Carbon dynamics of Oregon and Northern California forests and potential land-based carbon storage

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Abstract. Net uptake of carbon from the atmosphere (net ecosystem production, NEP) is dependent on climate, disturbance history, management practices, forest age, and forest type. To improve understanding of the influence of these factors on forest carbon stocks and flux in the western United States, federal inventory data and supplemental field measurements at additional plots were used to estimate several important components of the carbon balance in forests in Oregon and Northern California during the 1990s. Species- and ecoregion-specific allometric equations were used to estimate live and dead biomass stores, net primary productivity (NPP), and mortality. In the semiarid East Cascades and mesic Coast Range, mean total biomass was 8 and 24 kg C/m^2, and mean NPP was 0.30 and 0.78 kg C·m^{-2}·yr^{-1}, respectively. Maximum NPP and dead biomass stores were most influenced by climate, whereas maximum live biomass stores and mortality were most influenced by forest type. Within ecoregions, mean live and dead biomass were usually higher on public lands, primarily because of the younger age class distribution on private lands. Decrease in NPP with age was not general across ecoregions, with no marked decline in old stands (>200 years old) in some ecoregions. In the absence of stand-replacing disturbance, total landscape carbon stocks could theoretically increase from 3.2 ± 0.34 Pg C to 5.9 ± 1.34 Pg C (a 46% increase) if forests were managed for maximum carbon storage. Although the theoretical limit is probably unattainable, given the timber-based economy and fire regimes in some ecoregions, there is still potential to significantly increase the land-based carbon storage by increasing rotation age and reducing harvest rates.

Key words: carbon cycle; climate regime; coarse woody debris, CWD; inventory data; management; mortality rates; net primary production; west-coast forests, USA.

Introduction

The amount of carbon sequestered by forest ecosystems plays an important role in regulating atmospheric levels of carbon dioxide (Canadell et al. 2007, Denman et al. 2007). Factors affecting the amount and rate at which forests sequester carbon include climate, disturbance, management, land use history, and species composition (Peet 1981, Harcombe et al. 1990, Law et al. 2004, Krankina et al. 2005, Gough et al. 2007). Pending and future forest management policies are attempting to offset anthropogenic carbon dioxide emissions by increasing and maintaining land-based sinks of carbon (IPCC 2007). Thus, it is important to quantify current and potential forest carbon pools and fluxes, and to understand factors that account for geographic variation.

Of particular interest is examination of age-specific trends. Commonly accepted patterns of live biomass accumulation and NPP in relation to stand age show a stabilization or decline as stands age (Bormann and Likens 1969, Odum 1969, Peet 1981). These patterns

have been identified using a variety of small-scale ecological studies that tend to select homogeneous stands (McCune and Menges 1986). However, because federal inventory plots are located in all types of stands (including transitional forests, uneven-aged stands, and areas that have experienced partial disturbances), the patterns of growth that emerge from inventory data may not follow idealized trends. The distinction between patterns elucidated from a sample of forest plots selected based on defined structural criteria, and a sample of stands selected regularly from the entire population is important when validating process models applied across landscapes (e.g., Jenkins et al. 2001). For this reason the patterns of carbon pools and fluxes over time, identified in inventory data, are uniquely powerful in that they can reveal collective trends (i.e., average values) in addition to idealized trends (i.e., upper bounds or maximum values).

In this study, data from supplemental field plots (i.e., foliage and fine-root metrics) and federal inventory data (FIA) were used to examine patterns of NPP, mortality, and live and dead carbon stores in different ecoregions of Oregon and Northern California, USA. The objectives were to: (1) identify age-related patterns of mean and maximum live biomass, dead biomass, NPP, and mortality; (2) determine the influence of forest type,
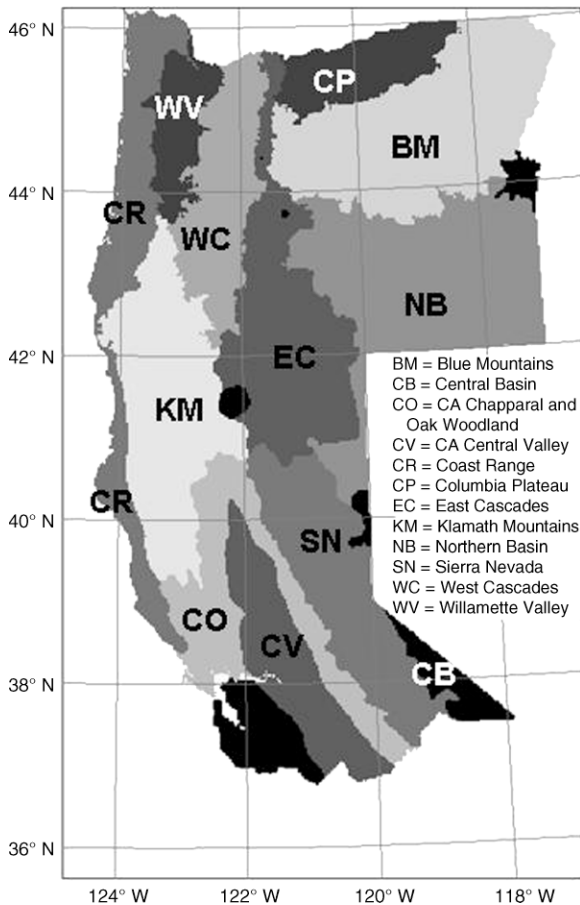
FIG. 1. ORCA study region (Oregon and Northern California, USA) divided by Omernik Level III ecoregions (Omernik 1987); different shades of gray show the different ecoregions.

BM = Blue Mountains
CB = Central Basin
CO = CA Chapparal and
    Oak Woodland
CV = CA Central Valley
CR = Coast Range
CP = Columbia Plateau
EC = East Cascades
KM = Klamath Mountains
NB = Northern Basin
SN = Sierra Nevada
WC = West Cascades
WV = Willamette Valley

carbon stocks using supplemental data and species- and ecoregion-specific allometrics.

METHODS

Study area

The ORCA project is part of the North American Carbon Program (NACP), where the goal is to quantify and understand the carbon balance of North America. The study area is the entire state of Oregon and the northern half of California (Fig. 1). The disturbance history of the region includes frequent windthrow near the coast, relatively short harvest cycles, and centuries-long fire cycles west of the Cascade crest, moderate-length harvest cycles with more frequent natural fire cycles to the drier east, and livestock grazing in the Great Basin.

The area was divided into 12 ecoregions using the U.S. EPA Level III Omernik classification scheme (Omernik 1987). The ecoregions are classified according to similar biotic and abiotic characteristics, including dominant land cover type, climate, soils, and topography. They encompass several cover types such as chaparral, juniper woodlands, coastal Douglas-fir and hemlock, and true fir alpine forests. Age-related patterns of biomass accumulation, NPP, and mortality were only examined for the dominant six ecoregions (Table 1). Totals and means were calculated for all ecoregions (Appendix: Tables A1 and A2). Approximately 50% of this area is forested land, with 56% under public ownership and 44% under private ownership (Table 1). There is a steep west to east climatic gradient, with annual precipitation ranging from 2510 mm in the Coast Range to 120 mm in the Central Basin.

Data were used from several different inventories collected by federal and state agencies and our field crews. Within plots, allometric calculations were made for each individual tree, shrub, and woody detritus record and summations were made to obtain plot total live and dead biomass carbon estimates per unit ground area and an NPP and mortality estimate per unit ground area per year.

FIA database

The federal inventory program (FIA, Forest Inventory and Analysis) has undergone recent changes in sampling protocols starting in 2001. Historically, states were measured in subsections with a complete inventory of the states completed within 10–12 years (referred to as periodic inventories). The last complete inventory (1991–1999) in Oregon and California is summarized in the Integrated Database version 2.0 or IDB (Waddell and Hiserote 2005). Under a more recent protocol (annual inventory), portions of each subsection are completed each year, with a complete inventory expected by 2010. We chose to use the earlier periodic database because it is the most recent complete cycle and thus more representative of the study region. Our results thus approximate conditions in the mid-1990s.

ecoregion (climate), and ownership (management) on these patterns; (3) quantify total and theoretical forest carbon stocks and NPP over the study region; and (4) investigate the potential for increased land-based carbon sequestration in Oregon and Northern California forests. We examined differences in carbon pools and fluxes due to species composition, climate, and management indicated by forest type, ecoregion, and ownership, respectively. We used the patterns to determine the current land-based total stocks (excluding forest floor and soil carbon) and NPP, as well as the theoretical stocks and NPP in the absence of stand-replacing disturbance. The theoretical estimates are representative of the potential for carbon sequestration in this region through management practices. This study complements studies by Hicke et al. (2007) and Van Tuyl et al. (2005) by including additional carbon pools and fluxes (dead wood and shrub biomass, NPP, and mortality), examining possible causes of variation due to management and climate, and by further refining the estimates of

TABLE 1. Ecoregion mean annual precipitation (MAP), mean winter and summer temperature (MAT), total and forested area, and stand age.

Ecoregion†	No. plots	MAT (°C) (winter/summer)	MAP (mm)	Total area (ha)	Forested area (ha)	Mean stand age (yr)‡			All plots, and plots >200 yr old (%)	
						All	Private	Public	Private	Public
BM	1266	−2/17	630	6 206 770	2 852 987	195 (3)	121 (9)	204 (3)	10, <1	90, 42
CR	737	7/18	2500	3 633 280	3 280 871	128 (4)	83 (3)	156 (6)	35, <1	65, 14
EC	1834	−3/17	500	4 795 480	2 971 042	185 (2)	133 (5)	190 (3)	8, 1	92, 36
KM	1526	3/21	1500	4 850 310	4 076 569	219 (4)	132 (6)	231 (4)	11, 1	89, 47
SN	1268	5/15	1500	3 931 700	3 059 246	196 (4)	146 (7)	201 (4)	9, 1	91, 38
WC	1896	4/16	2200	3 038 260	2 889 914	248 (4)	105 (36)	254 (4)	4, <1	96, 57
CB	26	4/11	150	834 689	165 932	210 (27)	84	219 (28)	4, 0	96, 50
CO	116	4/30	630	4 222 085	1 773 527	120 (6)	117 (7)	113 (14)	70, 7	30, 3
CP	4	0/21	250	1 756 090	40 046	145 (45)	145 (45)	...	100, 25	...
CV	0	10/17	450	2 656 190	49 832	...	...	...	...	...
NB	36	−1/18	250	6 556 370	174 125	150 (21)	184 (54)	177 (26)	17, 3	83, 22
WV	46	4/20	1270	1 373 040	504 923	109 (13)	86 (7)	162 (36)	70, 0	30, 9
Total	8755	2/18	1075	43 854 264	21 839 014	201 (2)	115 (2)	213 (1.5)	31, 1	41

Note: Ellipses in cells indicate that no data are available.

† BM, Blue Mountains; CR, Coast Range; EC, East Cascades; KM, Klamath Mountains; SN, Sierra Nevada; WC, West Cascades; CO, California Chaparral and Oak Woodlands; WV, Willamette Valley; NB, North Basin and Range; CB, Central Basin and Range; CP, Columbia Plateau; CV, Central California Valley.

‡ Standard errors in parentheses.

§ The first value is the percentage of total plots in private vs. public ownership. The second value after the comma is the percentage of total plots that are >200 years old in private vs. public ownership.

There were 14 188 plots with live tree data and 12 380 plots with woody detritus and understory data within the study area boundary (Fig. 1). The inventory design consists of 0.404-ha (1-acre) plots systematically placed across the landscape, encompassing a representative range of stand ages, disturbance histories, ownerships, and land cover types. The inventory data include tree diameter (dbh), actual height, wood increment, age, and species. Understory woody shrub data include percent cover, height, and species. Coarse woody debris and snag data include diameter, decay class, and species. We excluded plots that did not have enough increment data (1290 plots) to suitably calculate a stand age or a radial growth. One or more condition classes were assigned to plots that had more than one ownership, forest type, or disturbance history. Because we were interested in differences due to ownership and forest type, we chose to use plots with only one condition class. There were 4143 multi-condition plots distributed throughout the study area. A separate analysis of live biomass that included the multi-condition plots was done to determine if exclusion of these plots affected the overall results. The ecoregion means for total live biomass were slightly higher in the majority of areas, equivalent in some, and lower in the Coast Range by 0.90 kg C/m^2 (Appendix: Table A3). The regression of the 5-year age bin means for all plots vs. the corresponding single-condition bin means had values ranging from $r^2 = 0.75$ in the Blue Mountains to $r^2 = 0.91$ in the West Cascades.

After exclusions, 8755 plots remained with live tree and understory data, of which 8135 plots had measured woody detritus data. These plots were used to analyze NPP, mortality, and biomass for age-related trends as influenced by ecoregion, management, and forest type.

To evaluate and augment the federal inventory plots, we also used data from 170 supplemental field plots systematically dispersed among the ecoregions in the study area. Although these 1-ha plots cover a larger spatial area, the subplot and transect layouts, measurement protocols, and data collected met or exceeded the minimum standards of the federal inventory. Our plot locations were selected using a hierarchical random sampling design based on climate, forest type, and age (Law et al. 2006). The additional sampling was designed to allow a more comprehensive assessment of the carbon stocks and fluxes (Law et al. 2004, Sun et al. 2004, Van Tuyl et al. 2005, Law et al. 2006) by measuring foliage and soil carbon and nitrogen, leaf retention time, foliage and fine-root biomass and production (on selected plots), leaf area index, and litter stocks.

Stand age

Plot stand age was computed as the mean of the oldest 10% of trees (Spies and Franklin 1991, Van Tuyl et al. 2005). In cases where there were fewer than three trees in the oldest 10%, a mean of all aged trees on the plot was used. Stands older than 600 years were grouped into a single age class to account for an increasing trend in within plot variation. Although this method is the appropriate metric to best detect trends in growth and mortality, it is different than age based on time since disturbance and does not include effects of delayed establishment that vary widely (and probably with ecoregion, forest type, and ownership).

Ownership and forest types

Ownership was used as a surrogate for management practices because anthropogenic disturbances (i.e.,

clearcut harvest and thinning) have been more common on privately owned lands than on publicly owned lands in this region (Spies et al. 1994, Cohen et al. 2002). Public lands are defined as all non-private lands (federal, tribal, state, county, and so on). Private lands include small ownerships to large industrial properties.

Inventory plots were assigned a forest type code based on the dominant species on the plot. We grouped forest types into seven classes: (1) fir/Douglas-fir/hemlock, (2) larch and cedar/sequoia/redwood, (3) juniper, (4) spruce, (5) pine, (6) hardwoods, and (7) non-stocked. Non-stocked forest types are assigned to plots with a large percentage of ground area that is unsuitable for growth (i.e., rocky substrates).

Biomass

A database of volume and biomass allometric equations was compiled from prior studies (e.g., Means et al. 1994, Law et al. 2001, Van Tuyl et al. 2005) and new literature. We aimed to apply as many species-specific and ecoregion-specific equations as possible. Biomass estimates for trees included bole, bark, branch, foliage, and coarse roots (Appendix: Table A4). Species-specific wood densities (Maeglin and Wahlgren 1972, Forest Products Laboratory 1974) from wood cores obtained on our 170 supplemental plots were used to convert bole and coarse-root volume to biomass. For standing dead trees, wood densities were reduced according to decay class (Waddell 2002). Tree component biomass estimates were converted to kilograms per unit of ground area by multiplying by the tree-specific trees per hectare (TPH) and by 0.51 to obtain units of carbon (Law et al. 2001). TPH is a scaling factor for each tree record that is based on the sampled area and is supplied by the IDB specifically for generating plot-scale biomass estimates (Waddell and Hiserote 2005).

Fine-root biomass was estimated using an equation from earlier studies (Van Tuyl et al. 2005; Appendix: Table A4) relating leaf area index (LAI) and fine-root biomass. LAI is not measured on inventory plots, but was calculated by dividing foliage biomass (from the allometric equations) by the leaf mass per unit leaf area (LMA). LMA was obtained from a look-up table of species-specific values derived from measurements on the supplemental plots in each of the ecoregions. In some cases, a species-specific value was not available so a closely related (i.e., congeneric) species was used.

The conversion of shrub volume to biomass was from a database of allometric equations based on shrubs harvested at our supplemental plots. In total, 12 species were harvested, covering a wide range of morphology, leaf type, and leaf longevity, allowing for substitution of equations for all species where an equation could not be found. Shrub volume was calculated as the product of the recorded fraction of plot cover, plot area, and height. Coarse woody debris biomass was estimated following Waddell (2002). Biomass was calculated using piece volume, species-specific wood density, and a decay-class density reduction factor.

NPP and mortality

To calculate NPP for a plot, a radial increment is necessary for every tree on the plot. Federal inventory includes stem increment cores for a subsample of the trees on each plot. For our estimates, trees on a plot were divided into dbh quartiles and the mean radial increment of cored trees in each quartile was assigned to all other trees in the same quartile (Sun et al. 2004, Van Tuyl et al. 2005).

Net primary production of all tree woody components was estimated as the difference in biomass at two points in time and was divided by the remeasurement interval (usually about 10 years). A previous dbh and height for each tree were necessary to calculate a previous biomass. Previous dbh was derived by back-calculation from current dbh and the radial increment, and previous height was recorded for remeasured trees or was modeled for unmeasured trees in the previous inventory using height–diameter regression equations from our supplemental plot data and BioPak (Means et al. 1994).

Woody shrub, foliage, and fine-root NPP were calculated using look-up tables constructed from supplemental plot data. Foliage NPP was calculated by dividing foliage biomass per tree by the average foliage retention time (average number of years of foliage that a stand carries). An ecoregion species-specific look-up table of foliage retention values was constructed from data gathered on the supplemental plots. Woody shrub NPP was calculated as a percentage increase in biomass per year. Increment disks from several shrub species were collected on the supplemental plots to produce a look-up table of average percentage increase in biomass for the species in each ecoregion. Fine-root NPP was calculated as the product of fine-root biomass and average fine-root turnover (1.2 year^{-1}) obtained from the literature and supplemental plot data (Keyes and Grier 1981, Campbell et al. 2004).

Mortality in kilograms of carbon per meter squared per year was only computed for trees. The IDB has assigned a mortality rate, the probability (0–1) that a given tree may die in one year due to natural causes, to each tree record. It is derived from a ratio of dead-to-live trees that were tallied on plots throughout the inventory area and developed for different groups by species and/or location (Waddell and Hiserote 2005). The amount of mortality expressed as the biomass loss per year can be estimated by multiplying the total live tree biomass by the location and/or species-specific mortality rate.

Statistical analysis

S-PLUS version 7.02 (S-PLUS 2005) was used for all statistical analysis. The questions of interest were addressed by comparing the coefficients of the response functions fit to the age-based distributions. Plots with

stand ages greater than 600 years were grouped into a single age group. Because less than 1% of plots on private land had age groups greater than 200 years, statistical analysis for comparisons between ownerships were restricted to plots aged 200 years or less for both public and private land.

Historically, private land ownership has tended to be located in lower elevation forested areas characterized by higher productivity. We confirmed this difference by comparing mean site index (a measure of site potential productivity) across ownerships for the stand area. We found a significantly higher mean site index value for private lands ($P < 0.01$, by permutation test). To isolate effects of differences in stand age distribution between ownerships from differences in site potential, the public land data set in each ecoregion was randomly subsampled using a constrained range and distribution of site indexes that was defined by private land distributions in the same ecoregion. This distribution was then used for the comparisons across ownerships.

To compare the coefficients of the fitted functions, the data for each ecoregion, ownership, or forest type were first binned into 25-year age groups and a stratified random sample of observations was chosen to ensure that the sample included data points from the entire age range. The appropriate functions were then fit to the sample data set. The sampling process and curve fitting were repeated to obtain 10 different estimates of each coefficient (used to produce a stand error) for each ecoregion and for ownership and forest type within ecoregion. A weighted one-way ANOVA using the coefficient standard errors as the weight was run for each coefficient to test for significant differences. To determine the relative influence of ecoregion, ownership, and forest type on biomass stores, NPP, and mortality across the entire study area and within ecoregion, the data were $\log_e$-transformed and linear regression models were compared using Akaike's information criterion (AIC). For the entire study area, model weights for age only, age + ownership, age + forest type, and age + ecoregion were calculated and ranked to determine the most influential explanatory variable (Burnham and Anderson 2002). Within ecoregion, model weights were calculated for age only, age + ownership and age + forest type.

Chapman-Richards functions (Pienaar and Turnbull 1973) were fit to live biomass and mortality data to compare the amount (mean and maximum) of carbon stored in biomass as a function of age:

$$\text{biomass} = a[1 - \exp(-b \times \text{stand age})]^c \qquad (1)$$

where parameter a is the asymptote, or the maximum amount of biomass carbon; parameter b determines the rate in years that it takes to reach the maximum amount; and c is a shaping parameter that gives a Chapman-Richards relationship the characteristic sigmoid shape. Because we were interested in the age at which NPP peaked and started to decline, a peak function (three-parameter, log-normal) was fit to the NPP data:

$$\text{NPP} = a \times \exp\left\{-0.5[\ln(\text{stand age}/c)/b]^2\right\} \qquad (2)$$

where parameter a is the asymptote or the maximum NPP; b is the rate to reach maximum; and c represents the age of initial NPP decline.

Woody detritus data can be fit with a standard decay function plus a Chapman-Richards function (Janisch and Harmon 2002). Stands typically start with large stores of legacy dead wood from prior stand development or downed wood caused by disturbance and then start to accumulate dead biomass as they age. The decay function quantifies the decay of the legacy dead wood in clearcut/burned and very young stands and the Chapman-Richards function quantifies the accumulation of dead wood as the stand ages:

$$\text{biomass} = d \times \exp(-e \times \text{stand age}) \\ + a[1 - \exp(-b \times \text{stand age})]^c \qquad (3)$$

where parameter d is the initial carbon stores and e is the decay rate in years. Although we were able to fit this function to all of the data in each ecoregion, we were unable to detect a U-shaped pattern with stand age in the smaller random samples used to compare the coefficients of the fitted function. Therefore, the data were divided into three age classes and a permutation test for a difference of means in each age class (by ecoregion or ownership) was used.

All of the above-mentioned curves were fit to both the mean values in each 5-year age bin and to the 99th percentile (hereafter "upper bound") of each age bin. Curves fit to the mean values represent the average realized trends of biomass, mortality, and NPP, whereas the curve fit to the upper bounds should represent the maximum values of stands in the ecoregion given minimal disturbance and ideal site and growing conditions. Curves fit to the upper bounds could also represent what many ecological field studies have documented and therefore what many modelers have used to parameterize and validate model results.

Regional-scale analyses

Total biomass, NPP, and mortality estimates for each ecoregion, state, and the total ORCA study area were obtained as the sum of the product of the relevant forested area using land cover data from Advanced Very High Resolution Radiometer (AVHRR) composite images recorded during the 1991 growing season (USDA Forest Service and U.S. Geological Survey 2002) and the corresponding mean values across all plots. The same procedure was used with GIS ownership coverages (from USGS National Land Cover Data 1992) to isolate patterns by public and private ownerships. Theoretical values for live biomass, dead biomass, and NPP were determined for each forest type × ecoregion combination using the parameter estimates for the maximum (parameter a) from the curve fit to the mean values of the data (note that this was from the

mean trend, not the upper bounds). Although these values should represent the maximum amounts, given a range of site productivities, and also should allow for partial disturbance, the amounts calculated assume the absence of stand-replacing disturbance through full harvest or catastrophic wildfire. Uncertainty estimates for regional stocks and NPP were calculated with a Monte Carlo procedure using the ecoregion mean and standard errors for the current values and the ecoregion parameter *a* estimates and standard errors for theoretical values. Simulations were run using a random normal distribution. We tested the independence assumption by using correlation coefficients for no correlation (0.0) and perfect correlation (1.0). Because the results did not vary significantly, uncertainty estimates for the simulations assuming no correlation are reported. Maps (ArcGIS version 9.1; ESRI 2005) of current mean and potential maximum carbon stocks and NPP were produced using the above results and a forest type land cover layer (USDA Forest Service and U.S. Geological Survey 2002).

<center>RESULTS</center>

<center>*Ecoregion patterns*</center>

There is strong evidence ($P < 0.001$) that maximum amounts of live biomass and rate of accumulation differ by ecoregion (Fig. 2). The Chapman-Richards function appeared to be a good general equation to describe biomass accumulation (Appendix: Table A5), especially for the upper bounds data in the West Cascades. When fit to the mean values, the maximum amount of live biomass (*a* in Eq. 1) is highest in the Coast Range and Klamath Mountains (33–44 kg C/m²) and lowest in the East Cascades and Blue Mountains (7–10 kg C/m²). The rate (*b* in Eq. 1) at which biomass reaches the maximum is lowest in the Klamath Mountains, with maximum stores still increasing at 600 years. Rates are higher in the other ecoregions, yet biomass is still increasing in stands over 300 years in the Coast Range, the Sierra Nevada, and the West Cascades.

We were unable to measure the inputs to or outputs from dead biomass, but we were able to compare the dynamic balance between these processes across ecoregions as measured by the standing mass of dead wood in three age groups (Table 2). There is strong evidence ($P < 0.001$, from a permutation test) that mean dead biomass differs among ecoregions for young, mature, and old stands. The Coast Range and West Cascades had the highest mass of dead wood in all age groups (ranging from 3.1 kg C/m² in the young to 4.7 kg C/m² in the old). The East Cascades had the lowest mass of dead wood in all age groups (ranging from 0.8 to 1.7 kg C/m²) and the Klamath Mountains and Sierra Nevada had intermediate levels (ranging from 0.8 to 2.7 kg C/m²).

The theoretical U-shaped pattern of dead biomass over time (high levels initially after disturbance, followed by low levels as this legacy wood decays, then

by high levels as new dead wood is recruited) was mostly apparent in the West Cascades when fit to the upper bounds (Appendix: Table A6), and slightly apparent in the East Cascades and Sierra Nevada (Fig. 3). The pattern was only slightly apparent in the West Cascades when fit to the mean values.

There is strong evidence ($P < 0.001$) that maximum NPP differs among ecoregions (Fig. 4). Maximum NPP peaks earliest in the Coast Range and West Cascades at about 80 years. The most obvious cases of late-successional decline in NPP for the upper-bound data were in the ecoregions with highest maximum NPP (Coast Range, West Cascades, and Klamath Mountains). Interestingly, the Coast Range was the only case of a conspicuous decline in mean NPP with age.

There was strong evidence ($P < 0.001$) that both maximum mortality and the rate at which it is reached differs among ecoregions (Appendix: Table A5). Maximum mortality was highest in the Sierra Nevada, followed by the West Cascades and Klamath Mountains for both the mean trend and upper bounds of the data (Fig. 5). Mortality appeared to increase with stand age and become less predictable in older stands. As a percentage of live biomass, mortality ranged from 0.50% in the Coast Range to 1.20% in the Sierra Nevada for stands younger than 80 years, from 0.35% in the Coast Range to 1.30% in the Sierra Nevada for mature (80–200 year old) stands, and from 0.35% in the Coast Range to 1.35% in the Blue Mountains for old stands (>200 years old).

<center>*Ownership patterns*</center>

Stand ages varied from 0 to over 1000 years, with a higher frequency of younger stands on private land than public land and more old stands on public lands (Fig. 6). Mean stand age for private ownership ranged from 83 years in the Coast Range to 146 years in the Sierra Nevada (Table 1). Public ownership mean ages ranged from 156 years in the Coast Range to 244 years in the West Cascades, where most of the land is public. There are very few stands older than 250 years on private land.

After accounting for site index, there is strong evidence that mean and maximum biomass differed between ownerships in all but the Blue Mountains and East Cascades ($P < 0.001$), with generally higher values on public lands (parameter *a* in Eq. 1, Appendix: Table A7). Dead biomass was not as consistently influenced by ownership as was live biomass (Table 2).

There is also strong evidence that mean NPP differed between ownerships ($P < 0.001$), being generally lower on public lands. Maximum NPP (parameter *a* in Eq. 2) was lower on public lands in the Coast Range, East Cascades, and the West Cascades and showed no difference in the Blue Mountains and Klamath Mountains (Appendix: Table A7). The number of years required to reach maximum rates of NPP was higher on public land ($P < 0.01$) in the Blue Mountains, East Cascades, and Sierra Nevada. Maximum mortality was
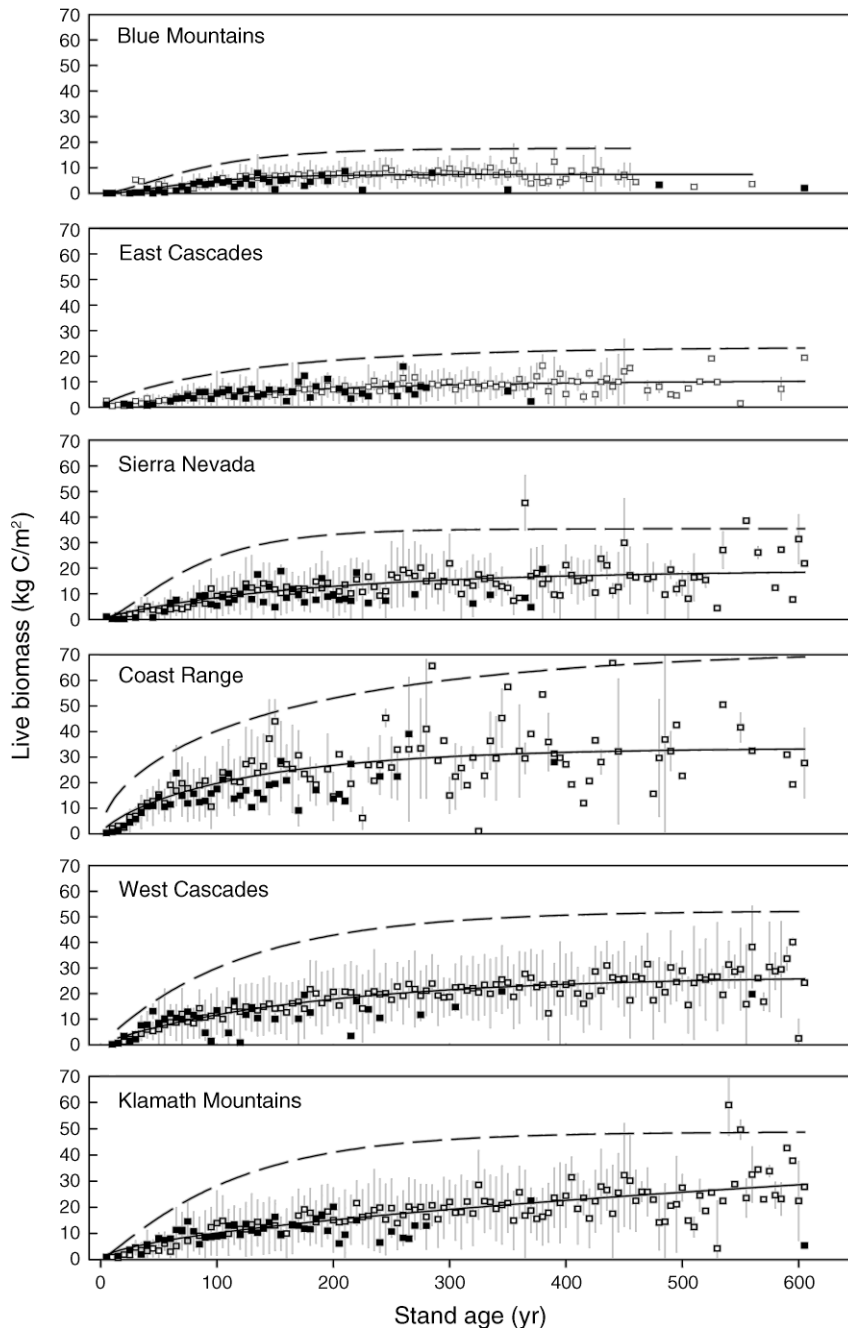
FIG. 2. Live biomass (trees and understory woody shrubs) vs. stand age. The dashed line (upper bounds) and solid line (mean trend) were fit using a Chapman-Richards function. Open (public) and solid (private) squares are the mean biomass for plots grouped into 5-year age bins. Gray vertical lines are the standard deviations in each bin. Note that, for clarity, plot mean values for the upper-bounds (99th-percentile) curve of the data are not shown on the figure.

higher on public land in the Blue Mountains and Sierra Nevada, but lower in the Coast Range.

Forest type patterns

Forest type differences were examined for live biomass and NPP. There was strong evidence ($P < 0.001$) that forest types within an ecoregion differ in

maximum live biomass accumulation, maximum NPP, years required to reach maximum NPP, and age at initial decline of NPP (Appendix: Table A8). The overall variation in age-related patterns of biomass accumulation was reduced in some ecoregions when the Chapman-Richards functions were fit to the data separated by forest type. Douglas-fir forest types had the highest

TABLE 2.   Estimates (mean with SD in parentheses) by age group, maximum of mean trend, and age at which maximum is reached for biomass, NPP, and mortality in each ecoregion and by ownership.

Ecoregion	Young	Mature	Old	Maximum	Age at max. (yr)	Young Private	Young Public	Mature Private	Mature Public
Live biomass (kg C/m²)									
BM	1.9 (2.1)	5.9 (3.6)	7.4 (4.1)	7.1 (0.2)	180	3.0 (2.7)	3.1 (2.3)	4.8 (2.9)	6.5 (3.7)
CR	10.9 (6.9)	22.7 (12.4)	30.0 (14.5)	33.4 (3.0)	310	10.5 (7.9)	12.7 (6.6)	16.1 (7.8)	25.9 (12.9)
EC	3.0 (2.7)	6.2 (4.6)	8.7 (5.5)	10.1 (0.8)	310	3.1 (2.9)	3.2 (2.1)	6.4 (4.5)	5.6 (3.7)
KM	5.2 (5.0)	13.0 (8.9)	20.0 (11.9)	44.2 (33.0)	600+	8.3 (6.0)	7.3 (6.2)	12.4 (7.3)	15.0 (9.4)
SN	3.8 (3.5)	11.1 (7.3)	14.9 (9.6)	19.4 (0.7)	500	3.2 (4.3)	3.8 (3.4)	9.4 (5.0)	11.7 (7.3)
WC	6.2 (5.2)	14.6 (9.8)	22.1 (11.9)	26.9 (2.0)	430	7.9 (5.6)	7.0 (5.5)	11.3 (7.1)	16.4 (10.7)
Dead biomass (kg C/m²)									
BM	1.0 (0.9)	1.9 (1.8)	2.1 (1.9)	2.1 (1.9)	200+	0.6 (0.0)	1.0 (0.8)	1.6 (1.2)	1.8 (1.8)
CR	3.1 (2.7)	3.6 (2.9)	4.7 (4.8)	4.7 (4.8)	200+	3.2 (2.5)	3.2 (2.8)	2.9 (2.4)	3.8 (3.0)
EC	0.8 (0.8)	1.3 (1.2)	1.7 (1.6)	1.7 (1.6)	200+	1.9 (1.3)	0.7 (0.7)	1.3 (1.2)	1.3 (1.1)
KM	1.5 (1.4)	1.6 (1.5)	2.6 (2.3)	2.6 (2.3)	200+	2.0 (1.2)	1.9 (2.1)	1.9 (1.5)	1.6 (1.5)
SN	0.8 (0.8)	1.9 (1.7)	2.7 (2.2)	2.8 (0.2)	200+	2.4 (1.7)	0.8 (0.7)	1.9 (1.4)	1.7 (1.6)
WC	3.1 (3.1)	2.5 (2.2)	4.9 (4.1)	9.5 (5.2)	200+	4.0 (3.6)	3.2 (3.2)	3.2 (2.6)	2.7 (2.2)
NPP (kg C·m⁻²·yr⁻¹)									
BM	0.16 (0.12)	0.27 (0.10)	0.29 (0.09)	0.30 (0.01)	125	0.23 (0.15)	0.23 (0.12)	0.28 (0.11)	0.29 (0.07)
CR	0.75 (0.31)	0.80 (0.24)	0.77 (0.27)	0.82 (0.03)	60	0.75 (0.36)	0.79 (0.23)	0.91 (0.29)	0.78 (0.19)
EC	0.24 (0.15)	0.33 (0.19)	0.36 (0.15)	0.38 (0.01)	155	0.25 (0.18)	0.25 (0.10)	0.37 (0.18)	0.29 (0.12)
KM	0.45 (0.33)	0.63 (0.34)	0.62 (0.27)	0.65 (0.01)	110	0.66 (0.30)	0.65 (0.44)	0.70 (0.28)	0.73 (0.38)
SN	0.29 (0.19)	0.48 (0.22)	0.49 (0.20)	0.51 (0.01)	125	0.25 (0.23)	0.30 (0.19)	0.50 (0.19)	0.46 (0.21)
WC	0.46 (0.26)	0.52 (0.21)	0.49 (0.15)	0.54 (0.01)	65	0.59 (0.31)	0.50 (0.24)	0.59 (0.26)	0.54 (0.21)
Mortality (kg C·m⁻²·yr⁻¹)									
BM	0.02 (0.02)	0.07 (0.02)	0.10 (0.08)	0.10 (0.00)	140	0.03 (0.03)	0.03 (0.02)	0.05 (0.04)	0.08 (0.07)
CR	0.05 (0.05)	0.06 (0.04)	0.08 (0.04)	0.09 (0.01)	270	0.06 (0.06)	0.05 (0.03)	0.08 (0.05)	0.05 (0.02)
EC	0.03 (0.03)	0.07 (0.09)	0.10 (0.12)	0.11 (0.01)	270	0.02 (0.02)	0.03 (0.03)	0.06 (0.06)	0.05 (0.05)
KM	0.03 (0.04)	0.08 (0.09)	0.13 (0.11)	0.29 (0.27)	600+	0.06 (0.05)	0.03 (0.02)	0.07 (0.07)	0.06 (0.04)
SN	0.04 (0.02)	0.13 (0.12)	0.17 (0.14)	0.20 (0.02)	250	0.03 (0.03)	0.04 (0.05)	0.10 (0.08)	0.13 (0.13)
WC	0.04 (0.03)	0.10 (0.08)	0.14 (0.09)	0.17 (0.01)	310	0.02 (0.02)	0.04 (0.03)	0.05 (0.04)	0.10 (0.07)

Notes: Age groups are defined as young, <80 years old; mature, 80–200 years old; and old, >200 years old (information is not available for private land for the "old" group). Ecoregion codes are as in Table 1. Means for each ownership type (last four columns) were calculated with site-index-corrected data, resulting in higher means than for the entire data set (described in *Methods: Statistical analysis*).

maximum NPP, whereas pine forest types had the oldest age of initial decline of NPP.

Regional-scale analyses

Across the entire ORCA study region and after accounting for stand age, variation in live biomass (model weights 0.0–1.0) and mortality (model weights 0.12–0.88) was most explained by forest type, whereas variation in dead biomass (model weights 0.40–0.60) and NPP (model weights 0.02–0.98) was most explained by ecoregion (Appendix: Table A9). Within each ecoregion or climate zone, forest type was the most important explanatory variable in all cases except for mortality in the Coast Range, where ownership was most important (higher on private lands).

Total live biomass of forests in the ORCA study region (4.4×10^7 ha of forest land) is estimated at 2.71 ± 0.28 Pg C, mean ± SD (Appendix: Table A1; Figs. 7 and 8a). Understory biomass ranged from 1% to 5% of live biomass in most ecoregions and exclusion would not have resulted in a significant underestimation of biomass. Private land accounts for 35% of live biomass (and 44% of the forested area), with nearly one-third of the regional biomass in the predominantly privately

owned Coast Range. The total live biomass, assuming that all stands are at maximum carbon storage as determined by the mean trend of the data, would nearly double to 5.19 ± 1.34 Pg C (Fig. 8b). Although it would take hundreds of years to reach these theoretical levels in all ecoregions, land-based stocks could increase by 15% in just 50 years (i.e., if all stands increased in age by 50 years). Total dead biomass for the ORCA study regions is estimated at 0.51 ± 0.19 Pg C (Fig. 8c). Total dead biomass stores would increase by 36% to 0.80 ± 0.15 Pg C at maximum levels from the mean trend of the data (Fig. 8d). Total mortality of biomass for the ORCA study regions is estimated at 0.021 Pg C/yr. Total NPP of forest in the ORCA study region is estimated at 0.109 ± 0.001 Pg C/yr, mean ± SD (Fig. 9a) and total NPP would increase to 0.118 ± 0.002 Pg C/yr, assuming that all stands were at maximum NPP (Fig. 9b).

DISCUSSION

Trends with age

The expected age related ecological patterns (i.e., Chapman-Richards logistic growth for biomass accumulation, U-shaped pattern for dead biomass accumulation, and a marked decline in NPP with stand age)
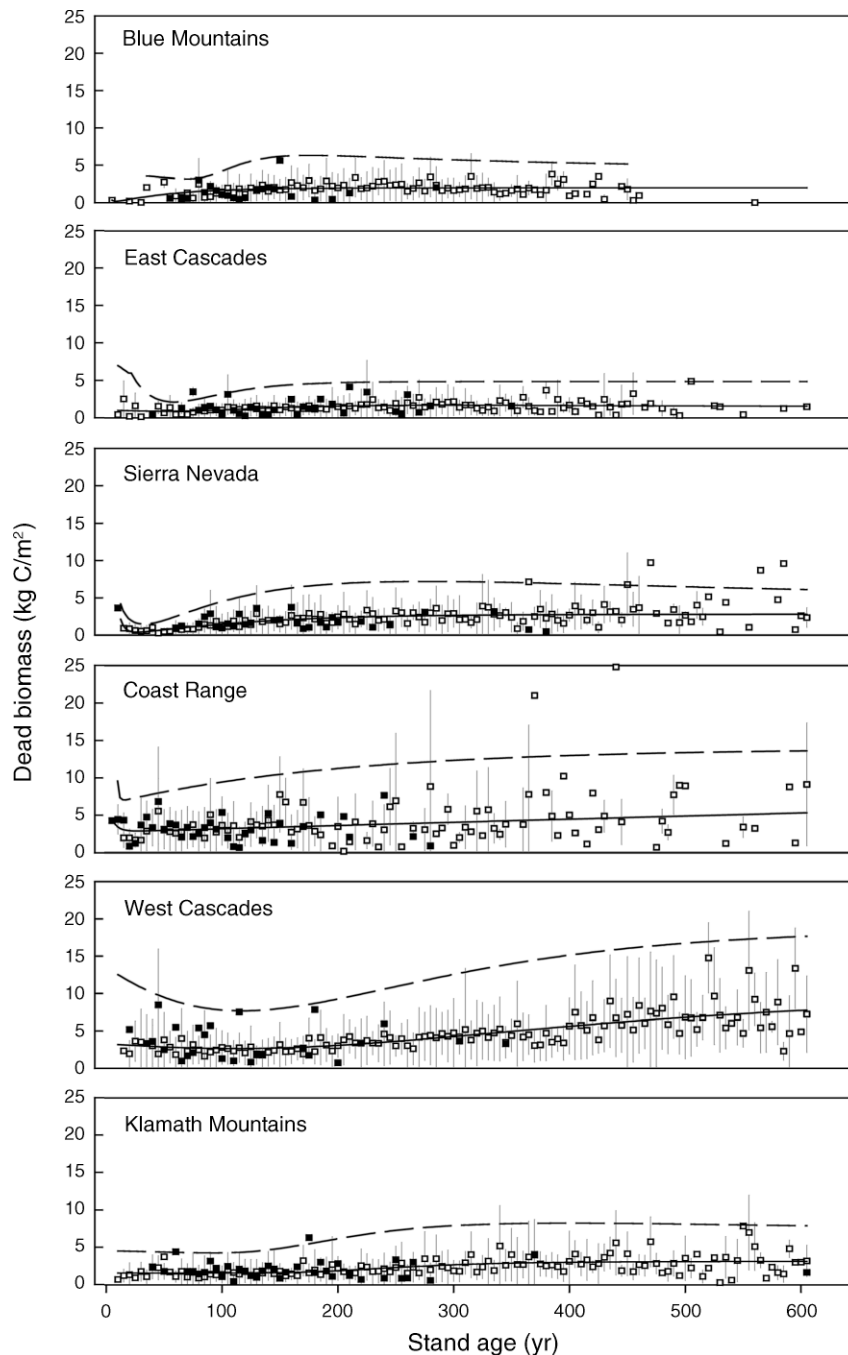
FIG. 3. Dead biomass (coarse woody debris [CWD] and standing dead trees) vs. stand age. The dashed line (upper bounds) and solid line (mean trend) were fit using a decay plus a Chapman-Richards function. Open (public) and solid (private) squares are the mean biomass for plots grouped into 5-year age bins. Gray vertical lines are the standard deviations in each bin. Note that, for clarity, plot mean values for the upper-bounds (99th-percentile) curve of the data are not shown on the figure.

were generally more distinguishable in the upper bounds of the data rather than in the age-specific mean values. In almost all cases, the West Cascades plot data were most suitably fit by these age related patterns. This is not surprising when considering that the ecological studies and data that were used to elucidate these patterns deliberately and appropriately targeted productive, smaller scale, undisturbed, mature plots, especially in the West Cascades (Acker et al. 2002, Janisch and Harmon 2002). In contrast, federal inventory sampling, by design, includes the full suite of factors that cause a given forest to grow at the full range of rates.
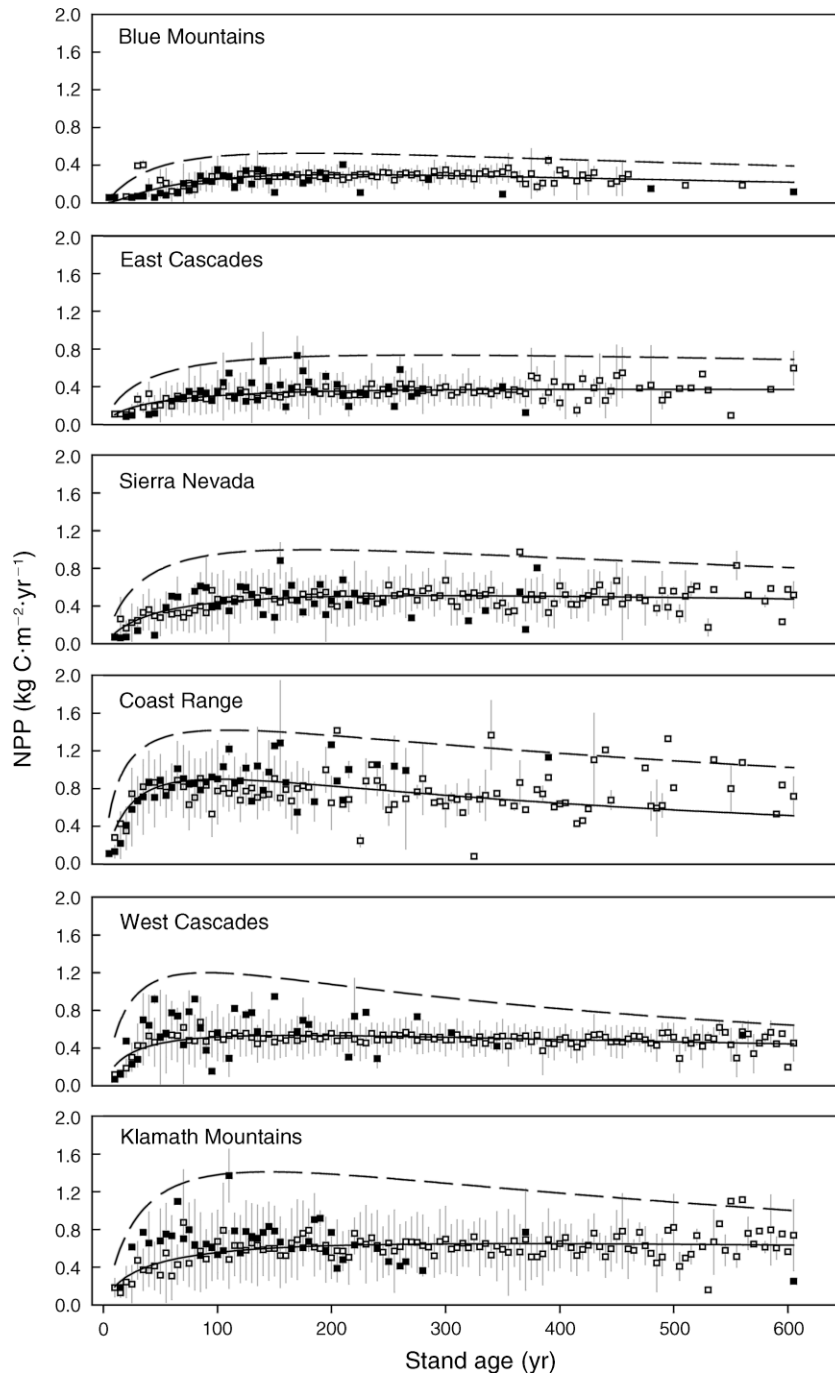
FIG. 4. Net primary productivity, NPP, of trees and understory woody shrubs vs. stand age. The dashed line (upper bounds) and solid line (mean trend) were fit using a Peak (three-parameter log-normal) function. Open (public) and solid (private) squares are the mean biomass for plots grouped into 5-year age bins. Gray vertical lines are the standard deviations in each bin. Note that, for clarity, plot mean values for the upper-bounds (99th-percentile) curve of the data are not shown on the figure.

With respect to coarse woody debris (CWD), the idealized U-shaped pattern arising from the combined and lagged effects of legacy wood decay and the recruitment of new dead wood (Harmon et al. 1986) was most apparent in the upper bounds. Coarse woody

debris biomass stores may be underestimated because the federal inventory CWD data required a minimum diameter measurement of 12.5 cm, rather than the 10 cm used by ecological studies or the 7.6 cm used by fire studies. Federal inventory data also do not include
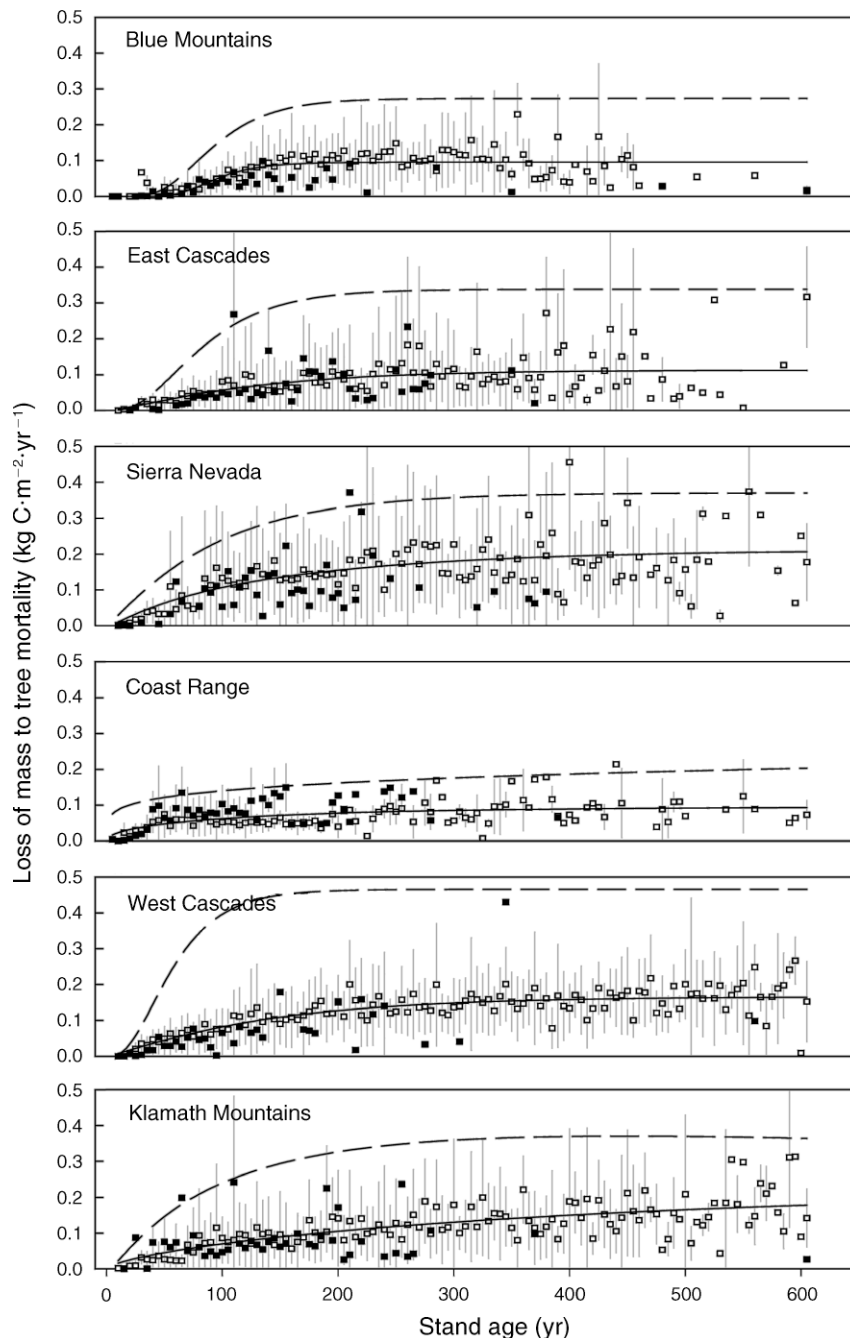
FIG. 5.   Mortality of trees (loss of live carbon mass due to the death of trees) vs. stand age. The dashed line (upper bounds) and solid line (mean trend) were fit using a Chapman-Richards function. Open (public) and solid (private) squares are the mean biomass for plots grouped into 5-year age bins. Gray vertical lines are the standard deviations in each bin. Note that, for clarity, plot mean values for the upper-bounds (99th-percentile) curve of the data are not shown on the figure.

stumps, which would increase biomass in recently harvested (young) stands causing the curve to follow a more U-shaped pattern.

Because mortality affects both the inputs to dead biomass and the rate of loss from live biomass, it is important to characterize the factors controlling it. Our analysis shows mortality (expressed as an amount) increasing with stand age and stabilizing in late succession (Fig. 5). Expressed as a fraction of live biomass, we found that mortality tends not to be a constant. For example, mortality increases nonlinearly with stand age in most ecoregions and then reaches equilibrium while live biomass continues to increase. Carbon cycle models that have been applied in the
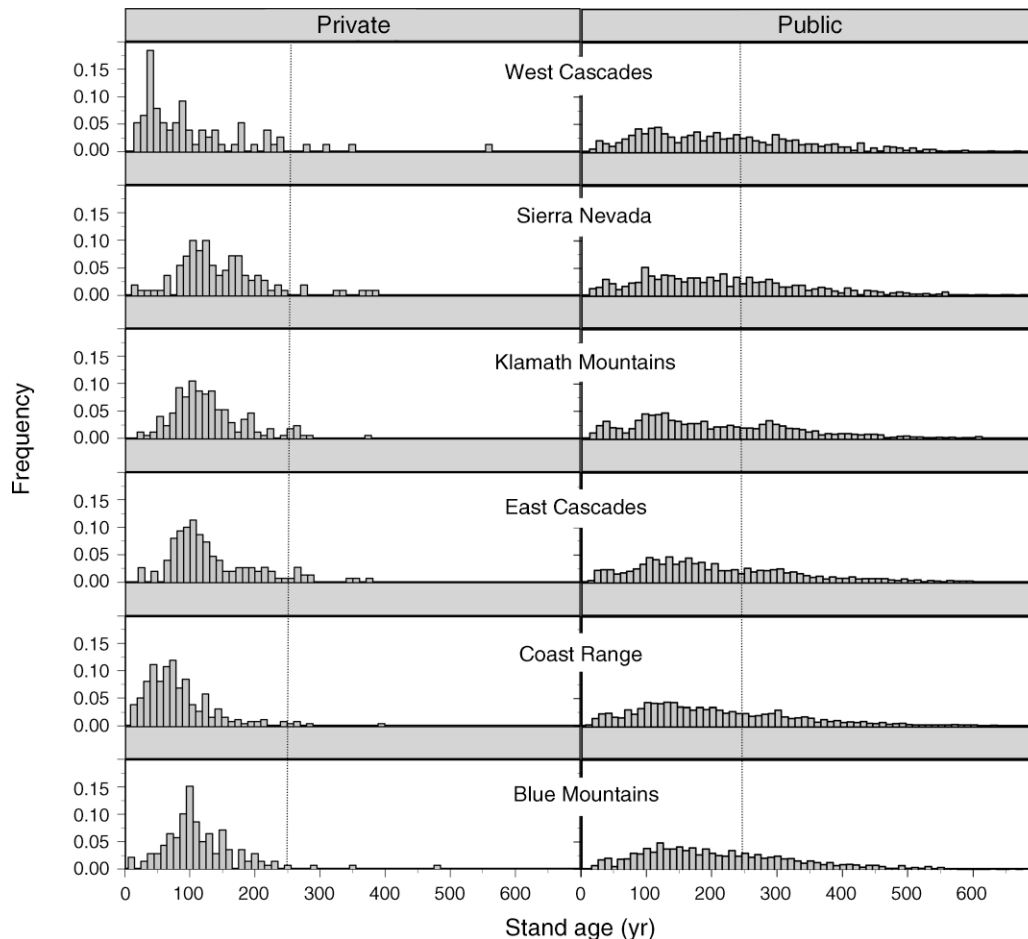
Fig. 6.   Frequency distributions of stand age by ecoregion and ownership class (private vs. public). Forests on private land tend to have more stands in lower age classes than stands on public lands. The light vertical lines delineate stands older vs. younger than 250 years.

Pacific Northwest (e.g., Turner et al. 2004) often represent mortality as a fixed percentage of live biomass and our results support the implementation of a dynamic mortality function in these models.

Increased mortality and decreased net primary production have been reported as equally responsible for late-successional stabilization of bole wood biomass in the West Cascades (Acker et al. 2002). The ecological studies upon which that conclusion is based are most relevant to our upper bound lines, and our results support these findings in some ecoregions (e.g., Coast Range, West Cascades, and Klamath Mountains). In those cases, upper bound NPP peaks at approximately 80 years and then declines (Fig. 4), and mortality (Fig. 5) increases with age to a stable rate that approximates bole-wood production. The FIA data suggest that in the most productive ecoregions, biomass continues to accumulate at low rates in very old stands.

In other ecoregions, there is less marked decline in NPP with age, or no apparent decline in NPP. For instance, pine forests in the Blue Mountains, East Cascades, and Klamath Mountains experienced NPP declines at significantly older ages than did other forest types in these ecoregions (Appendix: Table A5). The traditional explanation for NPP decline with age in forests, i.e., stable GPP and increasing autotrophic respiration, has largely been rejected in PNW forests (Ryan et al. 2004). The fact that decline is most apparent in the upper bound lines and least apparent for the relatively low productivity, more open-grown, pine forest type lends support to the hypothesis that competition-related changes in stand structure (Binkley et al. 2002) may be the critical driving factor.

Ecoregion patterns

In general, wetter ecoregions west of the Cascade Mountains crest (Klamath, Coast Range, and West Cascades) had much higher NPP and biomass stores at a given age than the drier ecoregions east of the crest (East Cascades and Blue Mountains). Despite the relatively high NPP and live biomass in the Klamath Mountains, dead biomass stores were 50–60% lower than in the

Coast Range and West Cascades. Although mortality rates are generally higher for both the Coast Range and West Cascades vs. the Klamath Mountains, the difference does not account for the large difference in dead biomass stores. Dead wood biomass is either being removed or consumed in the Klamath ecoregion at a much higher rate than in other ecoregions west of the Cascade crest. One explanation is differential decomposition rates. Decomposition is thought to be higher in the Klamath than in other west-side forests because of sufficient moisture and warm temperatures, but with fewer prolonged periods of moisture saturation, which can limit log decomposition (Harmon 1992). Others have proposed that historically frequent surface fires in the Klamath (every 5–75 years) consumed much of the coarse woody debris (Skinner 2002). It is most likely a combination of faster decomposition and shorter pre-suppression-era fire return intervals that underlie the lower amounts of dead biomass in the Klamath (Wright et al. 2002).

A consideration in interpreting biomass dynamics across ecoregions is the potential influence of 20th century fire exclusion, which has likely varied among regions. In dry forest types of some ecoregions (e.g., East Cascades, Sierra Nevada), fire suppression has resulted in long recent fire intervals relative to historical fire regimes that included frequent low-intensity surface fires (Agee 1993). These long intervals may allow greater live and dead biomass accumulations than under shorter fire intervals, as well as increases in stem densities that may affect patterns of stand productivity. By contrast, in wetter ecoregions (e.g., West Cascades, Coast Range), the fire suppression era has been brief relative to characteristic fire return intervals and probably has had little effect on biomass dynamics (Noss et al. 2006). Note that the chronosequence approach taken in our study is sensitive to the changes in disturbance regime over the last century. The effect of fire exclusion (and restoration) on carbon dynamics in different forest types remains an important direction for future research.

Ownership patterns and management implications

Forest management has always been somewhat different on private and public lands in the Coast Range, West Cascades, and Klamath Mountains (Spies et al. 1994), and reduced timber cut on federal lands in these ecoregions after implementation of the Northwest Forest Plan in 1990 has intensified the differences. Private lands in these ecoregions have, on average, less live biomass per unit area than do public lands because the typical harvest rotation (80 years) is much less than the age at which maximum biomass is reached (300 years). The frequency distribution of stand age could largely explain the differences in both live and dead biomass on public and private lands (Van Tuyl et al. 2005). Mean stand age of publicly owned forests is 50–150 years older than privately owned forests and mean carbon stores are 30–50% higher. Despite the fact that
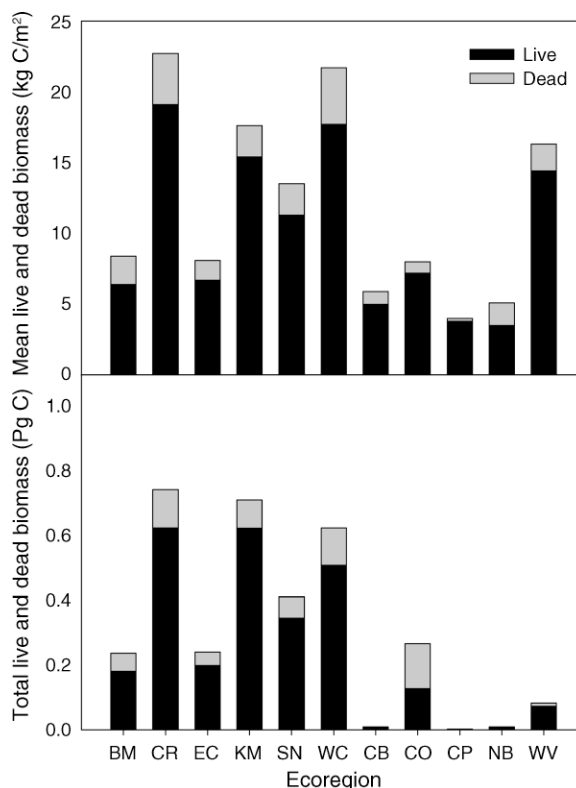

Fig. 7. Current mean and total carbon stocks in each ecoregion; mean and total live and dead biomass include trees, understory woody shrubs, and coarse woody debris.

the Coast Range has the highest percentage of private land (twice that of any other ecoregion), the lowest mean stand age, and the highest rate of removals by harvest (Law et al. 2004), it has the largest amount of biomass stored per unit area, presumably due to high NPP (climate), low natural mortality rates, and lack of recent major wildfires. Coast Range forests are among the most productive temperate forests in the world (Smithwick et al. 2002) and aboveground carbon stocks are comparable with tropical forest stocks (Houghton 2003, Sierra et al. 2007). Thus, there is high potential for increased land-based carbon storage with increased rotation age or reduction in harvest rates (Fig. 8b).

It is expected that management would affect NPP in younger stands because they are being managed for harvest and maximum wood volume production. After accounting for site index, our results supported this hypothesis, with maximum annual NPP of forests higher on private land than public land in all but the Blue Mountains and Klamath Mountains. An explanation for the lack of difference in these two ecoregions is difficult to ascertain because site index was accounted for in the analysis. There was also no difference in maximum live and dead biomass stores in the Blue Mountains. Maximum mortality is higher on public lands in the Blue Mountains, which could partially account for the decreased live biomass, but it may also
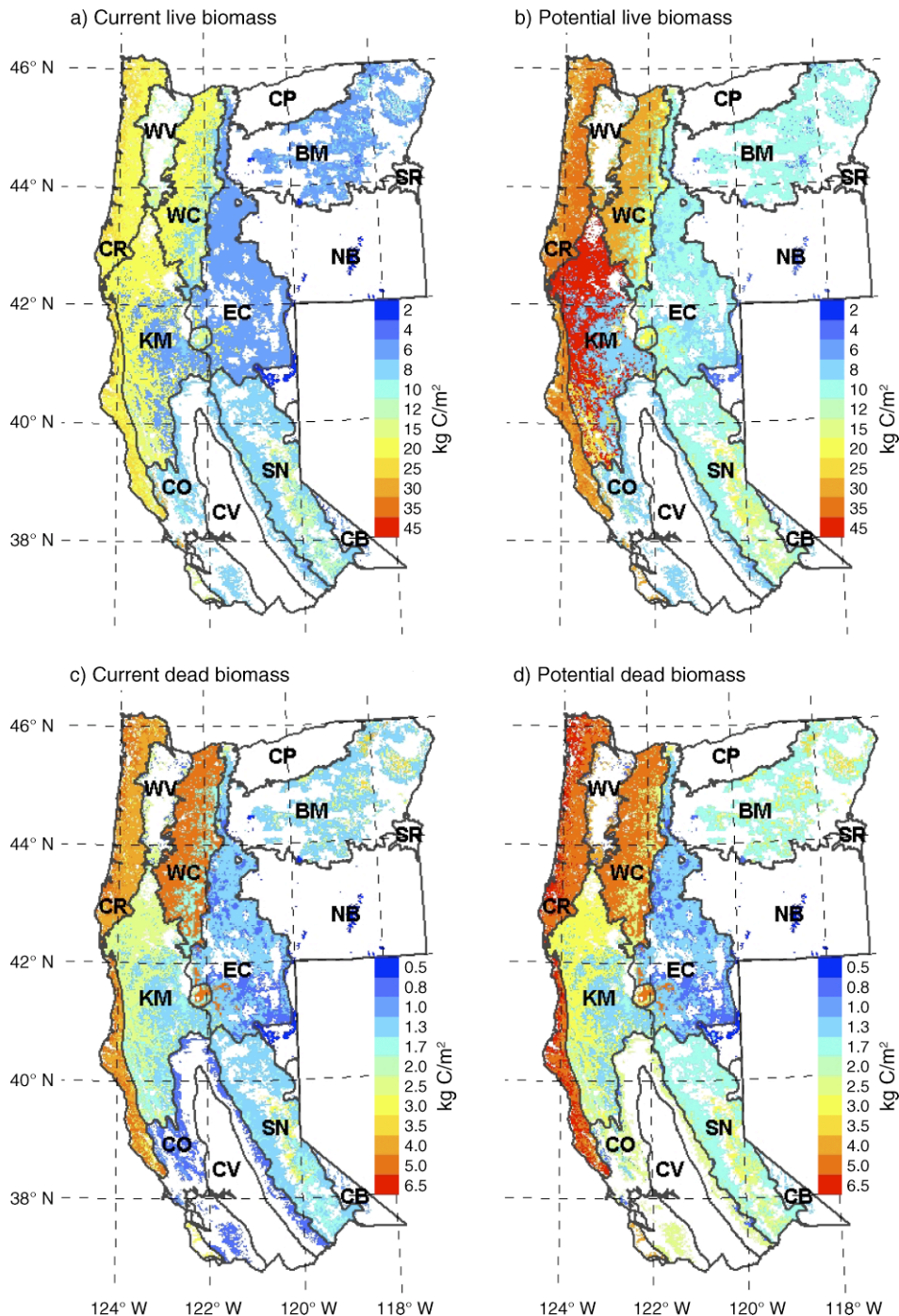
FIG. 8. Current and potential carbon stocks by forest type within ecoregion. Potential stocks were calculated using the mean trend maximums by forest type (Appendix: Table A6).

be that management practices are more similar on public and private land, as this ecoregion was also not affected by the Northwest Forest Plan.

Because ownership is associated with differences in mean biomass levels, a shift from current management on public land to a regime more like that on private land would gradually reduce mean carbon stocks on the land base. Decreasing rotation age to 50 years (i.e., mean age to 25 years) on all forested land in the Coast Range, Klamath Mountains, and West Cascades would reduce land-based live carbon stores by 53%. Some carbon can be sequestered in wood products derived from harvesting. However, due to manufacturing losses, only about 60% of the carbon harvested enters the products pool
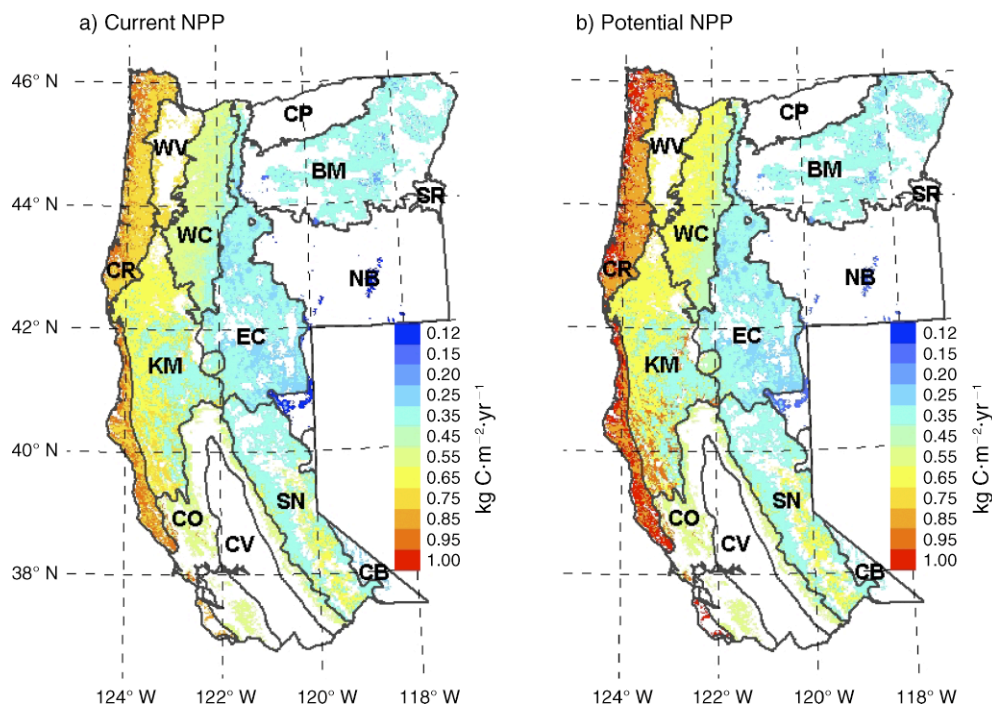
FIG. 9. Current and potential NPP by forest type within ecoregion. Potential NPP was calculated using the mean trend maximums of NPP by forest type (Appendix: Table A6).

(Harmon et al. 1996) and there are significant emissions from older products decomposing in landfills that tend to offset this carbon sink. Furthermore, with full carbon accounting there is a large carbon cost to the initial conversion of a landscape dominated by old forests to one dominated by young forests (Harmon et al. 1990).

Managing forests to maximize NPP may not have a positive effect on maximum regional carbon storage. Maximum NPP is reached much earlier in stand development than maximum biomass in all ecoregions (by hundreds of years) and limiting biomass accumulation to rotation ages based on maximum NPP would reduce land-based stocks. Examining current and potential productivity across the region is important when deciding regions where accumulation of biomass stores is most efficient. Highly productive ecoregions with infrequent fire such as the Coast Range are most likely to reach the potential stocks if managed for maximum biomass accumulation.

Modeling implications

As this study reaffirms, the processes driving forest carbon balance vary with stand age and forest type. Therefore estimates of regional carbon fluxes from modeling efforts depend in large part on our ability to accurately characterize stand age and forest type across the region (Turner et al. 2007). Including forest types as species groups in model parameterization could help further constrain model output for a specific area. Spatially explicit maps of age can be derived from remote imagery (Cohen et al. 2002), but the accuracy of these maps is dependent on pronounced canopy structural development (Law et al. 2006). Until accurate age maps can be developed for the entire region, the distribution of forest age among inventory plots is uniquely valuable in developing probabilistic-based maps of age (e.g., Ohmann et al. 2007).

Ecological studies have identified patterns of response in biomass and productivity with age that are based on homogeneous forests growing under ideal conditions, and in this study, we found that those patterns are more evident in the upper bounds of biomass or productivity for a given age rather than mean response. The structure of many process models used for scaling NEP is often developed based on ecological trends elucidated from field studies on idealized study plots or the upper bounds. Depending on exactly how a process model is structured, it may be best to parameterize it with curves fit to the upper maximum of the inventory data because these trends reflect the unconstrained behavior of vegetation in a given ecoregion. This is especially true for trends such as age-related mortality, age-related allocation, and age-related declines in NPP that need to be explicitly enforced, because these high-order trends fail to otherwise emerge in standard simulations. Mean trends in the inventory data, on the other hand, have a different, but equally important value to modeling since after incorporating the constraints of disturbance and climate across a region, model output is best validated against the mean trends apparent in the inventory data.

TABLE 3. Forest carbon stocks in different regions.

Region	Stocks (kg/m^2)	Components	Source
Oregon and N. California	6.5–19†,||	total tree biomass	this study
Oregon and N. California	17–70‡	total tree biomass	this study
West Coast USA	9.1–13.5†,||	total tree biomass	Woodbury et al. (2007)
PNW, Coast Range	63‡	total tree biomass	Smithwick et al. (2002)
PNW, Cascades	58‡	total tree biomass	Smithwick et al. (2002)
PNW, Eastside	12‡	total tree biomass	Smithwick et al. (2002)
Northern Rockies	8†	total tree biomass	Hicke et al. (2007)
Colorado Rockies	<8†	total tree biomass	Hicke et al. (2007)
Mid-Atlantic USA	16–29‡	total tree biomass	Jenkins et al. (2001)
Mid-Atlantic USA	7–11†,||	total tree biomass	Woodbury et al. (2007)
Eastern USA	7.5–25§	aboveground live tree biomass	Brown et al. (1999)
Russia	4.6–24§	total tree biomass	Krankina et al. (2005)
Canada	1–15†	total forest live biomass	Kurz and Apps (1999)
Latin America	13.5†	aboveground live tree biomass	Houghton (2005)
Tropical Asia	11.5†	aboveground live tree biomass	Houghton (2005)

Notes: Values reported as a range are the total estimates across different forest types or ecoregions. PNW is the Pacific Northwest.

† Includes foliage and coarse roots, but excludes fine roots.
‡ Reported as maximum levels for the study area.
§ Minimum to maximum levels across study area.
\|\| Mean levels across ecoregions.
¶ From small-scale ecological studies (not inventory).

For this reason we advocate the separate characterization of mean and upper bound trends in federal inventory data.

Comparison with other studies

Our estimates of live and dead biomass, NPP, and mortality compare favorably with other regional studies (Table 3). Most recent federal inventory estimates of state total live and dead tree (excluding fine roots) carbon per unit area were 9–11 kg C/m^2 (Woodbury et al. 2007) in Oregon and California. Our results produce a mean of 12 kg C/m^2 (including fine roots) for both states, but range from 3 to 24 kg C/m^2 across the ecoregions. Hicke et al. (2007) reports a range of 4–20 kg C/m^2 for mean live tree biomass (excluding fine roots) at the county level in Oregon and California. When compared with the IDB estimates of ecoregion means, aboveground woody biomass varied by 5–10%.

Smithwick et al. (2002) reported that Oregon tree (including snags) and understory biomass in very old undisturbed stands averaged 63, 58, and 12 kg C/m^2 in the Coast Range, West Cascades, and East Cascades, respectively. Our estimates of the upper bounds of tree (not including snags) and understory biomass (Fig. 2) were 55, 50, and 20 kg C/m^2 for each of these ecoregions. Our East Cascade upper bounds estimate is much higher, but is based on a much larger number of plots over a more extensive area. Our aboveground wood biomass increments averaged 0.17 kg C·m^{-2}·yr^{-1} in the East Cascades to 0.50 kg C·m^{-2}·yr^{-1} in the Coast Range. In comparison with other regions, maximum live tree biomass averaged 10 kg C/m^2 in softwood forest types and wood biomass increment averaged 0.24 kg C·m^{-2}·yr^{-1} in the mid-Atlantic region (Jenkins et al. 2001). In tropical regions, total tree live-tree biomass averaged a 15 kg C/m^2 (Sierra et al. 2007) in Columbia and ranged from 11 to 13 kg C/m^2 (aboveground biomass only) across all tropical forests (Houghton 2003).

Conclusions

The potential to store additional carbon in Pacific Northwest forests is among the highest in the world because much of the area has forests that are long-lived (e.g., Douglas-fir) and maintain relatively high productivity and biomass for decades to centuries. In Oregon and Northern California (4.4 × 10^7 ha), total live biomass of forests is estimated at 2.71 ± 0.28 Pg C, mean ± SD (mean of 12 kg C/ha) in the period 1991–1999. Total dead biomass (which does not include fine woody debris or litter stocks) of forests in the region was 0.51 ± 0.19 Pg C, and total NPP was 0.109 ± 0.001 Pg C/yr, mean ± SD. The majority of live and dead biomass (~65%) is on public lands (53% of forested land). Trends in NPP with age vary among ecoregions, which suggests caution in generalizing that NPP declines in late succession. Contrary to commonly accepted patterns of biomass stabilization or decline, biomass was still increasing in stands over 300 years old in the Coast Range, the Sierra Nevada and the West Cascades, and in stands over 600 years old in the Klamath Mountains. If forests were managed for maximum carbon sequestration total carbon stocks could theoretically double in the Coast Range, West Cascades, Sierra Nevada, and East Cascades and triple in the Klamath Mountains (Fig. 8). Our results indicate that Oregon and California forests are at 54% of theoretical maximum levels (3.2 ± 0.34 Pg C vs. 5.9 ± 1.34 Pg C) given the absence of stand-replacing disturbance. These theoretical levels are calculated using the mean trend of the data and account for variation in site quality, climate, and partial disturbance (i.e., thinning, insect outbreaks, non-cata-

strophic fire). An increase of 15% may be possible in just 50 years. However, these levels (if reached) may be unstable in high-frequency fire regions. A more realistic management approach to increase carbon storage on the landscape would be to increase rotation ages by 30–50 years or reduce the acreage that is harvested in areas more likely to reach the theoretical levels (Coast Range, West Cascades, Klamath Mountains). Initial conditions are important when considering management options. Maintaining mature and old forests that already store large amounts of carbon is a mitigation option, as suggested by the IPCC (2007).

LITERATURE CITED

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

Agee, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C., USA.

Binkley, D., J. L. Stape, M. G. Ryan, H. R. Barnard, and J. Fownes. 2002. Age-related decline in forest ecosystem growth: an individual-tree, stand-structure hypothesis. Ecosystems 5:58–67.

Bormann, F. J., and G. E. Likens. 1969. Pattern and process in forest ecosystems. Springer-Verlag, Berlin, Germany.

Brown, S. L., P. Schroeder, and J. S. Kern. 1999. Spatial distribution of biomass in forests of the eastern USA. Forest Ecology and Management 123:81–90.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Campbell, J. L., O. J. Sun, and B. E. Law. 2004. Supply-side controls on soil respiration among Oregon forests. Global Change Biology 10:1857–1869.

Canadell, J. G., C. Le Quere, M. R. Raupach, C. B. Field, E. T. Buitenhuis, P. Ciais, T. J. Conway, N. P. Gillett, R. A. Houghton, and G. Marland. 2007. Contributions to accelerating atmospheric CO_2 growth from economic activity, carbon intensity, and efficiency of natural sinks. Proceedings of the National Academy of Sciences (USA) 104:18866–18870.

Cohen, W. B., T. A. Spies, R. J. Alig, D. R. Oetter, T. K. Maiersperger, and M. Fiorella. 2002. Characterizing 23 years (1972–1995) of stand replacement disturbance in western Oregon forests with Landsat imagery. Ecosystems 5:122–137.

Denman, K. L., et al. 2007. Couplings between changes in the climate system and biogeochemistry. Pages 499–587 *in* S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller, editors. Climate change 2007: The physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergov-

ernmental Panel on Climate Change [IPCC]. Cambridge University Press, Cambridge, UK.

ESRI. 2005. ArcGIS version 9.1. ESRI (Environmental Systems Research Institute), Redlands, California, USA.

Forest Products Laboratory. 1974. Wood handbook: Wood as an engineering material. Forest Products Laboratory, Madison, Wisconsin, USA.

Gough, C. M., C. S. Vogel, K. H. Harrold, K. George, and P. S. Curtis. 2007. The legacy of harvest and fire on ecosystem carbon storage in a north temperate forest. Global Change Biology 13:1935–1949.

Harcombe, P. A., M. E. Harmon, and S. Green. 1990. Changes in biomass and production over 53 years in a coastal *Picea sitchensis–Tsuga heterophylla* forest approaching maturity. Canadian Journal of Forest Research 20:1602–1610.

Harmon, M. E. 1992. Long-term experiments on log decomposition at the H. J. Andrews Experimental Forest. USDA Forest Service General Technical Report PNW-GTR 280, Pacific Northwest Forest Experiment Station, Portland, Oregon, USA.

Harmon, M., et al. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15: 133–302.

Harmon, M. E., W. K. Ferrell, and J. F. Franklin. 1990. Effects on carbon storage of conversion of old-growth forests to young forests. Science 247:699–702.

Harmon, M. E., S. L. Garman, and W. K. Ferrell. 1996. Modeling historical patterns of tree utilization in the Pacific Northwest: Carbon sequestration implications. Ecological Applications 6:641–652.

Hicke, J. A., J. C. Jenkins, D. S. Ojima, and M. Ducey. 2007. Spatial patterns of forest characteristics in the western United States derived from inventories. Ecological Applications 17: 2387–2402.

Houghton, R. A. 2003. Revised estimates of the annual net flux of carbon to the atmosphere from changes in land use and land management 1850–2000. Tellus B 55:378–390.

Houghton, R. A. 2005. Aboveground forest biomass and the global carbon balance. Global Change Biology 11:945–958.

IPCC. 2007. Climate change 2007: mitigation. Pages 546–548 *in* B. Metz, O. R. Davidson, P. R. Bosch, R. Dave, and L. A. Meyer, editors. Contribution of Working Group III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [IPCC]. Cambridge University Press, Cambridge, UK.

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

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

Keyes, M. R., and C. C. Grier. 1981. Above- and belowground net production in 40-year-old Douglas-fir stands on low and high productivity sites. Canadian Journal of Forest Research 11:599–605.

Krankina, O. N., R. A. Houghton, M. E. Harmon, E. H. Hogg, D. Butman, M. Yatskov, M. Huso, R. F. Treyfeld, V. N. Razuvaev, and G. Spycher. 2005. Effects of climate, disturbance, and species on forest biomass across Russia. Canadian Journal of Forest Research 35:2281–2293.

Kurz, W. A., and M. J. Apps. 1999. A 70-year retrospective analysis of carbon fluxes in the Canadian forest sector. Ecological Applications 9:526–547.

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

Law, B. E., D. Turner, J. Campbell, O. J. Sun, S. Van Tuyl, W. D. Ritts, and W. B. Cohen. 2004. Disturbance and

climate effects on carbon stocks and fluxes across Western Oregon USA. Global Change Biology 10:1429–1444.

Law, B. E., D. Turner, M. Lefsky, J. Campbell, M. Guzy, O. Sun, S. V. Tuyl, and W. Cohen. 2006. Carbon fluxes across regions: Observational constraints at multiple scales. Pages 167–190 *in* J. Wu, B. Jones, H. Li, and O. Loucks, editors. Scaling and uncertainty analysis in ecology: methods and applications. Springer-Verlag, New York, New York, USA.

Maeglin, R. R., and H. E. Wahlgren. 1972. Western wood density survey. Report Number 2. USDA Forest Service Research Paper FPL-183, Madison, Wisconsin, USA.

McCune, B., and E. S. Menges. 1986. Quality of historical data on midwestern old-growth forests. American Midland Naturalist 116:163–172.

Means, J. H., H. A. Hansen, G. J. Koerper, P. B. Alaback, and M. W. Klopsch. 1994. Software for computing plant biomass—BioPak Users' guide. USDA Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-340, Portland, Oregon, USA.

Noss, R. F., J. F. Franklin, W. L. Baker, T. Schoennagel, and P. B. Moyle. 2006. Ecology and management of fire-prone forests of the western United States. Society for Conservation Biology Scientific Panel on Fire in Western U.S. Forests. Society for Conservation Biology, North American Section, Arlington, Virginia, USA.

Odum, E. P. 1969. The strategy of ecosystem development. Science 164:262–270.

Ohmann, J. L., M. J. Gregory, and T. A. Spies. 2007. Influence of environment, disturbance and ownership on forest vegetation of coastal Oregon. Ecological Applications 17: 18–33.

Omernik, J. M. 1987. Ecoregions of the conterminous United States. Map (scale 1:7,500,000). Annals of the Association of American Geographers 77:118–125.

Peet, R. K. 1981. Changes in biomass and production during secondary forest succession. Pages 324–338 *in* D. C. West, H. H. Shugart, and D. B. Botkin, editors. Forest succession: concepts and application. Springer-Verlag, New York, New York, USA.

Pienaar, L. V., and K. J. Turnbull. 1973. The Chapman-Richards generalization of Von Bertalanffy's growth model for basal area growth and yield in even-aged stands. Forest Science 19:2–22.

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

Sierra, C. A., et al. 2007. Total carbon stocks in a tropical forest landscape of the Porce region, Colombia. Forest Ecology and Management 243:299–309.

Skinner, C. 2002. Influence of fire on the dynamics of dead woody material in forests of California and southwestern Oregon. USDA Forest Service General Technical Report PSW-GTR 181:445–454.

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

Spies, T. A., and J. F. Franklin. 1991. The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington. Pages 91–111 *in* L. F. Ruggerio, K. B. Aubry, A. B. Carey, and M. H. Huff, editors. Wildlife and vegetation of unmanaged Douglas-fir forests. USDA Forest Service Pacific Northwest Research Station, General Technical Report PNW-GTR-285, Portland, Oregon, USA.

Spies, T. A., W. J. Ripple, and G. A. Bradshaw. 1994. Dynamics and pattern of a managed coniferous forest landscape in Oregon. Ecological Applications 4:555–568.

S-PLUS. 2005. S-PLUS version 7.02. Insightful Corporation, Seattle, Washington, USA.

Sun, O. J., J. Campbell, B. E. Law, and V. Wolf. 2004. Dynamics of carbon storage in soils and detritus across chronosequences of different forest types in the Pacific Northwest, USA. Global Change Biology 10:1470–1481.

Turner, D. P., M. Guzy, M. A. Lefsky, W. D. Ritts, S. Van Tuyl, and B. E. Law. 2004. Monitoring forest carbon sequestration with remote sensing and carbon cycle modeling. Environmental Management 33:457–466.

Turner, D. P., D. Ritts, B. E. Law, W. Cohen, Z. Yang, T. Hudiburg, J. L. Campbell, and M. Duane. 2007. Scaling net ecosystem production and net biome production over a heterogeneous region in the western United States. Biogeosciences 4:597–612.

USDA Forest Service and U.S. Geological Survey. 2002. Forest cover types: National Atlas of the United States. Earth Science Information Center, USGS, Reston, Virginia, USA. ⟨http://www-atlas.usgs.gov/metadata/foresti020l.faq.html⟩

Van Tuyl, S., B. E. Law, D. P. Turner, and A. I. Gitelman. 2005. 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. Forest Ecology and Management 209:273–291.

Waddell, K. L. 2002. Sampling coarse woody debris for multiple attributes in extensive resource inventories. Ecological Indicators 1:139–153.

Waddell, K. L., and B. Hiserote. 2005. The PNW-FIA integrated database [on CD]. Version 2.0. Released September 2005. Forest Inventory and Analysis Program, Pacific Northwest Research Station. Portland, Oregon, USA. ⟨http://www.fs.fed.us/pnw/fia/publications/data/data.shtml⟩

Woodbury, P. B., J. E. Smith, and L. S. Heath. 2007. Carbon sequestration in the U.S. forest sector from 1990 to 2010. Forest Ecology and Management 241:14–27.

Wright, P., M. Harmon, and F. Swanson. 2002. Assessing the effect of fire regime on coarse woody debris. USDA Forest Service General Technical Report PSW-GTR 181:621–634.

APPENDIX

Ecoregion, ownership, and forest type summary tables and statistics (*Ecological Archives* A019-008-A1).