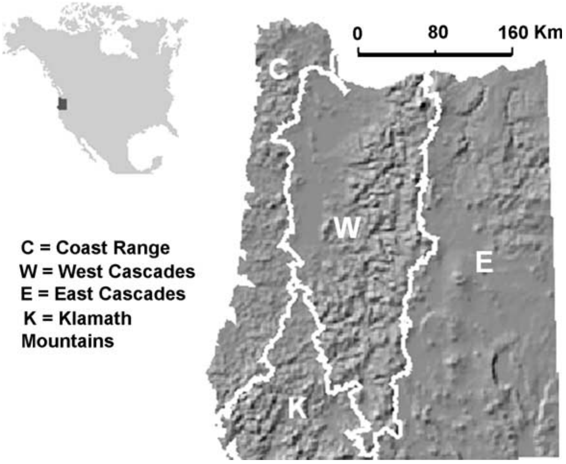

Fig. 1. Study area. Study region with the boundaries of four ecoregions identified.

The study region crosses a steep climatic gradient, ranging from maritime coastal forests in the west to semi-arid forests and woodlands in the east within approximately 250 km. Annual precipitation ranges from 2110 mm at the coast to 530 mm in the semi-arid ponderosa pine region on the east side of the Cascade Mountains. This range in climate in turn results in a large range in forest biomass and productivity, as determined from six study sites along the Oregon Transect (Runyon et al., 1994).

The study region includes long-term forest inventory plots as part of the Forest Inventory and Analysis program (FIA; http://fia.fs.fed.us) on non-federal lands and Current Vegetation Survey plots (CVS; http://www.fs.fed.us/r6/survey) on National Forest lands. Both of the inventory programs locate plots based on a systematic sampling design, though in our study area the plot selection methods differ in two ways. First, the spatial sampling intensity of the CVS inventory is four times denser than that of the FIA inventory, resulting in 3700 CVS plots and 900 FIA plots in the study area. Second, the FIA inventory excludes non-forested areas from its sampling while the CVS inventory locates plots in all cover types. The FIA data used for this project were collected between 1995 and 1997 while the CVS data were collected between 1993 and 1997.

We developed our own sampling program to supplement the inventory plots with measurements of additional carbon budget components, with 96 plots selected within the study area using a hierarchical random sampling design based on forest type, forest age, and climate regime (Law et al., 2005). Thirty-six of the plots were in three chronosequences: One in the maritime coastal forest, one in the west Cascade Mountains, and one in the semiarid east Cascade Mountains (three chronosequences, each with four age classes and three replications; Law et al., 2005). Of the 96 supplementary plots, the 36 chronosequence plots are referred to as ''intensive plots'' and the remaining 60 supplementary plots are referred to here as ''extensive plots.'' Details of sampling methods and analysis are in Law et al. (2003, 2005). Fig. 2 shows the distribution of stand ages for the forest inventory plots and our additional plots by ecoregion.

2.2. Stand age

We defined stand age as the approximate time since the last stand replacing disturbance. Both the FIA and CVS inventory programs report ages for a subset of the trees on each inventory plot. We used this data to estimate stand age for each inventory plot by determining the average age of the oldest 10% of trees on a plot, similar to a method used by Spies and Franklin (1991; average age of dominant trees). In a separate analysis, the results of a simple linear regression of predicted stand ages versus time since stand replacing disturbance for 15 plots (a subset of the 36 intensive plots that had reliable, independent stand ages) resulted in an intercept coefficient that was not significantly different from zero ($p = 0.58$) and a slope coefficient close to 1 ($p < 0.001$, slope 0.95, standard error of slope 0.09, $R^2 = 0.88$). These results suggest that our estimates of age are representative of time since disturbance, although the range of ages tested here is smaller than in our full study (0–250 years versus 0–815 years).

2.3. Biomass and productivity

The sampling methods for the two inventories are generally the same. In both inventories, components of data necessary for making broad estimates of biomass and productivity are collected (e.g., stem diameter, height, growth, etc.). Field sampling protocols for the FIA data used here employ variable radius sampling

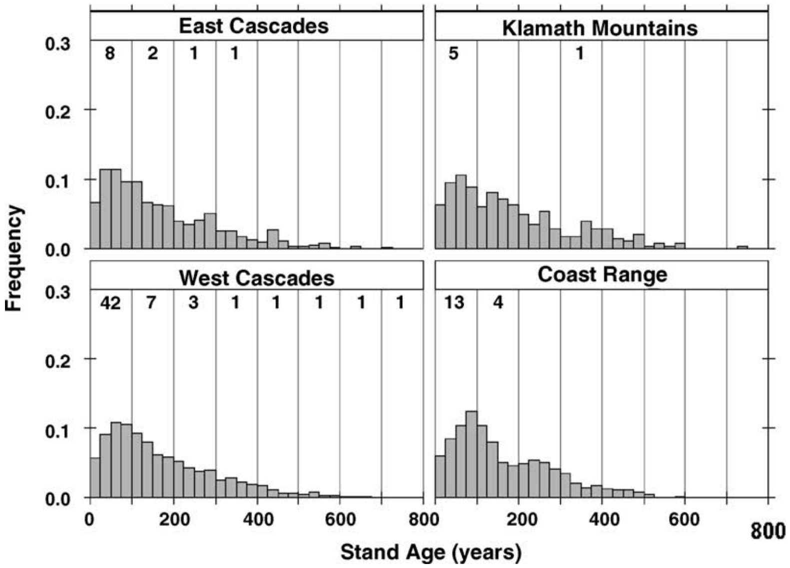

Fig. 2. Frequency distributions of stand age by ecoregion for inventory data and supplementary plot data. Frequency distributions by ecoregion are for CVS and FIA data combined. The number of supplementary plots (36 intensive and 60 extensive) are shown for each 100 year age class within each ecoregion (two plots in the West Cascades were not aged, but were less than 10 years old). Supplementary plot data cover a wide range of ages, with most plots clustered at early ages in order to capture successional changes in ecophysiological variables (fine root mass, foliage characteristics, etc.).

plots (USDA, 2001) while the CVS program uses a series of concentric fixed radius sampling plots (Johnson, 1998). This difference in sampling is not likely to result in differences in estimates of the components of biomass and NPP (Scott and Alegria, 1990). Variables include measurements on each tree (e.g., species, diameter at breast height (DBH)) and measurements on a subset of trees (increment cores, tree age, etc.) and the data are subsequently compiled by the inventory programs.

The method we used to estimate plot-level biomass and NPP from these inventories mirrors that commonly used for smaller scale estimates of plot-level carbon pools and fluxes (e.g., Law et al., 2001a; Janisch and Harmon, 2002), so we used the raw inventory data in our approach rather than the synthesized data products from the inventories.

2.4. Biomass

For each tree measured on the inventory plots, we estimated biomass for the following components: bole wood, branch wood, bark, and coarse roots. We estimated foliage and fine root biomass at the stand level. Biomass values were converted to kilograms of carbon per m^2 ground using 50% carbon content in wood, bark, foliage, and roots (e.g. Law et al., 2001a, 2004; Smithwick et al., 2002; Janisch and Harmon, 2002).

Bole wood biomass was estimated as:

$$\text{biomass}_b = \text{volume}_b \times \text{wood density} \quad (1)$$

where biomass_b is the bole wood biomass (kg m^{-2} ground), volume_b is the bole wood volume (see below), and 'wood density' is the dry density of wood. Bole wood, here, is defined as aboveground woody portion of the tree not including bark and branches.

We divided the study area into four ecoregions, each roughly corresponding to physiographic zones in Oregon: Coast Range, West Cascades, East Cascades, and Klamath Mountains (following Franklin and Dyrness, 1973). Where possible, we used species-specific allometric equations that had been developed in each of the four ecoregions to predict bole volume from diameter at breast height (DBH) and in some cases a combination of DBH and stem height. A full list of allometric equations and their sources can be found in Van Tuyl (2003). Where ecoregion and/or species-specific equations were not available, an equation from another ecoregion or similar species was chosen as a substitute. Of the approximately 400,000 trees in the CVS data, 27% were subject to equation substitution and 34% of the approximately 23,000 trees in the FIA data were subject to substitution. The volume equations typically use diameter at breast height (DBH: 1.37 m) and tree height as predictor variables.

Wood density data were acquired for most of the major hardwood and softwood species of western Oregon through wood density surveys conducted by the U.S. Forest Service (Western Wood Density Survey, 1965; Maeglin and Wahlgren, 1972). The wood density data from these surveys was collected at 850 forest inventory plots throughout our study area, many of which were likely associated with the inventory plots used in this study, with a total of 5622 wood cores sampled. Wood density was reported for wood cores as well as for the entire bole we use bole wood density values for this study. The wood density values we used in this study are species-specific regional averages (e.g. western Oregon). Where necessary, we acquired wood densities from another source (Forest Products Laboratory, 1974).

To refine our estimates of wood density, wood cores were collected from trees at the 96 intensive sites at DBH and evaluated for relationships between wood density and species, diameter, height, and stand age; however, no statistical model explained more than five percent of the variability in wood density. It is fair to note that wood density tends to vary vertically along the tree stem and with depth into the stem and that cores taken at DBH to a limited depth may not accurately represent this variability. However, the result of our wood density comparison at 96 plots across the study area is consistent with another regional study of wood density (e.g., Western Wood Density Survey, 1965) in which whole stem woody density was used. We therefore used the regional wood density values acquired from the above sources without correction for any of these other factors.

Branch and bark biomass was estimated with species-specific branch and bark biomass equations. Where equations for a given species were not available, substitutions were made based on growth form and plant type (pines grouped with pines, firs with firs, etc.). Most of the equations were selected from studies in the Pacific Northwest.

Foliage biomass was estimated as:

$$\text{biomass}_f = \text{LAI} \times \text{LMA} \tag{2}$$

where biomass_f is the foliage biomass (grams foliage per m^2 ground), LAI is the leaf area index (m^2 one-sided leaf area per m^2 ground), and LMA is the leaf mass per unit leaf area (grams of leaf material per m^2 leaf) scaled to the plot level. Leaf area index (LAI) data were derived for the inventory plots by intersecting the plot locations with a continuous surface of remotely sensed LAI (under the supervision of the FIA program, since plot locations are not released to the public). The LAI surface was derived from Landsat ETM+ remote sensing data (Law et al., 2005). Briefly, field measurements of LAI (LAI-2000, LICOR, Lincoln, NE) were corrected for clumping at multiple scales. Rather than use a standard spectral index (e.g. NDVI) which can be subject to saturation at high leaf area values, we used stepwise multiple regression to determine the best set of spectral variables for predicting LAI in each ecoregion. LAI from half of the 96 intensive plots and additional plot data that we collected in earlier studies (e.g. Law et al., 2001b) were used to develop spectral regression algorithms with the ETM+ data, and the remaining plots were used for accuracy assessment. Initial results suggested that East Cascades LAI was underestimated by ~20% which lead us to develop a separate LAI algorithm for the East Cascades making use of some additional plot-level LAI data from a previous project (Law et al., 2001b). The resultant multiple regression models explained 82% and 80% of variance in the East Cascades and remainder of the study are respectively (RMSE 0.742 and 11.606, respectively; Law et al., 2005) and did not show saturation at high leaf area index.

LMA was sampled on the 96 intensive plots by removing between 8 and 12 foliage samples from the dominant species on each plot. Leaf area of each sample was measured and then samples were dried 48 h and weighed. We compared all combinations of species specific LMA among ecoregions to determine if it was necessary to use ecoregion-specific LMA values. Only 10 of the 365 species pairs (3%) differed in LMA ($p < 0.001$, Tukey's HSD), so we used species-specific mean LMA across the study area. Species that were not sampled were assigned an average LMA by leaf/growth form groups (e.g., for unsampled *Abies* species we assigned an average LMA for the *Abies* species that were sampled). LMA was scaled to the plot-level by calculating a species basal-area weighted average.

Coarse root biomass equations were available for two species in the study area: *Pseudotsuga menziesii* (Gholz et al., 1979), and *Pinus ponderosa* (Omdal et al., 2001). We were unable to make comparisons among models to test for differences because the authors did not report sufficient regression statistics for such a comparison. An empirical analysis of the models suggested that results of using either the *P. menziesii* or *P. ponderosa* yield similar results. We chose to use the *P. menziesii* (Gholz et al., 1979) equation because the large range of tree sizes used to develop the model (2–135 cm DBH) encompassed greater than 95% of the trees in our study, potentially reducing error due to extrapolation beyond the limits of the original population used to develop the regression model. Coarse root biomass equations were converted to root volume equations by dividing the equation by a species specific (*P. menziesii*) wood density. The resultant equation was then applied to all species in the study area and converted from coarse root volume back to biomass by multiplying by the wood density of the given species.

Fine root biomass was measured on the 36 intensively measured chronosequence plots (6–25 soil cores per plot). Root material was dried, weighed, and converted to biomass per unit ground area. A regression model was used to estimate, empirically, fine root biomass from LAI at individual inventory plots:

$$\begin{aligned}\text{biomass}_{fr} = \exp(&4.4179 + (0.3256 \times \text{LAI}) \\ &- (0.0237 \times \text{LAI}^2))\end{aligned} \tag{3}$$

($p < 0.001$, $R^2 = 0.41$, $n = 36$).

2.5. Biomass comparisons

We used a permutation test to investigate whether there were differences between CVS and FIA data within each ecoregion. Parametric statistical methods for testing whether groups differ (e.g., a two-sample *t*-test), rely on standard error calculations that in turn rely on sample size. Because the sample size of our dataset is so large, these parametric methods could lead to results suggesting significant differences when there are none (i.e., with large sample sizes, the probability of a type 1 error is increased). The permutation test provides an appealing alternative, since no standard error calculation involving sample size is made—the observations are simply randomly permuted across the CVS and FIA groupings, a test statistic is recalculated, and the observed test statistic is compared to the distribution of recalculated test statistics. In the end, if the observed test statistic is substantially different from the distribution of recalculated test statistics, it suggests that the CVS and FIA data are different.

We compared the data types of the first 100 years since FIA data are limited to this range of ages. We conducted the following test separately for each ecoregion:

(a) Fit separate simple linear regression models to the FIA and CVS data.
(b) Calculate a test statistic from these models:

$$T = |\beta_0^{\mathrm{FIA}} - \beta_0^{\mathrm{CVS}}| + |\beta_1^{\mathrm{FIA}} - \beta_1^{\mathrm{CVS}}| \tag{7}$$

where β_0 and β_1 are the intercept and slope coefficients for the regression models, respectively.
(c) Pool FIA and CVS data.
(d) Randomly divide the pooled data into two groups with sizes corresponding to the original FIA and CVS sample sizes.
(e) Refit the separate simple linear regression models to the two new groups.
(f) Recalculate the test statistic (these are the permuted test statistics).
(g) Repeat steps (d) through (f) 1000 times.

At the end of this procedure, we compared the observed test statistic to the histogram of 1000 permuted test statistic values to determine if there were significant differences in biomass on FIA and CVS plots within each ecoregion.

2.6. Radial growth

There are radial growth estimates available for only a subset of trees on each FIA and CVS inventory plot, but because our method for estimating NPP relies on knowing the radial growth for every tree on a plot, it is necessary to estimate radial growth for unmeasured trees. Jenkins et al. (2001) made generalized estimates of radial growth for unmeasured trees by correlating diameter with radial growth of all trees of a given species in a state or region. This method, while useful for making generalized estimates of plot-level growth, may result in loss of within-plot and/or between plot variability in radial growth because relationships between diameter and radial growth may vary from site to site within a region (e.g. due to differences in local climatic and edaphic factors). To maintain as much of the plot-to-plot variability as possible, we estimated radial growth at the plot level.

Radial growth was estimated for FIA trees as the difference between current and previous tree diameter where data from previous inventories were available. Within each inventory plot, trees with measured radial growth were split into DBH quartiles and a mean radial growth for each quartile was calculated. The mean radial growth increment for the trees in each quartile was assigned to the unmeasured trees in the quartile, while trees with actual measurements of radial growth maintained their original values. Due to non-linearities in the DBH–radial growth relationship on some plots, we did not want to assume that a quartile without any radial growth values would have similar properties to the next lower or higher quartile. For this reason, we assigned the plot-wide average radial growth to trees in quartiles that had no measured radial growth values (10% of the plots and 12% of the trees in the study area). We tested the quartile method against using plot-level diameter to radial growth linear regression models for predicting radial growth for individual trees, a method commonly employed in smaller scale studies.

2.7. Bole, branch, bark, and coarse root NPP

Net primary production of the coarse woody components (bole, branch, bark, and coarse root) was estimated by taking the difference between current biomass and the back calculated biomass of individual trees based on radial growth estimates:

$$\mathrm{NPP_w} = \mathrm{biomass_{w2}} - \mathrm{biomass_{w1}} \tag{4}$$

where $\mathrm{NPP_w}$ is the NPP of woody components and $\mathrm{biomass_{w2}}$ and $\mathrm{biomass_{w1}}$ are the biomass of woody components at current and previous time steps, respectively. Previous height and current height for unmeasured trees was modeled using height-diameter equations developed in the region from forest inventory data (Garman et al., 1995). NPP values reported are the 10-year mean for CVS plots (plots with the most recent measurements made between 1993 and 1997) and 8–12 year means for FIA plots (plots with the most recent measurements made between 1995 and 1997).

Other components of woody NPP that are commonly calculated are ingrowth, ongrowth, and mortality (see Clark et al., 2001). Ingrowth and ongrowth are dealt with in the same manner as other live trees on the plot—that is, they are assigned a radial growth increment based either on actual measurements or on our annual radial growth estimation methods. If the assigned radial growth value for these trees is larger than the radius of the tree, we assume that the tree grew in its entirety in the past year. We do not account for the NPP that any dead trees experienced in the measurement interval. However, because estimates of radial increment attributable to trees before they die in the study area are relatively low (1% of NPP; Grier and Logan, 1977; Campbell et al., 2004), and the NPP potentially contributed by these dead trees is also relatively low, we assume that our live wood NPP increment adequately approximates actual wood NPP.

2.8. Foliage NPP

Foliage NPP was estimated as:

$$\mathrm{NPP_f} = \frac{\mathrm{biomass_f}}{\text{foliage retention time}} \tag{5}$$

where $\mathrm{NPP_f}$ is the foliage net primary production ($\mathrm{kg\,m^{-2}\,y^{-1}}$), $\mathrm{biomass_f}$ is the foliage biomass ($\mathrm{kg\,m^{-2}}$), and foliage retention time (FRT) is the average number of years of foliage a stand carries. This assumes that foliage production is uniformly distributed over the years foliage is present, and may result in underestimation of foliage production for evergreen coniferous stands in which foliage retention is not in steady stasis (e.g., young stands).

Foliage retention time observations (based on the number of years of foliage on each shoot sampled) were collected on the 96 supplementary plots and a one-way ANOVA test indicated there was evidence to suggest differences in retention time between species ($p < 0.001$, Tukey's HSD). Multiple comparisons were conducted to determine which groups differed, and only 19 of 190 (10%) species pairs were significantly different. Because the differences were not systematic, we assigned species-specific foliage retention values based on mean measured values. Species that were not adequately represented in our foliage sampling were grouped with species similar in growth form. FRT was scaled to the plot-level by calculating a species basal-area weighted average.

2.9. Fine root NPP

Fine root NPP was estimated at the 36 chronosequence plots by Law et al. (2005): Fine root production was computed as fine root biomass multiplied by ecoregion-specific estimates of fine root turnover. Fine root turnover was assumed to be 0.66 $\mathrm{y^{-1}}$ for plots in the Coast Range, West Cascades, and Klamath Mountains based on the average of measurements compiled by Santantonio and Hermann (1985) and 0.60 $\mathrm{y^{-1}}$ for plots in the East Cascades based on minirhizotron measurements made by C. Anderson (US EPA, Corvallis, OR, unpublished data) at several sites of varying age (Law et al., 2001a, 2001b).

A regression model was developed from measurements on the 36 intensive plots and used to estimate fine root NPP empirically from LAI at the plot level for all inventory plots:

$$\mathrm{NPP_{fr}} = \exp(3.8746 + (0.3514 \times \mathrm{LAI}) - (0.0250 \times \mathrm{LAI}^2)) \tag{6}$$

($p < 0.001$, $R^2 = 0.45$, $n = 36$).

2.10. Uncertainty analysis

Due to the many assumptions and generalizations necessary for estimating biomass and NPP at large spatial scales, we examined the potential for uncertainty in our estimates. It was not possible to conduct a proper uncertainty analysis such as a Monte Carlo simulation because most of the allometric models used to calculate biomass came from publications that lack regression statistics with which to determine errors in the models. In lieu of a proper uncertainty analysis we attempted to isolate some of the aspects of our design that could be responsible for large uncertainties including the choice of biomass equations, volume equations, and wood density values (responsible for uncertainties in biomass estimates) and the method used to estimate radial growth for unmeasured trees (responsible for uncertainties in net primary production).

We examined error in our biomass estimates using bole biomass as a surrogate for total biomass because bole biomass accounts for approximately 55% of total biomass on average, and because it allowed us to investigate the effects of errors in the volume and wood density components of biomass. Bole volume equations were plotted for each species to estimate how volume equations differ between ecoregions. Uncertainty associated with using wood density values from generic sources were estimated for our 36 intensive plots by comparing biomass estimates from the generic sources used for the inventory data with estimates from the plot-specific values.

Uncertainty in NPP estimates was evaluated in two ways. First, we tested our method of estimating radial growth at the plot level by comparing it with a typical approach to estimating radial growth for unmeasured trees—linear regressions developed to predict radial growth from tree diameter. NPP estimates for 36 plots at which plot-specific diameter to radial growth regressions have been developed were compared with estimates using the method for determining radial growth on the inventory plots. Second, uncertainty estimates were made for each inventory plot by defining the upper and lower 95% confidence interval for radial growth estimates and carrying out NPP calculations at these upper and lower intervals, a method similar to that used by Jenkins et al. (2001). This effectively gave us three estimates of NPP for each inventory plot: a lower (using lower 95% CI for radial growth), middle (based on estimate of radial growth), and upper estimate (using upper 95% CI for radial growth). While these methods did not treat uncertainty in foliage and fine root production, they do begin to account for the major sources of error in our estimates of bole wood production.

We also compared our estimates with those generated using a more generalized approach to using forest inventory data (e.g. Jenkins et al., 2001). We used national-scale biomass equations to estimate the aboveground components of biomass (Jenkins et al., 2003) and international-scale biomass equations to estimate the belowground components of biomass (Cairns et al., 1997). Aboveground wood NPP and belowground NPP were estimated as the difference between current and previous biomass estimated using the national- and international-scale biomass equations (Jenkins et al., 2004 and Cairns et al., 1997 respectively). Foliage NPP was estimated by dividing the generalized foliar mass (Jenkins et al., 2004) by our estimates of plot-level foliage retention time (see Section 2.8).

3. Results and discussion

3.1. Stand age

Stand age varied across the entire study area from zero to 815 years. Overall, stands on non-federal lands (FIA) tended to be younger than stands on national forest lands (CVS; means: 80 and 196 years, respectively), and variability in age tended to be less on non-federal lands than on national forests (standard deviations: 65 and 122 years, respectively).

The patterns within ecoregions were generally the same, with lower means and standard deviations of stand ages on non-federal than national forest lands (Table 1, Fig. 3). The majority of the mature and old stands (>100 years) are on national forest lands in the West Cascades, Klamath Mountains, and East Cascades ecoregions.

In the Coast Range, a series of large fires between 1850 and 1960 burned approximately 710,000 ha of forest (Miller, 1982). The fire disturbances, coupled with insect infestations and a typical harvest rotation length in the western Oregon of 50–80 years are likely driving the distribution of stand ages in this ecoregion, resulting in 75–85% of the stands between the ages of 0 and 125 years (Fig. 3).

In the West Cascades and Klamath Mountains ecoregions, 75% of the stands on non-federal land were between 0 and 125 years of age while this same proportion of stands on national forest land was between 0 and 350 years. The uniform distribution of ages in the national forests of the West Cascades suggests a less punctuated and extreme historical disturbance regime in this ecoregion over the past 800 years compared with the Coast Range.

In the East Cascades, 65% of the stands on non-federal lands were between 50 and 125 years. The distinct peak in the distribution of stand ages in this

Table 1
Summary of stand age, total biomass, and NPP for CVS and FIA plots in four ecoregions and six age classes (Coast Range, West Cascades, East Cascades, Klamath Mountains)

Ecoregion	Age class	Stand age	Mass (kg C m^{-2})	NPP (kg C m^{-2} y^{-1})	Count
CVS					
Coast range	0–13	11.2 (0.9)	5.1 (2)	1.28 (0.41)	14
	14–29	22.2 (4.4)	10.4 (4)	1.25 (0.32)	49
	30–50	40.7 (6.8)	15.3 (7.8)	1.09 (0.31)	29
	51–100	80.6 (15.3)	20 (9.6)	0.88 (0.24)	68
	101–200	132.7 (21.8)	30.4 (13.6)	0.88 (0.24)	155
	200+	346.5 (97.9)	36.5 (15.3)	0.85 (0.23)	57
	All plots	129.6 (109.7)	24.7 (14.9)	0.95 (0.3)	372
West cascades	0–13	11.1 (0.9)	1.9 (1)	0.63 (0.19)	20
	14–29	20.1 (4.6)	5.1 (3.2)	0.89 (0.31)	85
	30–50	37.7 (6.4)	7.7 (4.3)	0.91 (0.29)	60
	51–100	77.7 (14.9)	11 (7)	0.75 (0.28)	151
	101–200	150.2 (28.6)	17.4 (10.4)	0.68 (0.2)	396
	200+	351.9 (114.4)	25.9 (12.5)	0.67 (0.16)	867
	All plots	241 (153.8)	20.2 (13)	0.7 (0.21)	1579
East cascades	0–13	11.5 (1)	2.3 (3.3)	0.29 (0.08)	8
	14–29	20.7 (4.2)	2.8 (2.4)	0.36 (0.12)	26
	30–50	41.9 (6.1)	4.3 (3.2)	0.34 (0.13)	48
	51–100	74.9 (14)	4.7 (2.9)	0.31 (0.13)	327
	101–200	146.4 (29.3)	7.2 (4)	0.38 (0.15)	435
	200+	279.3 (63.2)	9.3 (4.4)	0.42 (0.16)	380
	All plots	160.9 (95.5)	6.9 (4.3)	0.37 (0.15)	1224
Klamath mountains	0–13	11.2 (0.3)	1.2 (0.2)	0.49 (0.08)	3
	14–29	20.5 (4.3)	4.9 (3)	0.91 (0.34)	17
	30–50	40.3 (5.1)	7.4 (7.4)	0.95 (0.67)	17
	51–100	79.7 (13.6)	16.2 (10.6)	0.96 (0.42)	70
	101–200	151.6 (28.3)	18.9 (10.9)	0.82 (0.34)	132
	200+	306.2 (92.6)	24.1 (10.7)	0.74 (0.23)	172
	All plots	193 (120.1)	19.4 (11.6)	0.82 (0.35)	411
FIA					
Coast range	0–13	10.5 (3.7)	5.9 (6.5)	0.71 (0.59)	15
	14–29	22.2 (4.7)	5.3 (4.7)	0.79 (0.61)	41
	30–50	40.3 (5.7)	9.2 (6.6)	0.86 (0.5)	91
	51–100	67.7 (13.4)	12 (8.4)	0.79 (0.5)	137
	101–200	133.4 (26.6)	15.7 (9.1)	0.82 (0.39)	35
	200+	223.2 (20.7)	24.7 (7.3)	0.91 (0.32)	3
	All plots	60.1 (37.9)	10.6 (8.2)	0.81 (0.51)	322
West cascades	0–13	5.6 (4.9)	5.8 (5.7)	0.55 (0.3)	17
	14–29	23.6 (4.6)	5.3 (5.6)	0.52 (0.47)	20
	30–50	40.1 (5.1)	6.9 (5.4)	0.72 (0.44)	55
	51–100	70 (13.7)	9.8 (6.8)	0.72 (0.39)	105
	101–200	130.8 (24.3)	15.8 (6.7)	0.82 (0.25)	43
	200+	290.7 (70.8)	13.8 (4.2)	0.62 (0.27)	14
	All plots	78 (65.9)	9.8 (7)	0.7 (0.39)	254
East cascades	0–13	11.2 (1.9)	3.3 (0.3)	0.34 (0.13)	2
	14–29	21.7 (4.8)	2.2 (1.9)	0.25 (0.13)	12
	30–50	39 (5.7)	3 (2)	0.27 (0.14)	33
	51–100	76.3 (15.5)	3.6 (2.1)	0.34 (0.15)	69
	101–200	132 (30.6)	7.2 (4.7)	0.45 (0.25)	51

Table 1 (*Continued*)

Ecoregion	Age class	Stand age	Mass (kg C m^{-2})	NPP (kg C m^{-2} y^{-1})	Count
	200+	264.4 (56.2)	9 (5)	0.54 (0.18)	17
	All plots	98.2 (69.2)	4.9 (4)	0.37 (0.2)	184
Klamath mountains	0–13	2.8 (3.9)	0.7 (0.3)	0.13 (0.01)	2
	14–29	22.3 (7)	7.3 (4.7)	0.57 (0.42)	4
	30–50	42.8 (7.6)	5.8 (5.4)	0.34 (0.21)	10
	51–100	79.6 (14.6)	7.9 (6)	0.7 (0.51)	36
	101–200	132.2 (24.7)	11.1 (3.9)	0.64 (0.35)	34
	200+	261.1 (46.2)	10.4 (6.3)	0.58 (0.21)	11
	All plots	110.9 (68.4)	8.9 (5.5)	0.61 (0.41)	97

Reported values are means with standard deviations in parentheses. Biomass and NPP values are for total above and belowground including bole, branch, bark, foliage, coarse root, and fine root.

region is the result of fire suppression as well as the removal of most of the old late-seral stands in eastern Oregon by early settlers (Everett et al., 1994). Similarly, 45% of the stands on national forest land were between 0 and 125 years. The typical age of harvest in Eastern Oregon is between 75 and 150 years (Lettman, 1995), implying that many stands are near harvest age if this rotation length is continued. The East Cascades have relatively low frequencies of stands in the 0–25 years range, indicative of the difficulty in stand regeneration after disturbance in the water limited climate of eastern Oregon (Coops et al., 2005) as well as a general reduction in the number of young stands due to management changes (Everett et al., 1994). Stand history data indicate that it can take 8–10 years of favorable summer rainfall for re-establishment to occur in this region, and the region has experienced frequent severe drought over the past decade (Law et al., 2001a).

3.2. Biomass

For the entire study region, stand biomass is higher on national forests than on non-federal land (means:

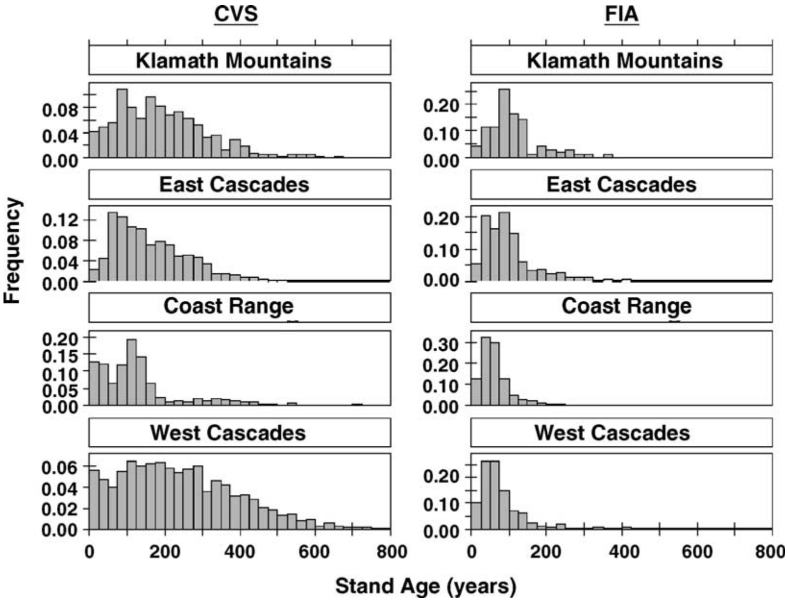

Fig. 3. Frequency distributions of stand age by geographic and data type. Forests in western Oregon tend to have fewer old stands on non-federal (FIA) lands than on national forest (CVS) lands. This trend is apparent in all geographic areas and may reflect forest management practices on non-federal lands that tend to have short rotation periods of 50–100 years.

CVS plots 16.07 kg C m^{-2}, FIA plots 8.94 kg C m^{-2}), and variability follows the same trend (standard deviations: 12.84 and 7.15 kg C m^{-2}, respectively). This trend is also true within each of the four ecoregions (Table 1). The difference in the distribution of ages appears to be primarily responsible for the overall difference in biomass between non-federal and national forest data. Because the national forest data tend to include more old stands and a wider range of stand ages, it follows that the mean biomass and the variance in biomass would be higher than for non-federal data.

The permutation test results suggest that, controlling for age, there is no difference between successional trends of biomass on national forest and non-federal lands in the West Cascades ($p = 0.22$) for the age classes represented in both land ownerships.

Because the FIA data have a restricted range of stand ages, we combined data from the two ownerships to evaluate broad long-term trends in biomass accumulation. Biomass in all four ecoregions rapidly increased with stand development, followed by a gradual reduction in the rate of biomass accumulation to a point of slowed net gain in older stands (Fig. 4). The age at which biomass accumulation appears to slow differs by ecoregion (200 years in West Cascades, 150 years in East Cascades, 200 years in the Klamath Mountains). The West Cascades and Klamath Mountains ecoregions show similar patterns of biomass accumulation through stand development with biomass increasing to a median of approximately 25–30 kg C m^{-2} and a maximum of about 60 kg C m^{-2}. Biomass of stands in the East Cascades reaches a median value of about 10 kg C m^{-2} and a maximum of 20 kg C m^{-2}. Because the lack of data for the Coast Range ecoregion beyond about 200 years, it is difficult to determine whether biomass continues to increase at its current rate or slows significantly in Coast Range stands, however, by 175 years, the Coast Range forests reach a median biomass of about 35–40 kg C m^{-2} and a maximum of about 60 kg C m^{-2}. The maximum biomass values for all of the ecoregions are large compared with maxima obtained in the rest of the country, including loblolly pine in the southeast U.S. (9 kg C m^{-2}; Jokela et al., 2004). This indicates the value of carbon storage in Pacific Northwest forests from a national perspective.

In all of the ecoregions, the biomass values from various field studies in the Pacific Northwest tend to approach the upper limits of our inventory based

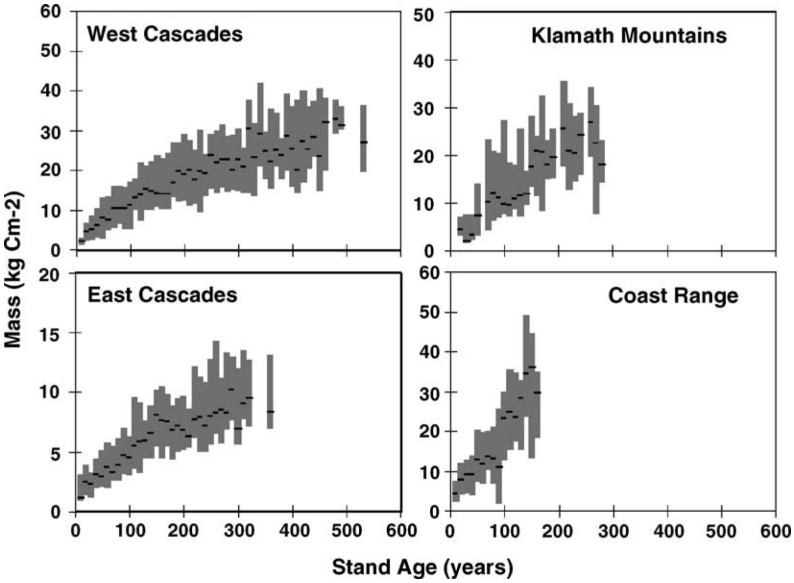

Fig. 4. Successional patterns of biomass. Trends in tree biomass accumulation with increase in stand age. Trajectories of biomass differ by ecoregion with biomass accumulation rates slowing at different ages in different ecoregions. Plots are grouped into 10-year age classes and box plots were made for each age class. Bars represent the age class interquartile range (25th percentile to 75th percentile) and the black bars indicate the median of each age class. Age classes that include fewer than 10 inventory plots were excluded for figure clarity.

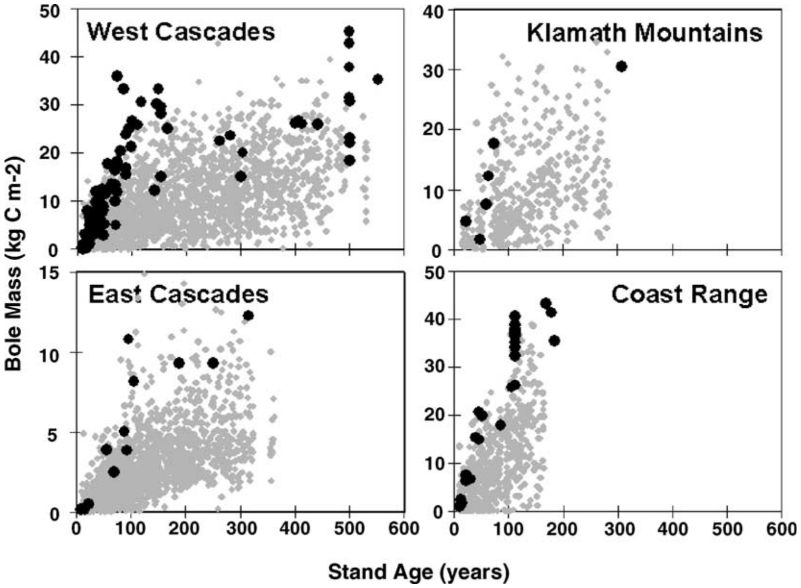

Fig. 5. Comparison of bole mass from this study and other studies in the Pacific Northwest. Change in tree bole mass with increase in stand age. Light dots are data from this study. Dark dots are data from other studies in the Pacific Northwest including our 36 intensive and 60 extensive supplementary plots: Acker et al. (2002), Janisch and Harmon (2002), Turner and Long (1975), Runyon et al. (1994), Gholz (1982), Harcombe et al. (1990) and Law et al. (2005).

estimates (Fig. 5). This result is not entirely surprising since the systematic sampling scheme allows inventory plots to be located in disturbed or otherwise heterogeneous stands while investigators in ecological studies typically select stands that represent relatively homogeneous forest conditions. This pattern has been previously observed in comparisons of forest inventory biomass data and data from ecological studies (Jenkins et al., 2001) and suggests that, when scaling plot-level estimate of biomass to larger spatial scales, the sampling design (systematic random versus non-random) and original intent of the investigators should be considered. Because biomass data from ecological studies tends to be higher than data from inventories, it is likely that estimates of carbon storage that use only data from ecological studies will be biased upwards (Botkin and Simpson, 1990).

We estimated total carbon storage in live trees for our study area by weighting the total area of forest in each ecoregion by the frequency distribution of biomass for each ecoregion. Our results suggest that the forests in our study area (the forested area of western Oregon) store 1.32 Pg C in live trees. This result is higher than the carbon storage in live trees reported by Turner et al. (1995) who estimate approximately 0.92 Pg C in Oregon. The estimates in Turner et al. (1995) rely heavily on inventory data from non-federal lands to make their estimates and if we recalculate our estimates based on non-federal lands we get a total carbon storage in live that is trees more comparable (0.83 Pg C). Conversely, if we make estimates based on national forests only, the total storage in live trees increases to 1.55 Pg C. This difference between storage in a national forest-like landscape compared with a non-federal-like landscape suggests that if disturbance regimes on national forests were more similar to those of non-federal lands, carbon storage in live trees could decrease considerably. Likewise, if forests on non-federal lands were managed for characteristics similar to those of national forests (e.g., more broad distribution of stand ages) the study area could store almost 20% more carbon in live trees.

Smithwick et al. (2002) estimate a maximum potential carbon storage in live trees for this study area at about 4 Pg C, indicating that western Oregon forests currently store 33% of their maximum potential in live trees (this does not include other pools such as necromass, soils, etc.). If the distribution of biomass across the study area were to emulate that of non-federal lands, these forests would hold 21% of the potential, while a biomass distribution similar to that of the national forests could hold 39% of the potential. A biomass distribution similar to that of the national forest lands could be achieved across the landscape of western Oregon by increasing rotation lengths on all forest lands. A lengthening of rotation time could result in even greater storage in carbon in other forest pools also. In our concurrent studies on regional soil carbon, we found that soil carbon accumulation following stand-replacing disturbance also slowed between 150 and 200 years (Sun et al., in press). A previous model simulation suggested that rotation lengths could be increased to increase the total amount of carbon stored on a landscape. For example, the simulations suggested that in highly managed forests in the Pacific Northwest, increasing the rotation length from 40 to 120 years increased landscape storage by more than 2.5-fold, and in minimally managed forests, the increase was about 20% (Harmon and Marks, 2002).

As an amendment to the Northwest Forest Plan (http://www.house.gov/defazio/073004EGRelease.shtml), legislation is proposed to increase timber sales on federal forests but prohibit cutting of trees older than 120 years, so that harvests can increase 3-fold while protecting old-growth forests. About 35% of the national forest stands were <120 years: 55%, 25%, 40%, and 30% of the Coast Range, West Cascades, East Cascades, and Klamath Mountains, respectively. This suggests that approximately 0.42 Pg C could be made available for harvest in our study area.

3.3. Net primary production

A comparison of age-specific NPP values estimated in our study with those of previous studies in the region shows consistency in the pattern across the climatic gradient in western Oregon (Gholz, 1982; Runyon et al., 1994). Both total light interception and light use efficiency decrease in moving from the mesic Coast Range across the Cascades to the xeric East Cascades ecoregion (Runyon et al., 1994), hence there is a trend to decreasing NPP. Ecoregion means for aboveground NPP in this region range from 0.16 to 0.60 kg C m^{-2} y^{-1}, a wider range than that of deciduous and evergreen forests in the mid-Atlantic U.S. where an analysis of FIA data showed means for aboveground production ranging from ~0.35 to 0.46 kg C m^{-2} y^{-1} (Jenkins et al., 2001).

Mean NPP and variability about the mean is slightly higher for plots on non-federal than federal lands (0.66 kg C m^{-2} y^{-1} and S.D.: 0.44 versus 0.63 kg C m^{-2} y^{-1} and S.D.: 0.30, respectively). This pattern may be partly due to differences in age distributions between plots on non-federal and federal lands (Table 1, Fig. 3). Because the plots on non-federal lands tend to be concentrated in the mature and young classes that have reached maximum canopy cover (mean 80 years, S.D.: 65), and because NPP is generally higher in mature stands than older stands and young stands that have not reach maximum canopy cover, it follows that mean NPP would be higher on non-federal plots.

Maximum NPP values were reached earlier in the more mesic ecoregions. In the West Cascades, NPP increased to a maximum at a stand age between 30 and 50 years (median 0.85 kg C m^{-2} y^{-1}, Table 1, Fig. 6) while the Coast Range forests reach a maximum NPP before 30 years (Table 1). Similar age trends are seen in bole wood production (data not shown) and these patterns have provided a basis for setting age-specific parameters in carbon cycle process models (Waring and McDowell, 2002; Law et al., 2005).

Previous studies indicated that NPP generally decreased in old forests to about half its maximum value (Ryan et al., 2004; Howard et al., 2004; Mund et al., 2002). However, many old forest stands are just as productive as young forest stands (Harmon, 2001). Data for the Klamath Mountains show that NPP can be relatively high (approximately 0.75 kg C m^{-2} y^{-1}) even between 80 and 90 years and decline only modestly after that point. NPP of the forests in the East Cascades clearly do not show the pattern of a distinct peak in NPP followed by a decline as seen in the Coast Range and West Cascades. Rather, NPP is generally stable at approximately 0.3 kg C m^{-2} y^{-1} during the first 100 years then tends to increase slightly between 100 and 300 years.

The pattern in NPP in the East Cascades may be explained by differences in stand dynamics between Eastern Oregon and western Oregon forests. It has been suggested that the theoretical NPP trajectory (peak then decline in NPP) can be explained as a

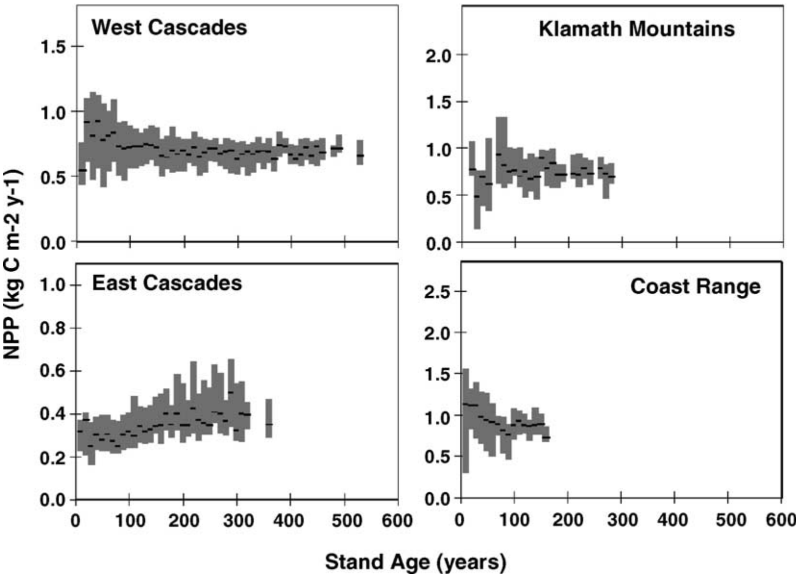

Fig. 6. Successional patterns of NPP. Plots are grouped into 10-year age classes and box plots were made for each age class. NPP is an 8–12 years average. Plots are grouped into 10-year age classes and box plots were made for each age class. Bars represent the age class interquartile range (25th percentile to 75th percentile) and the black bars indicate the median of each age class. Age classes that include fewer than 10 inventory plots were excluded for figure clarity.

function of stand community dynamics (Smith and Long, 2001), with canopy closure and the resultant self-thinning creating a decrease in stand-level NPP. However, Law et al. (2003) report that LAI in a chronosequence of ponderosa pine in Eastern Oregon did not decline significantly between stand ages ~75 and ~300 years. Forests in the East Cascades tend to grow at relatively low densities through stand development with leaf area index typically reaching levels no higher than 4 m^{-2} m^{-2} (no canopy closure). Competition for light is minor compared with competition for soil resources. Thus in the EC ecoregion, it is stand structure and community dynamics that permit maintenance of NPP with stand age.

The estimates for trends in allocation (Fig. 7) also reveal differences between the eastern and western ecoregions. The comparison shows that relatively more assimilated carbon is allocated belowground in young stands in the East Cascades, and this becomes a smaller fraction as stands age (Fig. 7). Earlier work has shown that stand re-establishment is slow and young pines in the East Cascades are severely drought stressed in summer, likely because of less developed roots for accessing deep soil water compared with mature and old trees (Irvine et al., 2002). In the Coast Range and West Cascades, stands exhibit the opposite pattern with relatively high carbon allocation aboveground in early stand development when there is competition for light resources. This is followed by a shift to more carbon allocation belowground as the dominant trees become assured of adequate light (~50–60 years). Similar data on the allocation of fixed carbon to above- and belowground components as a function of climate zone and biome are needed for developing algorithms that permit dynamic allocation in forest process models (e.g. Law et al., 2005).

3.4. Uncertainty analysis

Results of our uncertainty analysis for biomass components suggest that using site-specific allometry and wood density can result in large reductions in errors. We compared bole volume estimates from equations developed in each of the four ecoregions for each species and found that differences in bole volume estimates could be as great as 40%. While this level of error is unlikely to be the norm, we have no realistic way of testing appropriateness of each equation for the inventory plots. St. Clair (1993) demonstrate the

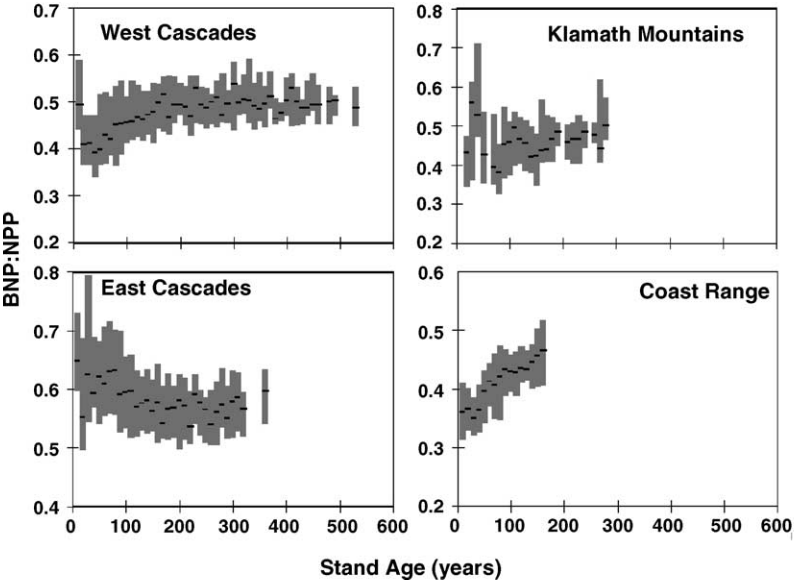

Fig. 7. Successional patterns of BNPP–NPP ratio. The ratio of belowground NPP to total NPP by stand age and ecoregion. Broad successional patterns of carbon allocation appear to differ among ecoregions. West Cascades and Coast Range forests allocate relatively more carbon aboveground in early succession while East Cascades forest allocate more carbon belowground in early succession.

importance of using site-specific allometrics because of variation in equations developed within a region. This, however, was not feasible in our study and generally is not feasible for other large-scale studies of this sort due to the destructive and labor-intensive nature of developing site-specific allometry at thousands of sites across a region. Other studies have approached this problem of using site-specific allometric equations across a large spatial area by pooling equations across a region (Jenkins et al., 2003). Systematically testing the spatial variability of tree allometry across large spatial scales and testing the effect of using pooled or generalized allometric equations are important steps towards understanding the sources of variability in biomass and NPP estimates made from forest inventory datasets.

Efforts to increase the specificity of wood density data could decrease error in biomass and NPP estimates. When regional averaged wood densities acquired from regional wood density surveys (see Section 2) were substituted for plot specific wood densities on 36 test plots, the average difference in biomass and NPP was 9% with a standard deviation of 13%. The errors associated with generalizing wood density were not systematic with stand age. The magnitude of the error associated with using regional average wood densities suggests the importance of using site-specific estimates of wood density where available, perhaps by initiating wood density sampling on different size classes of trees on inventory plots.

Overall, the error associated with our method of estimating radial growth does not introduce a significant amount of error in our NPP estimates. Comparisons of NPP for the 36 test plots using plot-specific diameter to radial growth regressions and using our bin-averaging approach show only a 1% change in NPP estimates with a standard deviation of 4%. There appears to be no age or ecoregion related pattern associated with this error. A benefit of the quantile approach to assigning radial growth values to unmeasured trees in large-scale studies is that the quantile method is able to detect, to some degree, nonlinear relationships between diameter and radial growth within individual plots (e.g. plots with slow growing small trees, fast growing moderate sized trees, and slow growing old trees).

When 95% confidence intervals of radial growth were propagated through the NPP calculations, the median percent change in NPP was approximately 11% for all stand ages. The inter-quartile range for most of the radial growth error estimates is from 9% to 14% with a general upward trend as stands age. This gives us confidence that our method of estimating radial growth for individual trees is relatively robust. The errors in NPP are likely the result of relatively low sample sizes of radial growth increments on individual inventory plots and could be alleviated by increasing sampling of growth increment on inventory plots.

It is also worth noting that the data collected on the 96 supplementary plots and used in the estimation of components of biomass and NPP may be subject to some level of bias. We have stated that sample plots from ecological studies tend to have biomass values higher than those from forest inventory programs and it may be the case that samples of components of biomass (e.g. LMA, wood density, etc.) from ecological plots are biased though the direction of the bias is uncertain due to a lack of data. However, we also found that the inventory plots often occur in disturbed areas, leading to low biomass estimates (i.e. skewed distribution). A move towards sampling more components of whole tree biomass and productivity on forest inventory plots, and increased noting of intermediate disturbances on inventory plots (e.g. thinning, fire) may be one way to alleviate these discrepancies.

Finally, while being a systematic sample, the forest inventory data may conceivably result in a biased estimate of the true condition on the landscape which may, in turn, result in biased estimates of some forest attributes at the landscape scale. Inventory programs such as FIA that currently using a multi-phase design (e.g. remote sensing and ground plots) might incorporate some attributes into their remote sensing sampling that could aid biomass and productivity estimates at the regional scale as well as aid other ecological research (e.g. regional modeling, etc.). For example, a complimentary approach to estimating stand age is 100% coverage with high spatial resolution (30 m) satellite remote sensing data, particularly for the ages classes below 30 years (length of the satellite record for change detection; Cohen et al., 1995; Turner et al., 2003; Law et al., 2005). This added information is likely to increase the reliability of large area estimates of carbon pools and fluxes the patterns of which are highly influenced by variability in stand age across the landscape (Law et al., 2005).

Total biomass estimates from the two methods (this study and the generalized method) were within about 10% of one another. Our methods were typically lower in the Coast Range, West Cascades, and Klamath Mountains. Differences were greatest in the East Cascades where our methods resulted in estimates about 50% higher than the generalized estimates. Allocation among above and belowground pools was similar between the methods, though the generalized method typically underestimated aboveground biomass by about 10% on average and overestimated belowground biomass by about 5%. Foliage mass was the most different between the methods with generalized estimates averaging 60% of our estimates and the underestimate averaged 300% in early seral stands (0–30 years).

The comparison of our methods with generalized methods showed that total NPP produced using the generalized methods was typically 30% lower than by using our methods. Aboveground NPP was 15% higher using the generalized methods when compared to our methods. Foliage NPP estimates are the primary cause of the discrepancies in aboveground NPP. Foliage NPP is, on average, 60% lower using the generalized methods though differences range from as much as 700% lower to 40% higher using the generalized methods. These differences are driven by the variability in leaf area index on our plots which results in similar variability in our foliage biomass and NPP estimates. This variability is in contrast to the general lack of variability in foliar mass and NPP when using the generalized method, which assumes foliage mass (and by association, NPP) are a constant fraction of aboveground mass. We have found in this study and others (e.g. Law et al., 2001a, 2001b) that LAI and foliage mass can vary widely among stands with otherwise similar characteristics (e.g. woody biomass). This suggests that accounting for plot-to-plot variability in foliage characteristics (e.g. using remote sensing rather than allometric equations) can have significant effects on estimates of foliar biomass and especially foliage productivity. Also, these differences are mostly found in early seral stands (0–13 years) where the aboveground biomass equations based on stem diameters alone may underestimate foliar mass. This seral stage is also when our method of estimating foliage properties with remote sensing may be detecting understory LAI (before full canopy closure).

We found that belowground NPP estimates are also quite different between the two methods—by 400% on average, again driven by the variability in LAI on our plots. The equations used for the generalized method are a function of total aboveground mass (current and previous) only while our methods take into account separate coarse root allometrics (based on tree diameters) and fine root allometrics (estimated from LAI). Ratios of BNPP to NPP are considerably lower for the generalized method (average: 0.21, S.D.: 0.01) than for our method (average: 0.47, SD: 0.08) as well as for previous studies in the regions (Law et al., 2003, average: 0.42, S.D.: 0.09; Runyon et al., 1994, average: 0.35, S.D.: 0.16).

4. Conclusions

The integration of data from forest inventories, satellite remote sensing, and intensive + extensive measurement sites has allowed us to make reasonable estimates of biomass and NPP components for these forests, and to explore trends in biomass and NPP with disturbance and management. We found that, in western Oregon, the distribution of stand ages on national forests versus non-federal lands is quite different. More old stands are present on national forest lands than on non-federal lands. The difference in stand age distributions results in a lower mean storage of carbon in live trees on non-federal lands across the study area. Productivity generally peaks earlier and at a higher level in the Coast Range than in the other ecoregions. Our data show that NPP does not necessarily decrease in old forests, and some old forests are just as productive as younger forests. Belowground allocation tends to increase in older stands, except in the East Cascades ecoregion. Our results suggest that because biomass and soil carbon pools continue to increase up to about age 200, forest management to maximize carbon stocks on forest land in this region would employ a cutting rotation cycle close to 200 years. This conflicts with forest management plans for large-scale forest thinning to reduce fire risk. Use of a nested hierarchy of observations as shown in this study can contribute to direct estimation of carbon stocks and fluxes as well as to calibration and validation of carbon cycle models that are applied across regions.

Acknowledgements

This study was funded by U.S. EPA National Center for Environmental Research (NCER) Science to Achieve Results (STAR) Program (Grant # R-82830901-0). FIA and CVS data were provided by USDA Forest Service. We thank Tony Olsen at U.S. EPA in Corvallis for assisting us with extensive plot study design to maximize representativeness of the region. We also thank Karen Waddell, Robert Brown, Dale Weyermann, Andy Gray, Janet Ohmann, and Otha Terry for assistance with the FIA and CVS datasets, and John Campbell, Michael Guzy, Michael Lefsky, Osbert Sun, Colin Edgar, and the 2001 field crew for field data collection and assistance in data analysis. Although the research described in the article has been funded wholly or in part by the U.S. Environmental Protection Agency's STAR program, it has not been subjected to any EPA review and therefore does not necessarily reflect the views of the Agency, and no official endorsement should be inferred.

References

Acker, S.A., Halpern, C.B., Harmon, M.E., Dyrness, C.T., 2002. Trends in bole biomass accumulation, net primary production and tree mortality in *Pseudotsuga menziesii* forests of contrasting age. Tree Physiol. 22, 213–217.

Botkin, D.B., Simpson, L.G., 1990. Biomass of the North American boreal forest. Biogeochemistry 9, 161–174.

Brown, S., Schroeder, P., Birdsey, R., 1997. Aboveground biomass distribution of US eastern hardwood forests and the use of large trees as an indicator of forest development. For. Ecol. Manage. 96, 37–47.

Brown, S.L., Schroeder, P., Kern, J.S., 1999. Spatial distribution of biomass in forests of the eastern USA. For. Ecol. Manage. 123, 81–90.

Cairns, M.A., Brown, S., Helmer, E.H., Baumgardner, G.A., 1997. Root biomass allocation in the world's upland forests. Oecologia 111, 1–11.

Campbell, J.L., Sun, O.J., Law, B.E., 2004. Disturbance and net ecosystem production across three climatically distinct forest landscapes. Global Biogeochem. Cycles 18 .

Clark, D.A., Brown, S., Kicklighter, D.W., Chambers, J.Q., Thomlinson, J.R., Ni, J., 2001. Measuring net primary production in forests: concepts and field methods. Ecol. Appl. 11, 356–370.

Cohen, W.B., Spies, T.A., Fiorella, M., 1995. Estimating the age and structure of forests in a multi-ownership landscape of western Oregon, U.S.A. Int. J. Remote Sensing 16, 721–746.

Coops, N.C., Waring, R.H., Law, B.E., 2005. Assessing the past and future distribution and productivity of Ponderosa Pine in the Pacific Northwest using a process model. 3-PG. 183, 107–124.

Everett, R., Hessburg, P., Jensen, M., Bormann, B., 1994. Eastside Forest Ecosystem Health Assessment: vol. I: Executive Summary. General Technical Report PNW-GTR-317. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station

Forest Products Laboratory, 1974. Wood Handbook: Wood as an Engineering Material. Forest Products Laboratory, Madison, WI, p. 72.

Franklin, J.F., Dyrness, C.T., 1973. Natural Vegetation of Oregon and Washington. USDA Forest Service General Technical Report PNW 8. Pacific Northwest Forest and Range Experiment Station.

Garman, S.L., Acker, S.A., Ohmann, J.L., Spies, T.A., 1995. Asymptotic Height-diameter Equations for Twenty-four Tree Species in Western Oregon. Forest Research Laboratory, Oregon State University, Corvallis, 22 pp. (Research Contribution 10).

Gholz, H.L., Grier, C.C., Campbell, A.G., Brown, A.T., 1979. Equations for estimating biomass and leaf area of plants in the pacific northwest. Research Paper 41. Forest Research Laboratory, Oregon State University, Corvallis, 37 pp.

Gholz, H.L., 1982. Environmental limits on aboveground net primary production, leaf area, and biomass in vegetation zones of the Pacific Northwest. Ecology 63, 469–481.

Grier, C.C., Logan, R.S., 1977. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: biomass distribution and production budgets. Ecol. Monogr. 47, 373–400.

Harcombe, P.A., Harmon, M.E., Greene, S.E., 1990. Changes in biomass and production over 53 years in a coastal *Picea sitchensis–Tsuga heyerophylla* forest approaching maturity. Can. J. For. Res. 20, 1602–1610.

Harmon, M.E., 2001. Carbon sequestration in forests: addressing the scale question. J. For. 24–29.

Harmon, M.E., Marks, B., 2002. Effects of silvicultural practices on carbon stores in Douglas-fir—western hemlock forests in the Pacific Northwest, U.S.A.: results from a simulation model. Can. J. For. Res. 32, 863–877.

Howard, E.A., Gower, S.T., Foley, J.A., Kucharik, C.J., 2004. Effects of logging on carbon dynamics of a jack pine forest in Saskatchewan, Canada. Global Change Biol. 10, 1267–1284.

Irvine, J., Law, B.E., Anthoni, P.M., Meinzer, F.C., 2002. Water limitations to carbon exchange in old-growth and young ponderosa pine stands. Tree Physiol. 22, 189–196.

Janisch, J.E., Harmon, M.E., 2002. Successional changes in live and dead wood carbon stores: implications for net ecosystem productivity. Tree Physiol. 22, 77–89.

Jenkins, J.C., Birdsey, R.A., Pan, Y., 2001. Biomass and NPP estimation for the mid-Atlantic (USA) using plot-level forest inventory data. Ecol. Appl. 11, 1174–1193.

Jenkins, J.C., Chojnacky, D.C., Heath, L.S., Birdsey, R.A., 2003. National-scale biomass estimators for United States tree species. For. Sci. 49, 12–35.

Johnson, M.D., 1998. Region 6 inventory and monitoring system: field procedures for the Current Vegetation Survey. Version 2.03. Natural Resource Inventory, Pacific Northwest Region, USDA Forest Service, Portland, OR.

Jokela, E.J., Dougherty, P.M., Martin, T.A., 2004. Production dynamics of intensively managed loblolly pine stands in the southern United States: a synthesis of seven long-term experiments. For. Ecol. Manage. 192, 117–130.

Law, B.E., Thornton, P.E., Irvine, J., Anthoni, P.M., Van Tuyl, S., 2001a. Carbon storage and fluxes in ponderosa pine forests at different developmental stages. Global Change Biol. 7, 755–777.

Law, B.E., Van Tuyl, S., Cescatti, A., Baldocchi, D.D., 2001b. Estimation of leaf area index in open-canopy ponderosa pine forests at different successional stages and management regimes in Oregon. Agric. For. Meteorol. 108, 1–14.

Law, B.E., Sun, O.J., Campbell, J., Van Tuyl, S., Thornton, P., 2003. Changes in carbon storage and fluxes in a chronosequence of Ponderosa Pine. Global Change Biol. 9, 510–524.

Law, B.E., Turner, D., Sun, O.J., Guzy, M., Campbell, J., Lefsky, M., Van Tuyl, S., Ritts, W.D., Cohen, W.B., 2004. Disturbance and climate effects on carbon stocks and fluxes across western Oregon, USA. Global Change Biol. 10, 1429–1444.

Law, B.E., Turner, D., Lefsky, M., Campbell, J.L., Guzy, M., Sun, O.J., Van Tuyl, S., Cohen, W.B., 2005. Carbon fluxes across regions: observational constraints at multiple scales. In: Wu, J., Jones, B., Li, H., Loucks, O. (Eds.), Scaling and Uncertainty Analysis in Ecology: Methods and Applications. Columbia University Press, New York, USA., in press.

Lettman, G., 1995. Timber management practices and land use trends on private forest land in Oregon: a final report to the sixty-eighth Oregon legislative assembly. Oregon Department of Forestry Forest Resources Planning Program.

Maeglin, R.R., Wahlgren, H.E., 1972. Western Wood Density Survey: Report Number 2. USDA Forest Service Research Paper FPL-183.

Miller, H.M., 1982. Forests, People, and Oregon: A History of Forestry in Oregon. Oregon State Forestry Department, Salem, OR.

Mund, M., Kummetz, E., Hein, M., Bauer, G.A., Schulze, E.-D., 2002. Growth and carbon stocks of a spruce forest chronosequence in central Europe. Forest Ecol. Manage. 171, 275–296.

Ni, J., Zhang, X., Scurlock, J.M.O., 2001. Synthesis and analysis of biomass and net primary productivity in Chinese forests. Ann. For. Sci. 58, 351–384.

Omdal, D.W., Jacobi, W.R., Shaw III, C.G., 2001. Estimating large-root biomass from breast-height diameters for Ponderosa Pine in Northern New Mexico. Western J. Appl. For. 16, 18–21.

Powell, D.S., Faulkner, J.L., Darr, D.R., Zhu, Z., MacCleery, D.W., 1993. Forest resources of the United States, 1992. United States Department of Agriculture Forest Service. Rocky Mountain Forest and Range Experiment Station. General Technical Report RM-234.

Runyon, J., Waring, R.H., Goward, S.N., Welles, J.M., 1994. Environmental limits on net primary production and light-use efficiency across the Oregon transect. Ecol. Appl. 4, 226–237.

Ryan, M.G., Binkley, D., Fownes, J.H., Giardina, C.P., Senock, R.S., 2004. An experimental test of the causes of forest growth decline with stand age. Ecol. Monogr. 74, 393–414.

Santantonio, D., Hermann, R.K., 1985. Standing crop, production, and turnover of fine roots on dry, moderate, and wet sites of mature Douglas-fir in western Oregon. Ann. For. Sci. 42, 113–142.

Scott, C.T., Alegria, J., 1990. Fixed versus variable-radius plots for change estimation. In: LaBau, V.J., Cunia, T. (Eds.), State-of-the-art Methodology of Forest Inventory: A Symposium Proceedings. General Technical Report PNW-GTR-263. USDA Forest Service Pacific Northwest Research Station, Portland, OR.

Smith, F.W., Long, J.N., 2001. Age-related decline in forest growth: an emergent property. For. Ecol. Manage. 144, 175–181.

Smithwick, E.A.H., Harmon, M.E., Remillard, S.M., Acker, S.A., Franklin, J.F., 2002. Potential upper bounds of carbon stores in forests of the Pacific Northwest. Ecol. Appl. 12, 1303–1317.

Spies, T.A., Franklin, J.F., 1991. The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington. In: Ruggiero, L.F., Aubry, K.B., Carey, A.B., Huff, M.H. (Eds.), Wildlife Habitat Relationships in Old-growth Douglas-fir Forests. USDA Forest Service General Technical Report PNW GTR-285.

St. Clair, J.B., 1993. Family differences in equations for predicting biomass and leaf area in Douglas-Fir (*Pseudotsuga menziesii* var. *menziesii*). For. Sci. 39, 743–755.

Sun, O.J., Campbell, J., Law, B.E., Wolf, V., in press. Dynamics of carbon storage in soils and detritus across chronosequences of different forest types in the Pacific Northwest, USA. Global Change Biol.

Turner, J., Long, J.N., 1975. Accumulation of organic matter in a series of Douglas-fir stands. Can. J. For. Res. 5, 681–690.

Turner, D.P., Koerper, G.J., Harmon, M.E., Lee, J.J., 1995. A carbon budget for forests of the conterminous United States. Ecol. Appl. 5, 421–436.

Turner, D.P., Guzy, M., Lefsky, M.A., Van Tuyl, S., Sun, O., Daly, C., Law, B.E., 2003. Effects of land use and fine scale environmental heterogeneity on net ecosystem production over a temperate coniferous forest landscape. Tellus B 55B, 657–668.

Van Tuyl, S., 2003. Carbon storage and fluxes in forests of western Oregon: successional patterns and environmental controls. M.S. Thesis. Oregon State University, 122 pp.

Waring, R.H., McDowell, N., 2002. Use of a physiological process model with forestry yield tables to set limits on annual carbon balances. Tree Physiol. 22, 179–188.

U.S. Department of Agriculture, Forest Service, 2001. Forest Inventory and Analysis National Core Field Guide, vol. 1: Field Data Collection Procedures for Phase 2 Plots, Version 1.5. U.S. Department of Agriculture, Forest Service, Washington Office. Internal Report. On file with: U.S. Department of Agriculture, Forest Service, Forest Inventory and Analysis, Washington, DC, p. 20250.

Western Wood Density Survey: Report Number 1, 1965. USDA Forest Service Research Paper FPL-27.