AN ABSTRACT OF THE THESIS OF

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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 flux in the western U.S., a combination of federal inventory data and supplemental ground measurements was used to estimate several important components of NEP in forests in Oregon and Northern California during the 1990's. The specific components studied were live and dead biomass stores, net primary productivity (NPP), and mortality. In the semi-arid Northern Basin and mesic Coast Range, mean total biomass was 4 and 24 Kg C m^{-2}, and mean NPP was 0.28 and 0.78 Kg C m^{-2} y^{-1}, respectively. These values were obtained using species- and ecoregion-specific allometric equations and tended to be higher than those obtained from more generalized approaches. There is strong evidence that stand development patterns of biomass accumulation, net primary production, and mortality differ due to climate (ecoregion), management practices (ownership), and forest type. Among those three factors and across the whole region, maximum NPP and dead biomass stores were most influenced by climate, while maximum live biomass stores and mortality were mostly influenced by forest type. Live and dead biomass, NPP, and mortality were most influenced by forest type. Decrease in NPP with age was not general across

ecoregions, with no marked decline in old stands (>200 years) in some ecoregions, and in others, the age at which NPP declined was very high (458 years in East Cascades, 325 in Klamath Mountains, 291 in Sierra Nevada). There is high potential for increasing total carbon storage by increasing rotation age and reducing harvest rates in this region. Only 1% of forest plots on private lands were >200 years old, whereas 41% of the plots were greater than 200 years old on public lands. Total carbon stocks could increase from 3.2 Pg C to 7.3 Pg C and NPP could increase from 0.109 Pg C y^{-1} to .168 Pg C y^{-1} (a 35% increase) if forests were managed for maximum carbon storage by increasing rotation age.

Climate, Management, and Forest Type Influences on Carbon Dynamics of West-Coast US Forests

by
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APPROVED:

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Tara M. Hudiburg, Author

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDIX TABLES

Climate, Management, and Forest Type Influences on Carbon Dynamics of West-Coast US Forests

Introduction

The amount of carbon sequestered by forest ecosystems plays an important role in regulating atmospheric levels of carbon dioxide (Dixon et al. 1994). 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 reduce atmospheric carbon dioxide levels by using current knowledge of forest carbon dynamics to increase and maintain the storage of carbon (IPCC 2007). Thus quantifying forest carbon pools and fluxes, as well as understanding the factors accounting for their geographic variation, is a significant research issue. In this study we used forest inventory data and supplementary field measurements to evaluate several components of the carbon budget over a large forested region in the western U.S.

In this study, inventory data was used to examine patterns of NPP, mortality, and live and dead carbon stores in different ecoregions of Oregon and Northern California. We incorporated measurements (i.e. foliage and fine root metrics) from supplemental field plots to augment the standard inventory plot data. We examined differences in carbon pools and fluxes due to species composition, climate, disturbance, and management as proxied by forest type, ecoregion, stand age, and ownership, respectively. This study compliments studies by Hicke et al., (In Press) 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 carbon stocks using supplemental data and allometrics. The objectives for examining carbon stocks and fluxes within and among ecoregions were:

1. Identify age-related patterns of mean and maximum live biomass, dead biomass, NPP, and mortality.
2. Determine the influence of forest type, ecoregion, and ownership on these patterns.
3. Quantify total and potential forest carbon stocks and NPP over the study region.

Literature Review

Net ecosystem production (NEP) is a critical flux in a carbon budget and is the difference between the two large fluxes of photosynthesis and autotrophic plus heterotrophic respiration. NEP can be estimated at the plot scale using a mass balance approach (Campbell et al. 2004b), at the ecosystem scale with eddy covariance techniques (Baldocchi et al. 2001, Law et al. 2003), and at the regional scale through a combination of measurements and modeling (Law et al. 2006). On the plot level, a mass balance or biometric approach to estimating NEP computes the difference between net primary production (NPP) and heterotrophic respiration. Quantification of NPP represents the difference between photosynthesis and autotrophic respiration. For estimates of heterotrophic respiration, dead wood mass should be included because it represents a large portion of the carbon stocks available for decomposition (Brown and Schroeder 1999, Janisch and Harmon 2002). In this study, we focus on estimating NPP and dead wood mass as well as live biomass and rates of mortality.

To produce unbiased regional estimates of carbon budget components from plot data, the plots should be representative of all forest types, ownerships, and climatic conditions. This can be accomplished through a probability-based design, like that of the federal forest inventory, FIA. The FIA database, as used here, provides measurement data and the temporal and spatial replication necessary for estimating carbon stocks and contributing fluxes of NEP at regional scales.

The large inventory datasets allow examination of factors controlling carbon uptake within and among areas of defined edaphoclimatic conditions. Milder climates with mesic conditions have faster rates of biomass accumulation and decomposition than semi-arid to arid regions (Campbell et al. 2004b). Management and the species present can also affect the rate of growth; managed stands are being cultivated to optimize growth for timber production and some species are physiologically adapted to faster growth (Lavigne and Ryan 1997). Such patterns of response can be examined through the use of ecoregions to stratify data, because ecoregions incorporate information on climate, physiography, soils, land use and geology (Omernik 1987, Hargrove et al. 2003).

Of particular interest when examining inventory wide patterns in carbon pools and flux are the age specific trends. Commonly accepted stand age related patterns of live biomass accumulation, NPP show a stabilization or decline as stands age (Bormann and Likens 1969, Odum 1969, Peet 1981). These patterns have mostly been identified using a variety of small scale ecological studies which tend to select homogeneous and unstressed 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 be as expected. 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 an important one when validating process models applied across real landscapes (e.g. Jenkins et al. 2001). For instance, it may be best to affirm model structure by validating output against trends quantified across idealized study plots. However, when these same models are used to simulate processes over entire regions the standard for validation should be the collective behavior of plots on the landscape that include a portion (possibly a majority) of idiosyncratic points. For this reason the patterns of production, mortality, and net carbon stocks over time identified in federal inventory data are uniquely powerful in that they can reveal both collective trends (i.e. average values) in addition to idealized trends (i.e. upper bounds or maximum values).

Simultaneous examination of accumulation, growth and mortality of all carbon pools on a landscape is important when trying to quantify and make predictions about the amount of carbon stored in relation to the amount that could be respired. Federal forest inventory data have been predominantly used to examine patterns of biomass accumulation and growth summarized by political boundaries (county or state) that can encompass several climate regimes and forest types (Caspersen et al. 2000, Smith and Heath 2004). There have been very few studies examining mortality and dead biomass stores on federal plots (Waddell 2002). Typically, NPP and live biomass estimates are computed from county or state level reports using generalized biomass expansion factors (Smith and Heath 2004), or plot level data using generalized allometric equations (Jenkins et al. 2003, Hicke et al. In press). Biomass expansion factors and general equations may not account for differences in growth due to tree species, site fertility, climate, or wood densities. Estimation of understory and downed wood carbon density has been reported, but were calculated using FORCARB2 which extrapolates the amount of carbon in these components from live tree biomass (Woodbury et al. 2007). To our knowledge, no studies have used federal inventory data of individual trees, understory, and coarse woody debris on each plot to compute biomass, NPP, and mortality.

Materials and Methods

Study Area

The ORCA project is part of the North American Carbon Program (NACP), for which the goal is to quantify and understand the carbon balance of North America. The study area covers the entire state of Oregon and the northern half of California (Figure 1). The disturbance history of the region includes frequent windthrow near the coast, relatively short harvest cycles but 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 11 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. Approximately 50 percent of this area is forested land, with 57 percent under public ownership and 44 percent 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. Total biomass, NPP, and mortality estimates for each ecoregion, state, and the total ORCA study area were obtained as the product of forested area using land cover data from Advanced Very High Resolution Radiometer (AVHRR) composite images recorded during the 1991 growing season (USDA Forest Service 2002) and mean values across all plots within the relevant area. The same procedure was used with GIS ownership coverages (from USGS National Land Cover Data, 1992) to isolate patterns by public and private ownerships.

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 a database made available from the PNW-FIA regional office known as the Integrated Database v2.0 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 periodic data as it is the most recent complete cycle and thus more representative of the study region. Our results thus approximate conditions in the mid 1990s.

We evaluated all periodic inventory plots (14,188 plots with live tree data and 12,380 plots with woody detritus and understory data) within the study area boundary (Figure 1). The inventory design consists of 0.404 hectare (one-acre) plots systematically placed across a landscape, thus encompassing a representative range of stand ages, disturbance histories, ownerships, and land cover types. To account for this variability, field crews assigned one or more condition classes to each plot to account for within-plot variability. Reasons for assignment and location of plot condition classes were not recorded. Because we were interested in differences due to ownership and forest type, we chose to use plots with only one condition class. The data collected on inventory plots include tree diameter breast height (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. Plots that did not include enough increment data to suitably calculate a stand age or a radial growth were also excluded. 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. While these one-hectare plots cover a larger spatial area, the subplot and transect layouts, measurement protocols, and data collected meet the minimum requirements of the federal inventory plots. Their locations were selected using a hierarchical random sampling design based on climate, forest type and age (Law et al. 2006). Besides the standard FIA measurements, the additional sampling was designed to allow a more comprehensive assessment of the carbon stocks and fluxes (Law et al. 2004, Law et al. 2006, Sun et al. 2004, Van Tuyl et al. 2005). Additional measurements included foliage and soil carbon and nitrogen, leaf retention time, foliage and fine root biomass and production, leaf area index, and litter stocks.

Stand Age

Stand age is computed to approximate the age since last stand replacing disturbance. Each plot was assigned an age based on the mean of the oldest 10 percent of trees (Spies and Franklin 1991, Van Tuyl et al. 2005). Many inventory plots did not have enough recorded tree ages to appropriately use this method (i.e. there were fewer than 3 trees in the oldest 10 percent). In cases where there were fewer than three trees, a mean of all aged trees on the plot was used. While 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 likely 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 etc). Private land includes 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 7 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 (Means et al. 1994, Van Tuyl et al. 2005) and a literature search was performed to locate as many species-specific and ecoregion-specific equations as possible. Biomass estimates for trees were computed for bole, bark, branch, foliage, and coarse roots. A second database to compute biomass for woody shrubs was compiled using equations developed from shrubs harvested at our supplemental plots. A total of 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.

Bole wood biomass ($Biomass_b$) was calculated as the product of the bole wood volume (allometrically derived from bole diameter) and wood density (obtained from the US Forest service wood density survey for western Oregon (Maeglin and Wahlgren 1972)), the Forest Products Laboratory wood handbook (1974) , and from wood cores obtained on our supplemental plots. Wood densities were reduced according to decay class for standing dead trees (Waddell 2002). Branch ($Biomass_{br}$) and bark ($Biomass_{ba}$) biomass were calculated separately for all evergreen-needleleaf (ENF) and some deciduous broadleaf trees (DBF). Many of the ecoregion specific volume equations for DBF trees calculate bole, branch and bark mass as a single estimate. Foliage biomass ($Biomass_f$) was calculated using DBH and/or height regression equations downloaded from BIOPAK (Means et al. 1994). Tree component biomass estimates were converted to kilograms of carbon per unit of ground area by multiplying by the trees per hectare (TPH). TPH is a multiplier supplied by the IDB to convert biomass estimates to per unit area estimates which are summable by plot to get a total plot biomass estimate of biomass per unit area. All biomass values were multiplied by 0.5 to obtain carbon amount per unit area.

Fine root biomass ($\text{Biomass}_{\text{fr}}$) was estimated using an equation relating leaf area index and fine root biomass developed by Van Tuyl et al. (2005).

$$\text{Biomass}_{\text{fr}} = (\exp(4.4179+(.3256*\text{LAI})-(.0237*\text{LAI}^2))$$

LAI is not measured on inventory plots, but can be calculated from foliage biomass and the leaf mass per unit leaf area (LMA):

$$\text{LAI} = \text{Biomass}_{\text{f}} / \text{LMA}$$

Where, LMA was obtained from a look-up table of species-specific values obtained from measurements on the supplemental plots in each of the ecoregions. In some cases, a species-specific value was not available and therefore a closely related species was used. Coarse root biomass (Biomasscr) was calculated with a volume equation developed for Pseudotsuga menziesii and species-specific wood densities (Van Tuyl et al. 2005).

We calculated biomass of understory woody shrubs and coarse woody debris including downed trees. Total shrub biomass ($\text{Biomass}_{\text{s}}$) was calculated from shrub volume using the following equation:

$$\text{Biomass}_{\text{s}} = a*(1-(\exp(-b*V)))$$

where V is shrub volume in cubic meters. Shrub volume is obtained from the product of the recorded fraction of plot cover, plot area, and height. The parameters ‘a’ and ‘b’ are regression coefficients that vary by species in the equation database. Coarse woody debris biomass was estimated using the method described in (Waddell 2002). Volume per unit ground area was calculated with a modified cylinder equation:

$$\text{Volume}_{\text{cwd}} = (9.869/(8*L))*(D^2)$$

Where, L is the transect length in meters and D is the diameter of the piece in centimeters. The volume per unit ground area is converted to biomass by multiplying by a decay class adjusted species-specific density:

$$\text{Biomass}_{\text{cwd}} = \text{Volume}_{\text{cwd}} * \text{Density} * \text{DC\_multiplier}$$

where Density in kilograms per cubic meter is reduced by the DC_multiplier.

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 sub-sample 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. Plots without a measured increment in each quartile (when that quartile was represented in the full range of tree sizes) were not included in the analysis.

Net primary production of all tree woody components was estimated as the difference in biomass at two points in time and 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 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 foliage 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. 2004a). Studies from our supplemental plots suggest a close equivalence of fine root productivity and leaf biomass (Van Tuyl et al., 2005).

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, 2005 Insightful Corp., Seattle, WA) was used for all statistical analysis. The questions of interest required that each response variable be compared while accounting for stand age. This was done by comparing the coefficients of the response functions (see below) fit to the age-based distributions. For the statistical analyses, plots with stand ages greater than 600 years were grouped into a single age group. Because less than 1 percent 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 and finding a significantly higher mean 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 dataset 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 was first binned into 25 year age groups and a stratified random sample of observations was chosen to ensure the sample included data points from the entire age range. The appropriate functions (see below) were then fit to the sample dataset. 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 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:

$$(1)\quad \text{Biomass} = a*(1 - \exp(-b*\text{Stand Age})^{c}$$

Where, parameter a is the asymptote, or the maximum amount of biomass carbon. Parameter b determines the rate in years 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 (3-parameter, log normal) was fit to the NPP data:

$$(2)\ \text{NPP} = a*\exp(-.5*(\ln(\text{Stand Age}/c)/b)^2)$$

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 clear-cut/burned and very young stands and the Chapman-Richards function quantifies the accumulation of dead wood as the stand ages:

$$(3)\ \text{Biomass} = d*\exp(-e*\text{Stand Age}) + a*(1 - \exp(-b*\text{Stand Age}))^c$$

where, parameter d is the initial carbon stores, and e is the decay rate in years. While 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 was 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 while the curve fit to the upper bounds should represent the maximum potential of stands in the ecoregion given minimal disturbance and ideal 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.

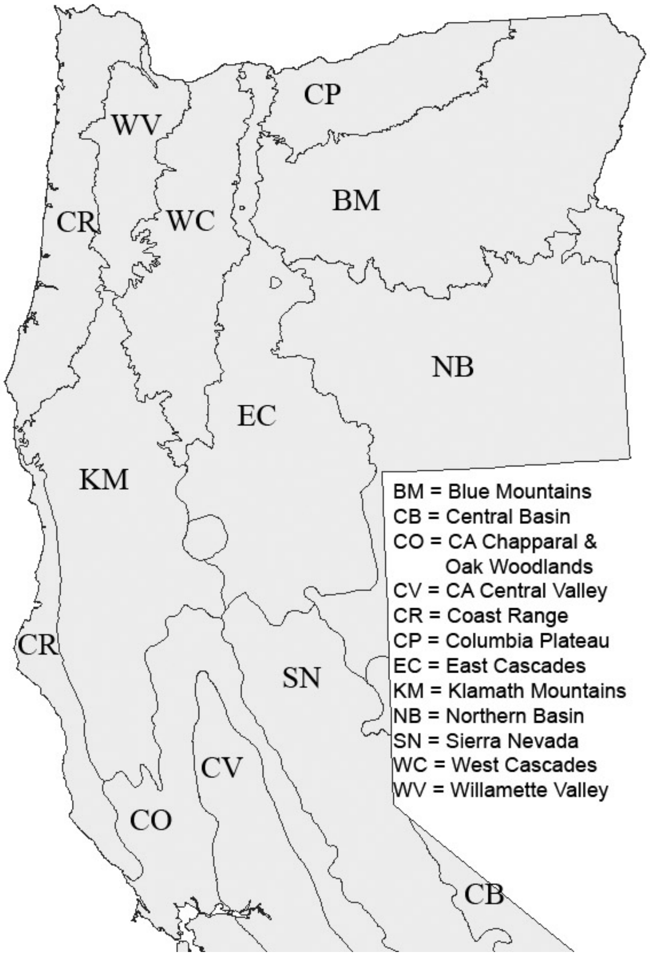


Figure 1. ORCA study region (Oregon and Northern California) divided by Omernik Level III ecoregions.

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

Ecoregion	Plots	MAT (degrees C) (Winter/Summer)	MAP (mm)	Total Area (ha)	Forested Area (ha)	Mean Stand Age[2]	% Plots[3]		% >200yrs[4]	
							Private	Public	Private	Public
BM[1]	1266	-2/17	630	6206770	2852987	195 (3)	10	90	<1	42
CR	737	7/18	2500	3633280	3280871	128 (4)	35	65	<1	14
EC	1834	-3/17	500	4795480	2971042	185 (2)	8	92	1	36
KM	1526	3/21	1500	4850310	4076569	219 (4)	11	89	1	47
SN	1268	5/15	1500	3931700	3059246	196 (4)	9	91	1	38
WC	1896	4/16	2200	3038260	2889914	248 (4)	4	96	<1	57
CO	116	4/30	630	4222085	1773527	120 (6)	70	30	7	3
WV	46	4/20	1270	1373040	504923	109 (13)	70	30	0	9
NB	36	-1/18	250	6556370	174125	150 (21)	17	83	3	22
CB	26	4/11	150	834689	165932	210 (27)	4	96	0	50
CP	4	0/21	250	1756090	40046	145 (45)	100	0	25	-
CV	0	10/17	450	2656190	49832	-	0	0	-	-
Total	8755	2/18	1075	43854264	21839014	201 (2)			1	41

[1] 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

[2] Standard deviations in parentheses

[3] Percentage of total plots in ecoregion

[4] Percentage of total plots within ownership over 200 years old in each ecoregion

Results

Stand Age

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 (Figure 2). Variability of stand age is also higher on public land with a more even distribution of stand ages between 100 and 300 years. Mean stand age for private ownership ranged from 83 in the Coast Range to 146 years in the Sierra Nevada. Public ownership mean ages ranged from 150 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.

Ecoregion Patterns

There is strong evidence ($P < 0.001$) that maximum amounts of live biomass and rate of accumulation differ by ecoregion (Figure 3). The Chapman-Richards function fit much better in some ecoregions than others, but appeared to be a good general equation to describe biomass accumulation (Appendix A, Table 1). The fits ranged from an adjusted R^2 of 0.39 in the Coast Range to 0.69 in the West Cascades. When fit to the mean values by age bin, maximum amount of live biomass (a in equation 1) is highest in the Coast Range and Klamath Mountains (33-44 kg C m^{-2}) and lowest in the East Cascades and Blue Mountains (7-10 kg C m^{-2}) . The rate (b in equation 1) at which biomass reaches the maximum is lowest in the Klamath Mountains with maximum stores still increasing at 600 years. Rates were 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.

While we were unable to measure the inputs to or outputs from dead biomass, 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 between ecoregions for young, mature and old stands. The Coast Range and West Cascades had the highest mass of dead wood in all age groups (ranged from 3.1 kg C m^{-2} in the young and 4.7 kg C m^{-2} in the old). The East Cascades had the lowest mass of dead wood in all age groups (ranged from 0.7 to 1.6 kg C m^{-2}) and the Klamath Mountains and Sierra Nevada had intermediate levels (ranged from 1.0 to 2.6 kg C m^{-2}).

The theoretical u-shaped pattern of dead biomass over time--high levels initially following disturbance, followed by low levels as this legacy wood decays, followed again by high levels as new dead wood is recruited--was mostly apparent in the West Cascades when fit to the upper bounds and slightly apparent in the East Cascades and Sierra Nevada (Figure 4). The pattern was only slightly apparent in the West Cascades when fit to the mean values. Initial stores (*d* in equation 3) and decay rates (*e* in equation 3) did not have reliable estimates (*P* >0.05) for any of the ecoregions regardless of whether equations were fit to the mean values or the upper bounds (Appendix A, Tables 1 and 2). However, estimates for maximum amounts (*a* in equation 3) were highest for the West Cascades, and lowest in the Blue Mountains, Sierras, and the Klamath Mountains when fit to the mean values.

There is strong evidence (*P* < 0.001) that maximum NPP differs between ecoregions (Appendix A, Table 1), however the rate at which maximum NPP is reached did not differ significantly (*P* = 0.36). When fit to the mean values, maximum NPP in the Sierra Nevada was equal to the West Cascades and highest in the Coast Range and Klamath (Figure 5). In some ecoregions the mean fit was much better than others; adjusted R^2 ranged from 0.17 in the Coast Range to 0.57 in the Blue Mountains.

The most obvious cases of late successional decline in NPP for the upper bound plots were in the ecozones with highest maximum NPP (CR, WC, KM). The Coast Range was the only case of a conspicuous decline with age in mean NPP.

There was strong evidence (P <0.001) that both maximum mortality and the rate at which it is reached differs among ecoregions (Appendix A, Table 1). In some ecoregions the mean fit was much better than others, adjusted R^2 ranged from 0.24 in the Coast Range to 0.64 in the West Cascades (Figure 6). 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. The number of years required to reach maximum mortality was highest in the Klamath Mountains for the mean values of the data, but highest in the West Cascades for the upper bounds. Mortality appeared to increase with stand age and become less predictable in older stands. Average mortality rates 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 years) stands, and from 0.35% in the Coast Range to 1.35% in the Blue Mountains for old stands (greater than 200 years).

Ownership Patterns

After accounting for site index, there is strong evidence that maximum biomass differed between ownerships in all but the Blue Mountains and East Cascades (*P* <0.001). Maximum live biomass is higher on public lands (parameter *a* in equation 1, Appendix A, Table 3), with the largest difference in the Coast Range (17 kg C m^{-2} vs. 27 kg C m^{-2} by age 200). Mean dead biomass differed (*P* <0.05) by ownership in the young age class in the East Cascades and Sierra Nevada, and in the mature age class in the Coast Range. Mean dead biomass was higher on private land in the East Cascades and the Sierra Nevada, but lower in the Coast Range (Table 2).

There is also strong evidence that maximum NPP (parameter *a* in equation 2) differed between ownerships (*P* <0.001). Maximum NPP 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 A, Table 3). The number of years required to reach maximum rates of NPP were higher on public land (*P* <0.01) in the Blue Mountains, East Cascades, and Sierra Nevada. Maximum mortality was 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 that forest types within an ecoregion differ in live biomass maximum accumulation (*P* <0.001) and rate or the number of years to maximum biomass (*P* <0.001). In the Blue Mountains, maximum biomass was highest for spruce and lowest for juniper and non-stocked groups. In the Coast Range, only two forest types had enough observations, fir and hardwoods. Surprisingly, there was no significant difference in maximum biomass levels (Appendix A, Table 4), but there is strong evidence ($P = 0.01$) that fir reached maximum biomass more quickly. Coast Range fir groups reached maximum biomass in an average of 170 years while hardwood biomass was continuing to increase in the largest age classes. All forest types in the East Cascades and the Klamath Mountains (hardwoods, fir, pine, and non-stocked) differed significantly in maximum live biomass, but again only fir had a faster rate of accumulation, reaching maximum biomass 100 years faster than other groups. The Sierra Nevada was similar to the Klamath and East Cascades as far as forest type differences for maximum biomass levels, but there was evidence that fir and pine had a lower rate of accumulation than hardwoods in this ecoregion (P=0.02). In the West Cascades, maximum biomass was higher for fir than pine and hardwoods, but no rates were significantly different.

There was strong evidence to support the hypothesis that forest types differ in maximum NPP, years required to reach maximum NPP, and age at initial decline of NPP (Appendix A, Table 4). In the Blue Mountains, maximum NPP, years to maximum NPP, and age at decline of NPP were highest for pine. In the Coast Range, fir had a significantly higher maximum NPP (P <0.001) than other forest types, but no difference between rate or age at decline (P=0.14 and 0.28 respectively). All forest types in the East Cascades, Klamath Mountains and Sierra Nevada differed significantly in maximum NPP (P< 0.001). Again, age of decline in NPP was much higher in pine. Finally, in the West Cascades, maximum NPP was higher for hardwoods than for fir (P=0), while fir reached maximum NPP most quickly.

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 ecoregion while variation in dead biomass (model weights 0.40-0.60) and NPP (model weights 0.02-0.98) was most explained by forest type (Appendix A, Table 7). 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 Pg C (Appendix A, Table 5). About 65 percent of live biomass is on public lands, with a relatively large amount, 0.476 Pg C, in the West Cascades ecoregion. Private land accounts for 35 percent of live biomass with nearly a third of the regional biomass in the predominantly privately owned Coast Range. Fir/Hemlock biomass dominates totals in all ecoregions except the East Cascades and Central Basin where pine stands dominate, and the Chaparral/Oak Woodlands where hardwoods dominate (Figure 7a). The total live biomass assuming all stands reach approximate equilibrium carbon storage would nearly triple to 6.38 Pg C (Figure 7b). An additional 0.17 Pg C could potentially be stored by converting grasslands in the Willamette Valley to Douglas-fir stands.

Total dead biomass for the ORCA study regions is estimated at 0.492 Pg C. While the Klamath Mountains have more total live biomass than the Coast Range and West Cascades, the amount of dead biomass was up to 25 percent less. About 64 percent of dead biomass is on public lands with the largest amount, 0.087 Pg C, in the West Cascades. Private land accounts for 36 percent of the dead biomass, with nearly half in the Coast Range. Fir/hemlock dead wood biomass dominates totals in all ecoregions except the East Cascades and Central Basin where pine stands dominate and in the Chaparral/Oak Woodlands where it is equaled by hardwoods (Figure 7c). Total dead biomass stores would approximately double to 0.922 Pg C under full equilibrium (Figure 7d).

Total NPP of forests in the ORCA study region is estimated at 0.109 Pg C y^{-1}. Approximately 53 percent of NPP is on public lands with the largest amount, 0.016 Pg C y^{-1}, in the Klamath Mountains. Private land accounts for 47 percent of NPP with 0.018 Pg C y^{-1} in the Coast Range. Fir/Hemlock NPP dominates totals in all ecoregions except the East Cascades and Central Basin where pine stands are greater and the Blue Mountains where they are equivalent (Figure 8a). Total NPP would increase from 0.109 to 0.168 Pg C yr^{-1} assuming all stands reached maximum NPP (Figure 8b).

Total mortality of biomass for the ORCA study regions is estimated at 0.021 Pg C y^{-1}. About 64 percent of mortality is on public lands with the largest amounts, 0.003 Pg C y^{-1} each, in the Klamath Mountains and Sierra Nevada. Private land accounts for 36 percent of the mortality, and the largest amount is in the Coast Range, probably due to windthrow. Fir/hemlock biomass mortality dominates totals in all ecoregions, but is nearly equal to pine stands in the East Cascades.

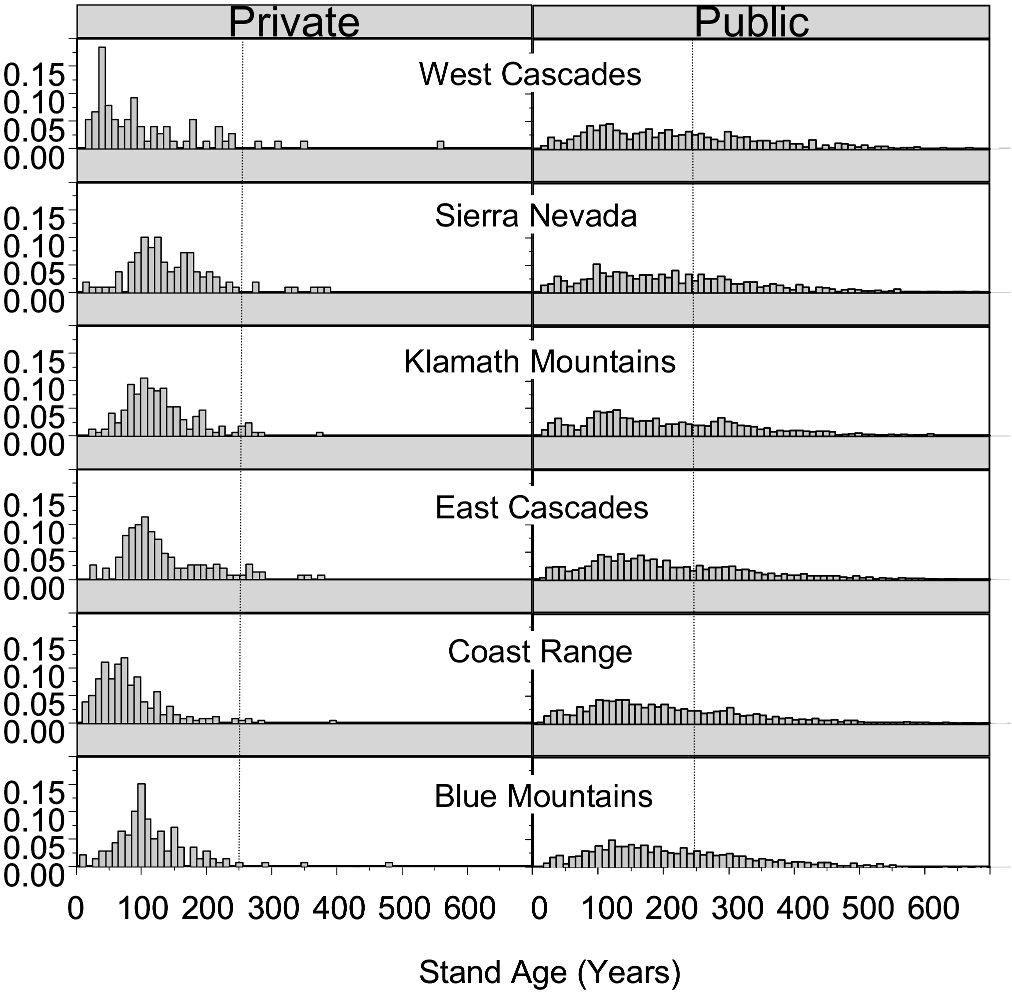


Figure 2. Frequency distributions of stand age by ecoregion and ownership. Forests on private land tend to have more stands in lower age classes than stands on public lands. Vertical line delineates stands older vs. younger than 250 years.

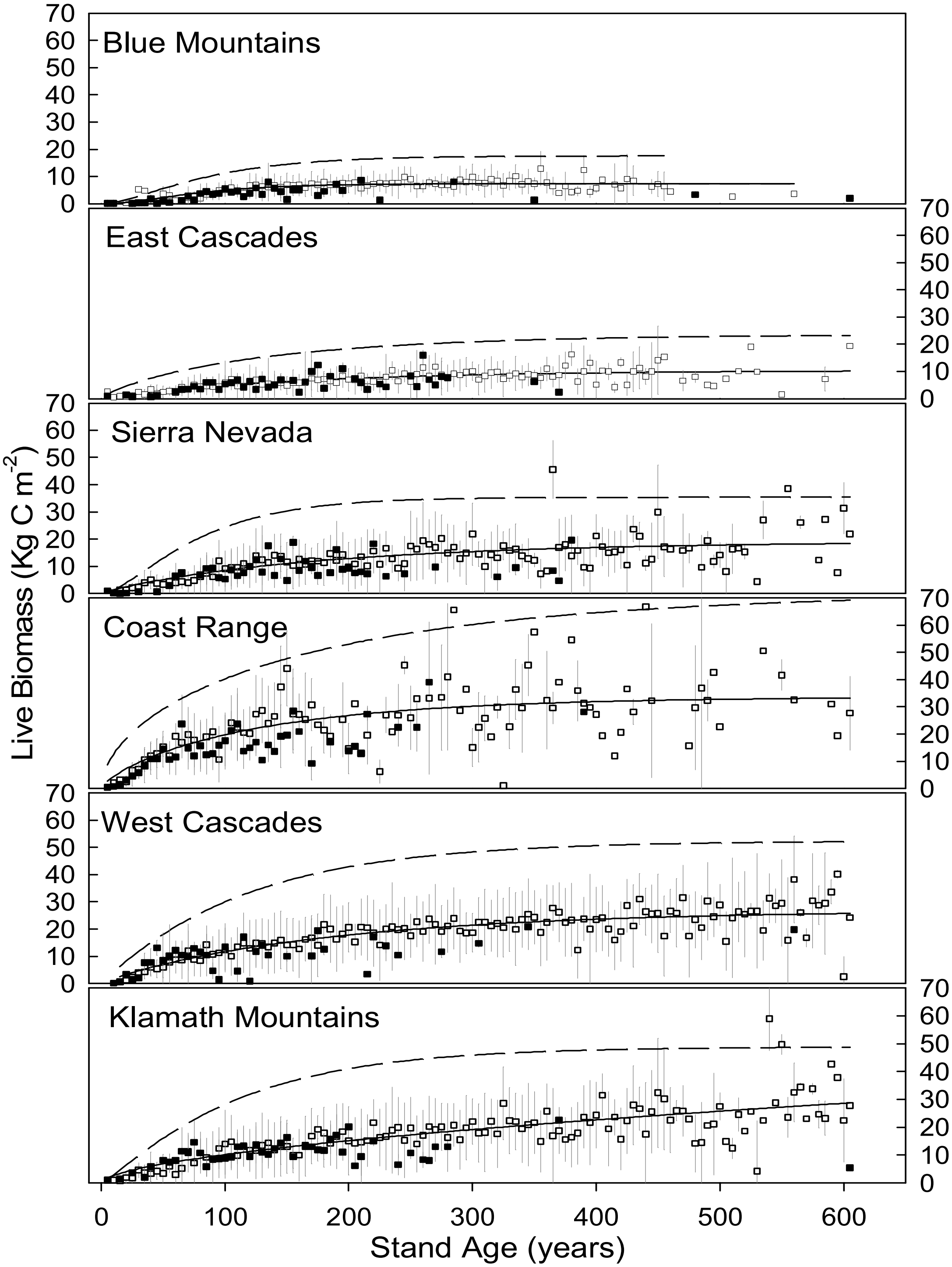


Figure 3. Live biomass (trees and understory woody shrubs) versus stand age. Dotted line (upper bounds) and solid line (mean trend) were fit using a Chapman-Richards function. Open (public) and solid (private) squares are the mean biomass for plots grouped into 5-year age bins. Gray lines are the standard deviations in each bin.

Table 2. Mean estimates by age group[1] and maximum of upper bounds for biomass, NPP, and mortality in each ecoregion and ownership[2]. Standard deviations are in parentheses. Ecoregion codes are as in Table 2.

Ecoregion	Young	Mature	Old	Maximum	Age at Max	Young		Mature	
Live Biomass (kg C m^{-2})						Private	Public	Private	Public
BM	1.9 (2.1)	5.9 (3.6)	7.4 (4.1)	17.8 (0.9)	215	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)	70.8 (15.8)	445	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)	22.5 (1.7)	255	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)	49.1 (1.9)	245	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)	36.3 (1.8)	195	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)	53.2 (1.8)	275	7.9 (5.6)	7.0 (5.5)	11.3 (7.1)	16.4 (10.7)
Dead Biomass (kg C m^{-2})						Private	Public	Private	Public
BM	1.0 (0.9)	1.9 (1.8)	2.1 (1.9)	6	180	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)	14	500	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)	5	150	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)	8	300	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)	6.5	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)	17	600	4.0 (3.6)	3.2 (3.2)	3.2 (2.6)	2.7 (2.2)
NPP (kg C m^{-2} y^{-1})						Private	Public	Private	Public
BM	0.16 (0.12)	0.27 (0.10)	0.29 (0.09)	0.53 (0.02)	75	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)	1.42 (0.06)	45	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)	0.74 (0.02)	105	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)	1.40 (0.04)	65	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)	1.00 (0.03)	75	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)	1.05 (0.02)	45	0.59 (0.31)	0.50 (0.24)	0.59 (0.26)	0.54 (0.21)

Table 2 Continued

Mortality (kg C m^{-2} y^{-1})						Private	Public	Private	Public
BM	0.02 (0.02)	0.07 (0.02)	0.10 (0.08)	0.27 (0.01)	225	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)	0.25 (0.10)	70	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)	0.34 (0.02)	175	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)	0.37 (0.02)	245	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)	0.45 (0.02)	115	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)	0.37 (0.01)	260	0.02 (0.02)	0.04 (0.03)	0.05 (0.04)	0.10 (0.07)

[1] Young = < 80 years, Mature = 80-200 years, Old = > 200 years (not available for private land)

[2] Ownership means calculated with site index corrected data

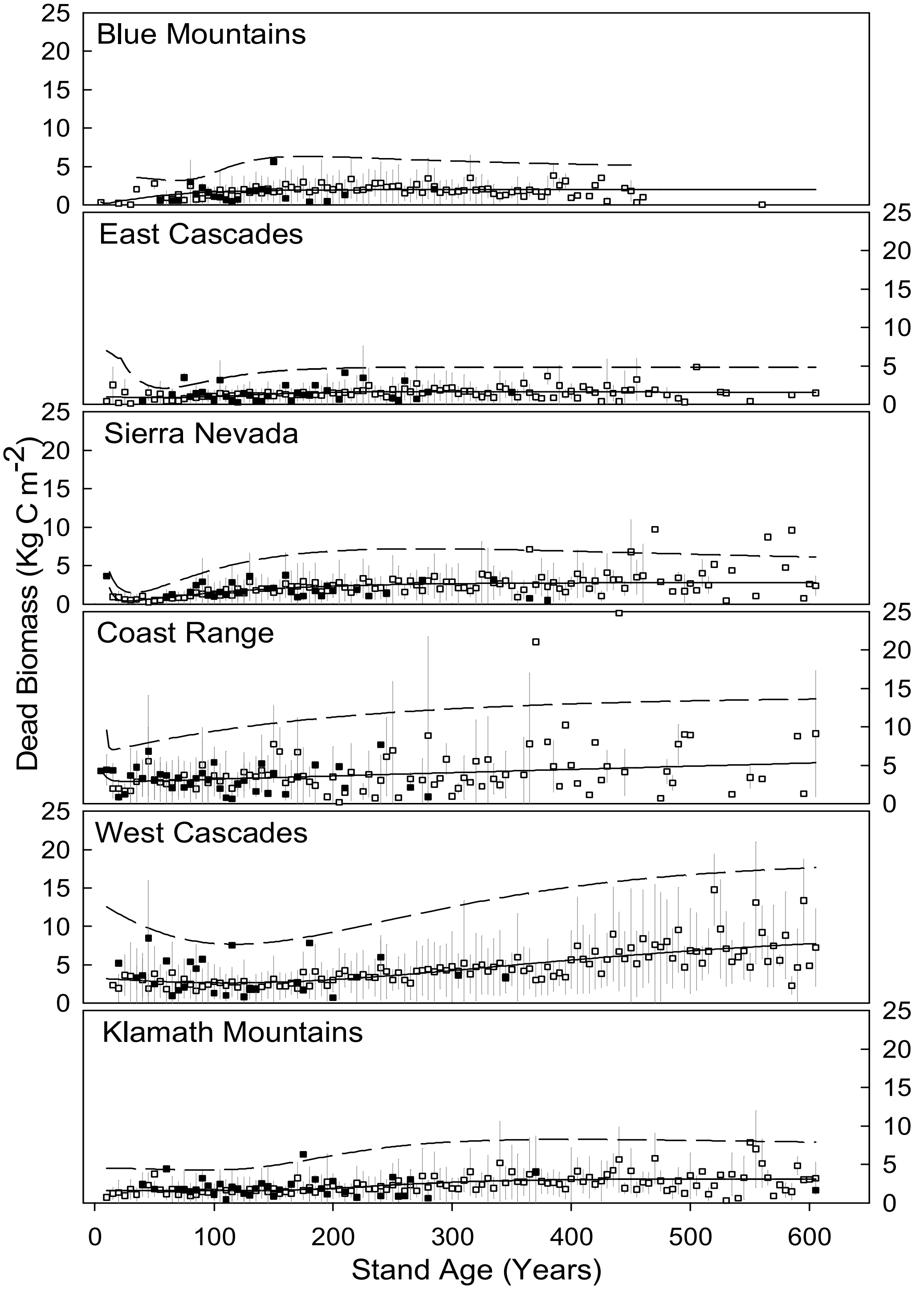


Figure 4. Dead biomass (CWD and standing dead trees) versus stand age. Dotted line (upper bounds) and solid line (mean trend) were fit using a decay plus a Chapman-Richards function. Open (public) and solid (private) squares are the mean biomass for plots grouped into 5-year age bins. Gray lines are the standard deviations in each bin.

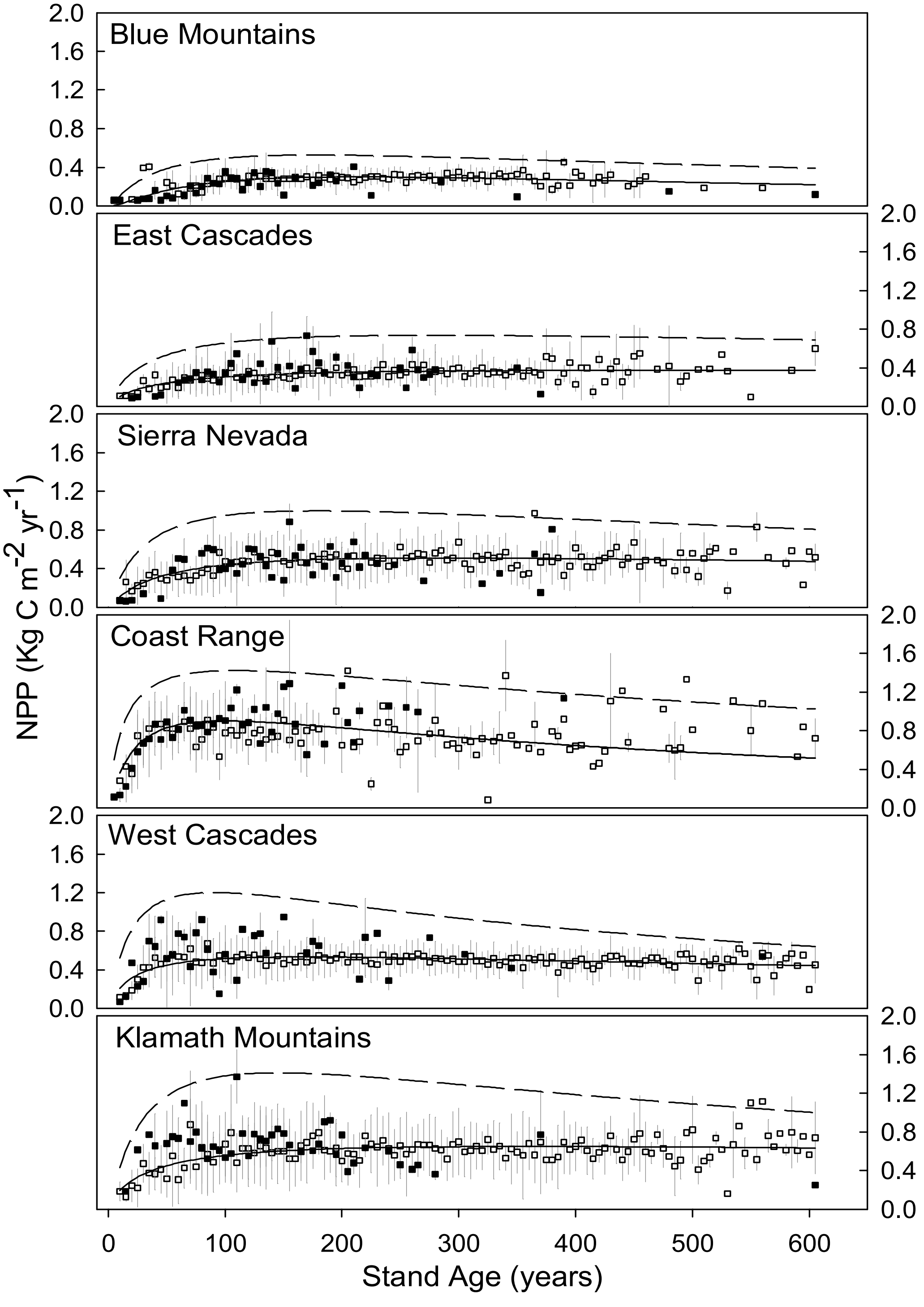


Figure 5. NPP (trees and understory woody shrubs) versus stand age. Dotted line (upper bounds) and solid line (mean trend) were fit using a Peak (3 parameter log-normal) function. Open (public) and solid (private) squares are the mean biomass for plots grouped into 5-year age bins. Gray lines are the standard deviations in each bin.

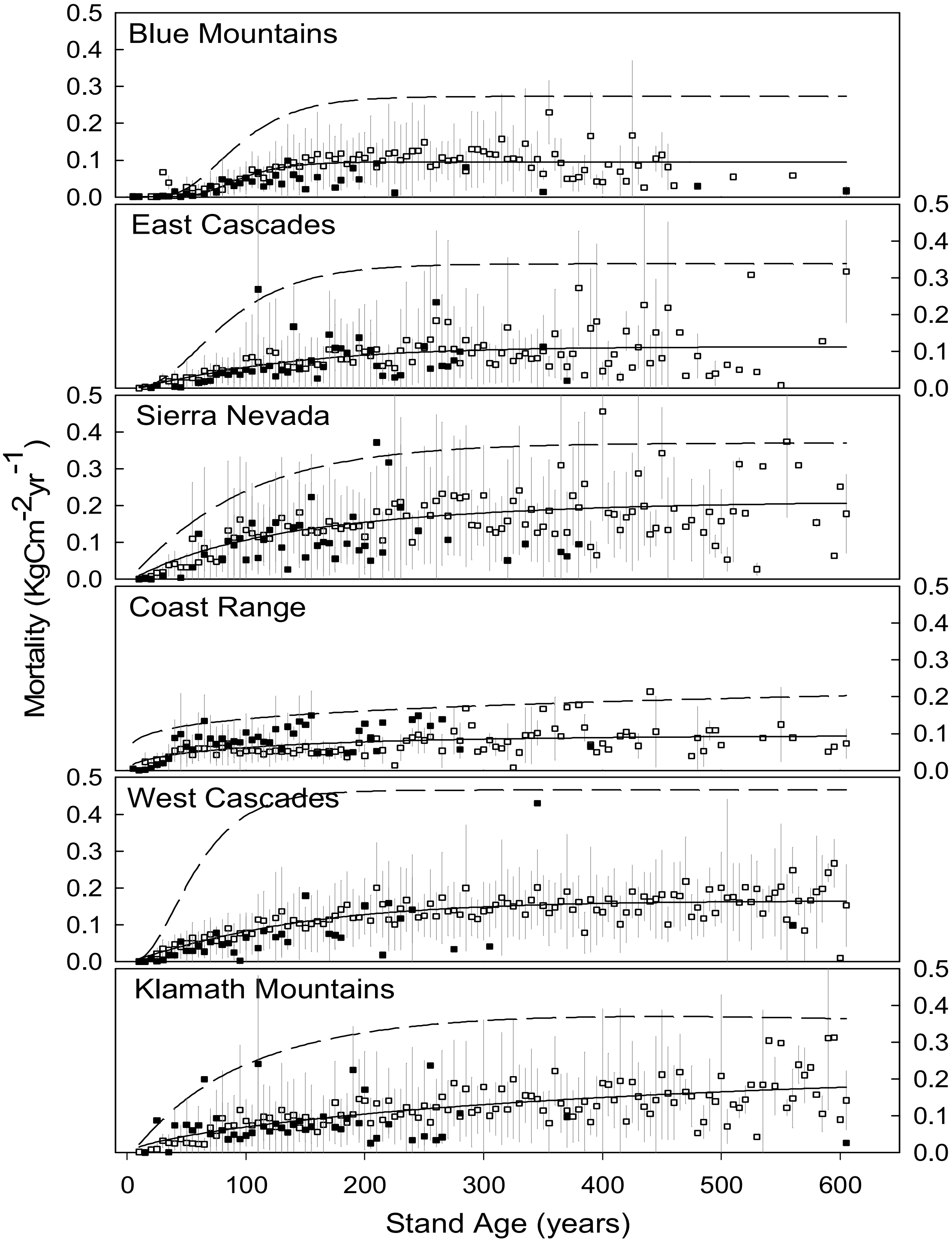
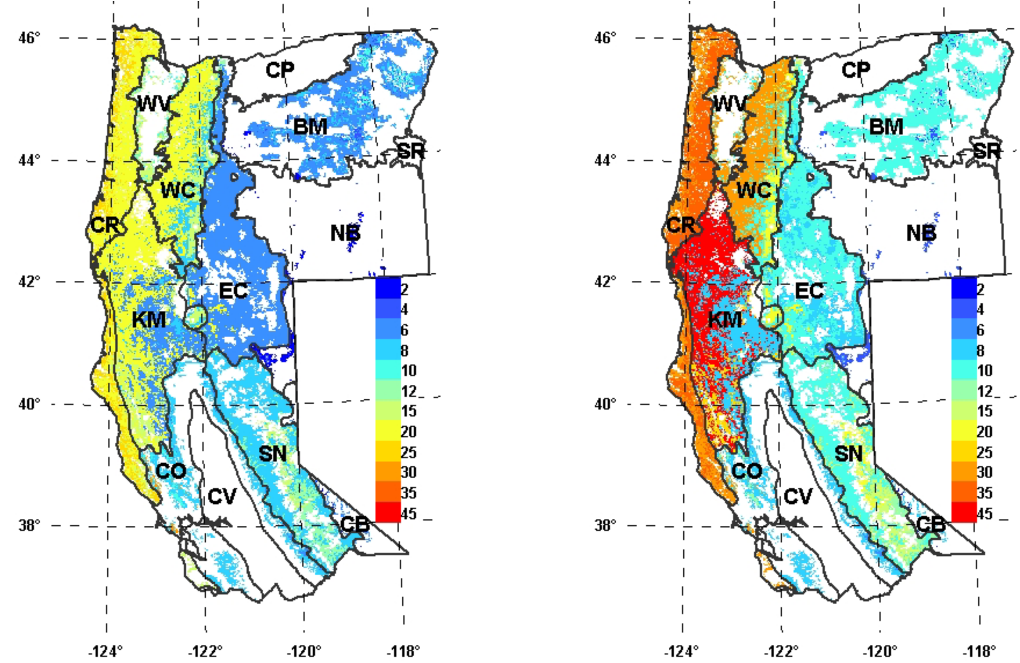


Figure 6. Mortality (trees) versus stand age. Dotted line (upper bounds) and solid line (mean trend) were fit using a Chapman-Richards function. Open (public) and solid (private) squares are the mean biomass for plots grouped into 5-year age bins. Gray lines are the standard deviations in each bin.

(a) Current Live Biomass (kg C m^{-2}) (b) Potential Live Biomass (kg C m^{-2})



(c) Current Dead Biomass (kg C m^{-2}) (d) Potential Dead Biomass (kg C m^{-2})

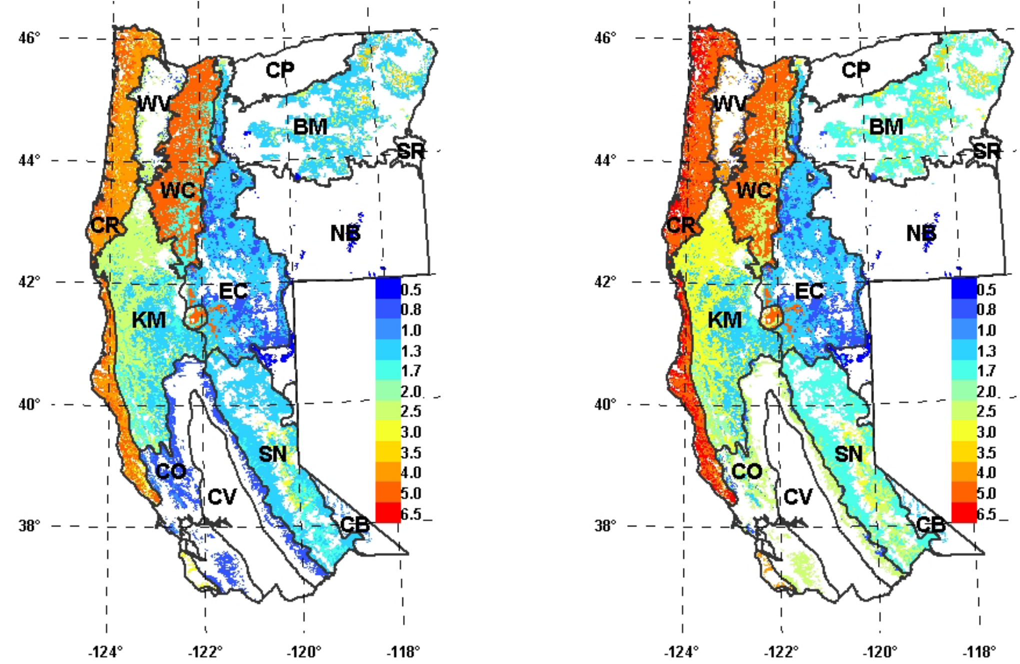
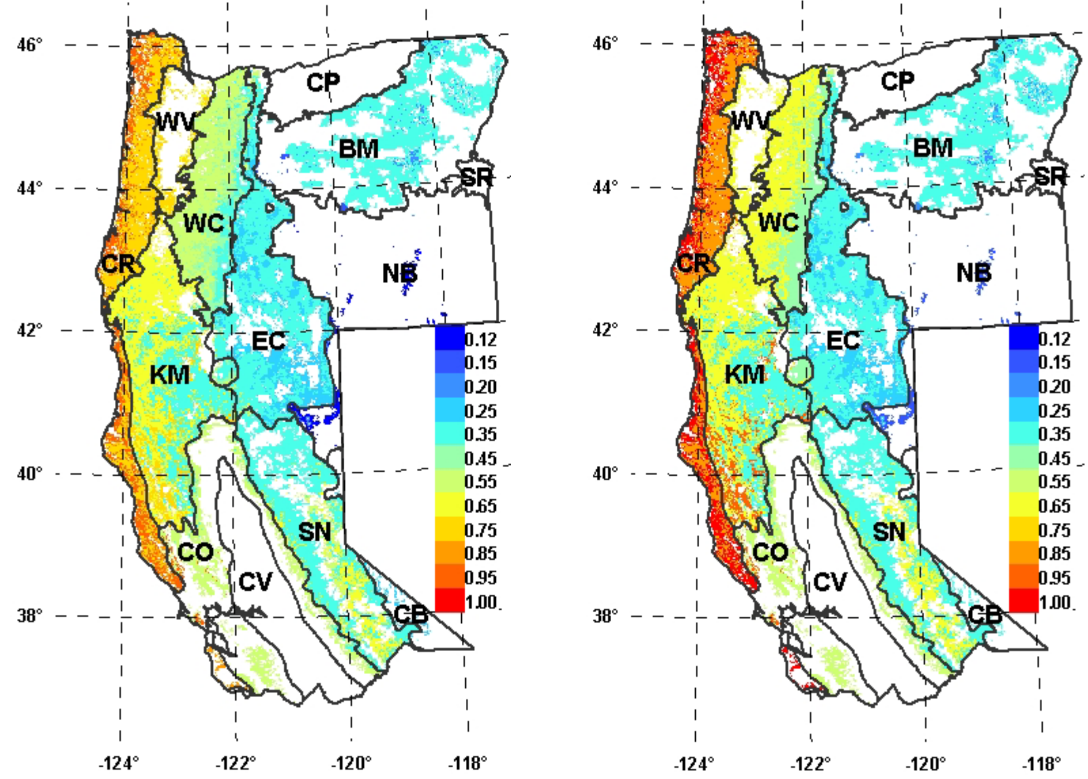


Figure 7. Current and potential carbon stocks (kg C m-^{2}) by forest type within ecoregion. Potential stocks were calculated using the mean trend maximums by forest type (Appendix A, Table 1).



(a) Current NPP (kg C m^{-2} yr^{-1})

(b) Potential NPP (kg C m^{-2} yr^{-1})

Figure 8. Current and potential NPP (kg C m^{-2} yr^{-1}) by forest type within ecoregion. Potential NPP was calculated using the mean trend maximums of NPP by forest type (Appendix A, Table 1).

Discusssion

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) were generally more distinguishable in the upper bounds of the data rather than the mean. In almost all cases, the West Cascades plot data was 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); while federal inventory sampling, by design, includes the full suite of factors that cause a given forest to grow at rates less than the optimal.

With respect to 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. Dead biomass stores may be underestimated by federal inventory data since the CWD diameter minimum required for measurement is 12.5cm rather than the 10cm used by ecological studies or the 7.6cm used by fire studies. Federal inventory data also does not include stumps which would increase biomass in recently harvested (young) stands causing the curve to follow a more U-shaped pattern.

Since 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. Expressed as a fraction of live biomass, we found that mortality tends not to be a constant (Figure 6). For example, mortality increases non-linearly 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 Pacific Northwest (e.g. Turner et al. 2004) often represent mortality as a fixed percent 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), but this is not the case in many of the ecoregions. 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, mean NPP peaks at approximately 80 years then declines (Figure 5) and mortality increases with age to a stable rate that approximates bolewood production. Despite the decline in NPP in the Coast Range, and West Cascades, we see biomass continuing 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 A, Table 4). 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). NPP and biomass in all age classes in the Sierra Nevada ecoregion were generally lower than in the Klamath Mountains despite similar mean annual precipitation. Forest types vary between the two with more abundant (less productive) pine in the Sierra Nevada. The lower overall productivity may be accounted for by the greater evaporative demands associated with warmer temperatures in the SN ecoregion.

Despite the relatively high NPP and live biomass in the Klamath Mountains, dead biomass stores were 50-60 percent lower than in the Coast Range and West Cascades. For this to be true, dead wood biomass is either being removed or consumed in the Klamath ecoregion at a much higher rate than 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). If frequent surface fires are controlling CWD dynamics in the Klamath, then we should expect to see an increase in CWD in stands originating after the onset of effective fire suppression (~70 years and younger) relative to older stands, which developed in part during the era of frequent surface fires. Examination of CWD in the Klamath Mountains does reveal that median dead biomass pools are dramatically less in most stands older than 60 years; moreover, this date-dependent drop in CWD mass is not seen in the upper bounds (99th percentile), suggesting that the inevitable few stands that escaped pre-suppression era wildfire continued to accumulate dead wood but at rates still less than in the Coast Range (see Figure 4). This supports the hypothesis that a combination of slower decomposition and shorter pre-suppression era fire return intervals may 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 background 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. Also, while younger stands (<100 yr) in these types were created by timber harvests or stand-replacing fires, resulting in relatively even-aged structure, older stands (> ~100 yr) developed under partial disturbances with small patch sizes and complex age distributions (Agee 1993). 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 has likely had little effect on biomass dynamics (Noss et al. 2006). In between these two extremes are the variable mixed-severity fire regimes, which occur in parts of most ecoregions (particularly in mixed conifer forest types in the Klamath, Blue Mountains, and Sierra Nevada); effects of fire exclusion relative to the variable fire intervals and effects typical of these areas are more difficult to define (Noss et al., 2006). The effects of fire exclusion (and restoration) on carbon dynamics in different forest types remains an important direction for future research.

Differences in maximum live biomass between the Coast Range and the West Cascades (33 versus 27 kg C m^{-2} respectively) may be primarily due to greater mortality and lower maximum NPP in the WC. West Cascade mortality was nearly twice that of the Coast Range and maximum NPP was about 60 percent of the Coast Range. The greater amount of dead biomass in the West Cascades further indicates that natural mortality of live biomass exceeds that in the Coast Range. Differences in age specific mean NPP could be due to ownership, as public land area accounts for 32% of total forest land in the Coast Range, but 75% in the West Cascades. Maximum NPP is lower on public lands in both of these ecoregions and given the difference in land areas managed by these ownerships, reduced NPP on public land would affect biomass accumulation.

Ownership patterns and management implications

Management of forests on private and public lands in the Coast Range, West Cascades and Klamath Mountains has always been somewhat different (Spies et al. 1994) and reduced timber cut on federal lands in these ecoregions after implementation of the Northwest Forest Plan in 1990 intensified the differences. Private lands in these ecoregions have on average less live biomass per unit area than public lands as the typical harvest rotation (80 yrs) 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 more than privately owned forests and mean carbon stores are 30-50 percent greater. Despite the fact that the Coast Range has the highest percentage of private land (twice any other ecoregion), the lowest mean stand age, and the highest rate of removals by harvest (Law et al. 2004), it nevertheless has the largest amount of biomass stored per unit area—due presumably 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). Thus, there is high potential for increased total carbon storage with increased rotation age or reduction in harvest rates (Figure 7b).

Unlike live biomass, dead biomass stores were not consistently influenced by ownership. Only in Coast Range mature stands was mean dead biomass per unit area significantly greater on public lands. Moreover, in the East Cascades and Sierra Nevada mean dead biomass was greater in young stands on private land. Typical management practices of Coast Range industrial land include thinning and removal of trees that would have contributed to the CWD pool especially in mature stands. The larger amounts of dead wood in young stands in the East Cascades and Sierra Nevada could be due to a combination of increased fire suppression on private land and more intensive management of woody detritus (e.g. pile and burn) on federal forests.

It is expected that management would affect NPP in younger stands as 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 since 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 be that management practices are more similar on public and private land as this ecoregion was also not affected by the Northwest Forest Plan.

Since ownership is associated with differences in mean biomass levels, a shift from current management on public land to a regime more like private land would likely significantly reduce carbon sequestration in forests. Decreasing rotation age to 50 years on all forested land in the Coast Range, Klamath Mountains, and West Cascades would reduce total live carbon stores by 35% (2.7 versus 1.8 Pg C). Public land has seen an increase in carbon storage since reducing harvest in 1990, but the increase is thought to have stabilized (Smith and Heath 2004). Our results indicate that Oregon and California forests are at 42% of potential maximum levels (2.7

versus 6.4 Pg C) given full equilibrium conditions and the absence of catastrophic wildfire.

While current NPP could potentially be increased by 35%, managing forests to maximize NPP would not have a positive effect on maximum 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 result in greatly reduced 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.

Forest type patterns

By examining the patterns of accumulation by forest type in each ecoregion, the variation in biomass in each age class bin is greatly reduced as forest type within ecoregion reflects the influence of local climate and soil fertility. Forest types affect the potential amount of carbon stored as they differ in growth rates, susceptibility to death by fire or insect outbreak, and physiological adaptation to local climate. For example, maximum biomass levels ranged from 3.0 kg C m-2 in juniper forests to 9.7 kg C m-2 in fir and spruce forests of the Blue Mountains. These within ecozone differences suggest caution in how FIA data is stratified for applications such as parameterization and validation of carbon cycle process models.

Forest type had the strongest influence on live biomass accumulation and mortality of carbon stores across the entire region while dead biomass stores and NPP were most influenced by climate. It is recognized that the distribution of forest types is strongly influenced by climate (e.g. firs in more mesic areas), so that changes in forest type distribution with climate change will also affect carbon sequestration. Future climate change scenarios suggest a warmer and wetter climate for the Pacific Northwest (IPCC 2007). While this change could increase growth rates, decomposition rates will also likely increase, and it is the relative change in these two processes that will determine NEP. Regional simulations of vegetation response to climate change are beginning to disaggregate forest ecosystems into forest types (Shafer et al. 2001) and the interpretation of the influence of forest type redistribution on carbon balance, and hence on the sign of the biospheric feedback to climate change, will be improved by comparisons of simulations to FIA data stratified at the same level.

Comparison and uncertainty

Our estimates of live and dead biomass, NPP, and mortality can be compared 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 aggregated at the state level produce a mean of 14 kg C m^{-2} for both states, but range from 3 to 24 kg C m^{-2} when aggregated by ecoregion. Besides the fact that our mean estimates included fine roots and understory biomass, the discrepancy is likely due to differences in the methods used to scale stem inventories to biomass and the method of aggregation (i.e. state instead of ecoregion). While we used ecoregion and species-specific equations applied at the stem level and then summarized for the plot, the study by Woodbury et al. (2007) and others (Smith and Heath 2004) used regional equations to convert reported plot-level growing stock volumes to biomass. Growing stock volumes are limited to a classification of timber inventory that includes commercial species of specified quality. This method may be appropriate for examining general trends at large scales, but may grossly overestimate or underestimate stocks and growth on some plots due to site variability (Jenkins et al., 2001). We believe we have constructed the most specific equation database available and we include all stems recorded on a plot. Our estimates of biomass are more comparable with studies using similar methods (i.e. ecoregion specific equations or lower levels of aggregation). Hicke et al. (in press) 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%. The IDB uses a less extensive ecoregion and species-specific equation database, resulting in more substitutions.

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 (Figure 3) 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 which are not limited to two areas. 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).

Modeling implications

As this study reaffirms, the processes driving forest carbon balance vary with stand age, therefore estimates of regional carbon fluxes from modeling efforts depend in large part on our ability to accurately characterize stand age across the region (Turner et al. 2006). Spatially explicit maps of forest age can be derived from remote imagery and used as input for carbon process models applied regionally. In our regional analyses, we use Landsat TM data (25m resolution) to map age for model input because the scale of stand replacing disturbance is < 60 m (Cohen et al., 2002). However, the accuracy of stand age maps based on remote sensing varies greatly by ecoregion and forest type, with the highest accuracy achieved in mesic forest where canopy structural development is most pronounced (Law et al. 2006). In addition to difficulties in remotely detecting age, there exist inevitable ambiguities in the definition of age since many forests in the Pacific Northwest are not even aged stands recruited immediately after a stand-replacing disturbance. The definition of age used in this study (the mean of the oldest 10 percent of trees in a plot) is simple and appropriate, but it still can result in some stands appearing very old with relatively low biomass (and vice-versa) if the increment data used to age the plot were not a representative sample and there were a very small number of trees left on a plot following a recent stand replacing disturbance. Until accurate and meaningful 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 such as those generated by GNN analysis (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 those patterns are more evident in the upper bounds of biomass or productivity for a given age rather than mean response. The variation in both maximum accumulation and rate of accumulation of live and dead biomass, NPP, and mortality for forest type within each ecoregion should be incorporated into modeling efforts when attempting to scale NEP across regions. The structure of many process models used for scaling NEP was developed based on ecological trends elucidated from field studies on idealized study plots. Theoretically, these trends would match those fit to the upper bounds in this study. 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 since 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 since 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. For this reason we advocate the separate characterization of mean and upper bound trends in federal inventory data.

Table 3. Forest carbon stocks in different regions

Region	Stocks	Components	Source
Western US	74[1]	Total tree biomass[1]	Hicke et al., in press
West Coast	50-200[1]	Total tree biomass[1]	Hicke et al., in press
West Coast	91-135[1]	Total tree biomass[1]	Woodbury et al., 2007
PNW- Coast Range	630[2]	Total tree biomass[4]	Smithwick et al., 2002
PNW- Cascades	580[2]	Total tree biomass[4]	Smithwick et al., 2002
PNW- Eastside	120[2]	Total tree biomass[4]	Smithwick et al., 2002
Oregon and N. California	65-190[1]	Total tree biomass	This study
Oregon and N. California	170-700[2]	Total tree biomass	This study
Northern Rockies	80[1]	Total tree biomass[1]	Hicke et al., in press
Colorado Rockies	<80[1]	Total tree biomass[1]	Hicke et al., in press
Mid-Atlantic	157-291[2]	Total tree biomass	Jenkins et al., 2001
Mid-Atlantic	70-110[1]	Total tree biomass[1]	Woodbury et al., 2007
Eastern US	75-250[3]	Aboveground live tree biomass	Brown et al., 1999
Russia	46-240[3]	Total tree biomass	Krankina et al, 2005
Canada	12-150[1]	Total forest live biomass	Kurz and Apps 1999
Latin America	135[1]	Aboveground live tree biomass	Houghton et al., 2005
Tropical Asia	115[1]	Aboveground live tree biomass	Houghton et al., 2005

[1] Includes foliage and coarse roots, but excludes fine roots

[2] Reported as maximum levels

[3] Minimum to maximum levels

[4] From small-scale ecological studies (not inventory)

Conclusion

In Oregon and Northern California (4.4×10^7 ha), total live biomass of forests is estimated at 2.71 Pg C (mean of 12 kg C ha^{-1}) in the period 1991-1999. Total dead biomass (does not include fine woody debris or litter stocks) of forests in the region was 0.492 Pg C , and total NPP was 0.109 Pg C. Mean stand age of publicly owned forests is 50-150 years higher than privately owned forests and mean carbon stores are also 30-50 percent higher. The majority of live and dead biomass (~65%) is on public lands. Trends in NPP with age vary among ecoregions, which suggests caution in generalizing that NPP declines in late succession. Biomass was still increasing in stands over 300 years in the Coast Range, the Sierra Nevada and the West Cascades, and in stands over 600 years in the Klamath Mountains, contrary to commonly accepted patterns of biomass stabilization or decline. If forests were managed for maximum carbon sequestration by reducing harvest or increasing rotation age, total carbon stocks could potentially double in the Coast Range, West Cascades, Sierra Nevada, and East Cascades and triple in the Klamath Mountains (Figure 7). Conversely, if rotation age is decreased as to a rotation age of 50 years in the Coast Range, Klamath Mountains, and West Cascades, total live carbon stocks could decrease from 2.71 Pg C to 1.80 Pg C.

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Appendix

Appendix A

Table 1. Equation^1 parameters fit to the mean values of each 5 year age bin.

Live Biomass	Maximum (A)	Rate (B)	Shape (C)	Years to Max^2		Adj. r^2
BM	7.1±0.2	0.028 ±0.008	7.20 ±5.21	180		0.61
EC	10.1±0.8	0.008 ±0.003	1.10 ±0.44	310		0.49
SN	19.4±0.7	0.004 ±0.003	0.81 ±0.31	500		0.47
CR	33.4±3.0	0.007 ±0.004	0.87 ±0.42	310		0.39
WC	26.9±2.0	0.005 ±0.002	0.86 ±0.20	430		0.69
KM	44.2±33.0	0.001 ±0.002	0.62 ±0.18	600+		0.63
NPP	Maximum (A)	Rate (B)	Decline Age (C)			
BM	0.30 ±0.01	1.30 ±0.10	216 ±14	125		0.57
EC	0.38 ±0.01	2.39 ±0.46	458 ±197	155		0.38
SN	0.51 ±0.01	1.92 ±0.22	291 ±45	125		0.42
CR	0.82 ±0.03	2.29 ±0.38	162 ±32	60		0.17
WC	0.54 ±0.01	2.09 ±0.15	162 ±12	65		0.39
KM	0.65 ±0.01	2.37 ±0.35	324 ±75	110		0.31
Dead	Maximum	Rate (B)	Shape (C)	Initial	Decay Rate	
BM	1.39 ±1.10	0.05 ±0.04	276 ±1576	1.83 ±0.9	0.01±0.01	0.15
EC	1.68 ±0.10	0.02 ±0.01	2.51 ±0.01	5.46 ±2	0.05±0.03	0.12
SN	2.80 ±0.17	0.01 ±0.01	1.61 ±.93	-	-	0.35
CR	-	-	-	-	-	-
WC	9.54 ±5.19	0.004 ±0.004	3.81 ±5.31	3.26 ±1.00	0.003 ±0.01	0.53
KM	1.57 ±1.93	0.015 ±0.02	33.00 ±166	1.59 ±0.30	0.00 ±0.00	0.24
Mortality	Maximum (A)	Rate (B)	Shape (C)	Years to Max^2		
BM	0.10 ±0.00	0.035 ±0.015	23.2 ±33.00	140		0.48
EC	0.11 ±0.01	0.007 ±0.006	1.43 ±1.00	270		0.26

Table 1 Continued

Mortality	Maximum (A)	Rate (B)	Shape (C)	Years to Max[2]		
SN	0.20 ±0.02	0.008 ±0.004	1.13 ±0.62	250		0.34
CR	0.09 ±0.01	0.006 ±0.005	0.48 ±0.27	270		0.24
WC	0.17 ±0.01	0.008 ±0.002	1.20 ±0.34	310		0.64
KM	0.29 ±0.27	0.001 ±0.003	0.61 ±0.23	600+		0.50

[1] Equation Forms: Live Biomass = A*(1 - exp(-B*SA)^C, Dead Biomass = D*exp(-E*SA) + A*(1 - exp(-B*SA))^C, NPP = A*exp(-.5*(ln(SA/C)/B)^2), Mortality = A*(1 - exp(-B*SA)^C where SA is stand age

[2] Equation solved for the stand age where A is 90% of maximum

Table 2. Equation[1] parameters fit to upper bounds (99th percentile) of data.

Live Biomass	Maximum (A)	Rate (B)	Shape (C)	Years to Max[2]		Adj. r^2
BM	17.8 ±0.9	0.013 ±0.005	1.44 ±0.67	215		0.51
CR	70.8 ±15.8	0.004 ±0.004	0.58 ±0.24	445		0.44
EC	22.5 ±1.7	0.009 ±0.004	1.01 ±0.46	255		0.39
KM	49.1 ±1.9	0.010 ±0.003	1.14 ±0.34	245		0.39
SN	36.3 ±1.8	0.014 ±0.006	1.61±0.89	195		0.69
WC	53.2 ±1.8	0.008 ±0.002	0.93 ±0.21	275		0.62
Dead	Maximum (A)	Rate (B)	Shape (C)	Initial (D)	Decay Rate (E)	
BM	1.4 ±1.1	0.050 ±0.040	276.0 ±1577	1.83 ±0.87	0.004 ±0.008	0.15
CR	-	-	-	-	-	-
EC	4.9 ±0.3	0.030 ±0.020	5.8 ±11.0	17.10 ±5.99	0.050 ±0.020	0.13
KM	5.0 ±6.0	0.020 ±0.020	17.6 ±71.0	4.58 ±1.22	0.001 ±0.005	0.19
SN	-	-	-	-	-	-
WC	18.6 ±3.0	0.007 ±0.004	3.6 ±5.3	13.48 ±4.26	0.008 ±0.009	0.29
NPP	Maximum (A)	Rate (B)	Decline Age (C)	Years to Max		
BM	0.53 ±0.02	1.60 ±0.21	176 ±21	75		0.28
CR	1.42 ±0.06	2.12 ±0.29	110 ±17	45		0.17
EC	0.74 ±0.02	2.10 ±0.46	278 ±86	105		0.32
KM	1.40 ±0.04	1.73 ±0.13	144 ±11	65		0.12
SN	1.00 ±0.03	1.86 ±0.17	179 ±16	75		0.56
WC	1.05 ±0.02	1.83 ±0.09	104 ±6	45		0.34
Mortality	Maximum (A)	Rate (B)	Shape (C)	Years to Max		
BM	0.27 ±0.01	0.020 ±0.010	8.89 ±9.60	225		0.39
CR	0.25 ±0.10	0.001 ±.004	0.02 ±0.10	70		0.24
EC	0.34 ±0.02	0.020 ±.010	3.58 ±4.05	175		0.26
KM	0.37 ±0.02	0.010 ±.005	1.15 ±0.62	245		0.11
SN	0.45 ±0.02	0.030 ±.020	3.36 ±3.53	115		0.5

Table 2 Continued

WC	0.37 ±0.01	0.010 ±.004	1.38 ±0.55	260		0.32

[1] Equation Forms: Live Biomass = A*(1 - exp(-B*SA)^C, Dead Biomass = D*exp(-E*SA) + A*(1 - exp(-B*SA))^C, NPP = A*exp(-.5*(ln(SA/C)/B)^2), Mortality = A*(1 - exp(-B*SA)^C where SA is stand age

[2] Equation solved for the stand age where A is 90% of maximum

Table 3. Regression parameters for equations[1] fit to mean values of each 5 year bin (maximum of 200 years) by ownership.

Public					
Live	Maximum (A)	Rate (B)	Shape (C)	Years to Max[2]	Adj. r^2
BM	11.2±4.4	0.006±0.005	1.04±0.40	390	0.76
CR	27.0±2.7	0.020±0.011	1.75±0.98	145	0.66
EC[3]	8.8±1.5	0.011±0.009	1.36±0.77	235	0.86
KM	18.1±2.7	0.014±0.006	1.76±0.67	205	0.84
SN	14.0±1.2	0.020±0.006	2.65±1.02	165	0.86
WC	21.2±2.9	0.011±0.005	1.38±0.36	280	0.91
NPP	Maximum (A)	Rate (B)	Decline Age (C)	Years to Max	
BM	0.33±0.12	3.16±2.08	250+	250+	0.33
CR	0.81±0.03	1.69±0.23	87±11	45	0.45
EC	0.34±0.02	1.91±0.41	233±115	95	0.70
KM	0.63±0.03	1.50±0.29	165±51	85	0.62
SN	0.58±0.11	2.22±0.63	250+	185	0.78
WC	0.55±0.01	1.31±0.10	96±6	55	0.79
Mortality	Maximum (A)	Rate (B)	Shape (C)	Years to Max	
BM	0.172±0.076	0.009±0.007	2.14±1.03	335	0.84
CR	0.054±0.002	0.103±0.042	7.41±7.71	45	0.59
EC	0.093±0.013	0.017±0.008	2.07±1.01	105	0.78
KM	0.112±0.014	0.020±0.009	2.48±1.38	155	0.74
SN	0.160±0.010	0.029±0.009	4.05±2.25	125	0.80
WC	0.170±0.040	0.009±0.005	1.23±0.36	280	0.89
Private					
Live	Maximum (A)	Rate (B)	Shape (C)	Years to Max	Adj. r^2
BM	4.8±0.4	0.05±0.03	31.1±64.8	115	0.57
CR	17.1±1.0	0.04±0.02	3.0±2.2	85	0.67
EC	7.9±1.1	0.03±0.02	6.4±11.0	135	0.32

Table 3 Continued

KM	14.6±2.1	0.02±0.02	2.0±2.1	160	0.36
SN	10.2±1.2	0.03±0.02	4.4±5.8	125	0.55
WC	16.8±6.6	0.01±0.02	1.0±1.2	240	0.42
NPP	Maximum (A)	Rate (B)	Decline Age (C)	Years to Max	
BM	0.27±0.02	0.83±0.17	143±24	105	0.60
EC	0.43±0.08	1.30±0.54	245±187	135	0.53
SN	0.52±0.03	0.91±0.20	119±17	75	0.51
CR	0.96±.04	1.45±0.25	121±25	65	0.65
WC	0.66±0.05	1.42±0.44	104±36	55	0.27
KM	0.76±.04	1.63±0.50	100±27	45	0.13
Mortality	Maximum (A)	Rate (B)	Shape (C)	Years to Max	
BM	0.051±0.005	0.063±0.036	75±221	105	0.63
CR	0.093±0.005	0.155±0.111	152±583	45	0.51
EC	0.081±0.016	0.065±0.064	132±664	175	0.25
KM	0.082±0.010	0.070±0.121	3.6±13.1	55	0.17
SN	0.150±0.031	0.018±0.021	2.5±4.5	175	0.43
WC	0.180±0.081	0.006±0.008	1.6±1.3	250+	0.32

[1] Equation Forms: Live Biomass = A*(1 - exp(-B*SA)^C, NPP = A*exp(-.5*(ln(SA/C)/B)^2), Mortality = A*(1 - exp(-B*SA)^C where SA is stand age

[2] Equation solved for the stand age where A is 90% of maximum

[3] Data included for age groups up to 250 (live biomass only) for EC and BM because values were still significantly increasing in both ownerships

Table 4. Regression parameters for equations[1] fit to mean values of each 5 year bin by forest type.
Regressions could not be fit to some forest types in some ecoregions as there were not enough age classes with data.

1: Douglas-fir/Hemock					
Live	Maximum (A)	Rate (B)	Shape ©	Years to Max^2	Adj. r^2
BM	9.1±0.5	0.023±0.010	5.95±6.55	175	0.31
CR	33.4±2.1	0.012±0.006	1.23±0.66	210	0.41
EC	14.9±2.3	0.006±0.005	0.91±0.52	345	0.34
KM	42.4±24.9	0.001±0.002	0.65±0.21	600$^+$	0.58
SN	17.7±0.9	0.014±0.006	1.77±1.03	205	0.37
WC	28.0±2.0	0.005±0.002	0.78±0.18	420	0.69
NPP	Maximum (A)	Rate (B)	Decline Age ©	Years to Max	
BM	0.32±0.01	1.20±0.19	224±21	130	0.20
CR	0.78±0.03	2.55±0.48	159±34	50	0.12
EC	0.51±0.03	2.25±0.72	472±322	170	0.23
KM	0.64±0.01	2.27±0.34	320±70	120	0.28
SN	0.56±0.01	1.71±0.18	228±24	110	0.31
WC	0.56±0.01	2.03±0.13	149±10	60	0.43
Mortality	Maximum (A)	Rate (B)	Shape ©	Years to Max	
BM	0.16±0.01	0.023±0.011	7.13±8.47	185	0.30
CR	0.10±0.02	0.004±0.005	0.53±0.30	430	0.26
EC	0.21±0.02	0.012±0.008	2.05±1.84	250	0.27
KM	0.21±0.05	0.003±0.003	0.74±0.27	600$^+$	0.49
SN	0.21±0.01	0.02±0.010	1.97±1.58	150	0.25
WC	0.17±0.01	0.008±0.002	1.15±0.34	310	0.62
2: Cedar/Larch					
Live	Maximum (A)	Rate (B)	Shape ©	Years to Max	Adj. r^2
BM	8.4±0.5	0.044±0.072	2.73±8.00	600$^+$	0.06
NPP	Maximum (A)	Rate (B)	Decline Age ©	Years to Max	

Table 4 Continued

CR	0.97±0.06	1.89±0.47	118±29	50	0.23
Mortality	Maximum (A)	Rate (B)	Shape ©	Years to Max	
CR	0.08±0.01	0.169±0.188	249±1605	50	0.22
KM	0.21±0.05	0.003±0.003	0.74±0.27	600$^+$	0.49
3: Juniper					
Live	Maximum (A)	Rate (B)^2	Shape ©	Years to Max	Adj. r^2
BM	3.0±0.3	0.018±0.009	2.68±2.17	190	0.50
EC	4.5±2.6	0.005±0.050	0.15±0.57	140	0.00
NPP	Maximum (A)	Rate (B)	Decline Age ©	Years to Max	
BM	0.16±0.01	1.56±0.30	233±48	115	0.35
Mortality	Maximum (A)	Rate (B)^2	Shape ©	Years to Max	
BM	0.03±0.00	0.023±0.018	4.12±5.88	160	0.29
4: Spruce – NONE					
5: Pine					
Live	Maximum (A)	Rate (B)^2	Shape ©	Years to Max	Adj. r^2
BM	9.7±3.9	0.003±0.004	0.54±0.26	580	0.43
EC	9.2±0.9	0.005±0.002	0.75±0.21	410	0.64
KM	8.0±3.7	0.005±0.010	0.61±0.61	370	0.11
SN	8.3±0.4	0.026±0.014	1.84±1.47	120	0.29
WC	8.9±0.4	0.082±0.044	21.91±41.0	70	0.38
NPP	Maximum (A)	Rate (B)	Decline Age ©	Years to Max	
BM	0.32±0.01	2.74±0.97	422±310	120	0.18
EC	0.33±0.01	2.99±0.60	527±283	130	0.43
KM	0.29±0.03	3.41±3.74	170±236	35	0.00
SN	0.35±0.01	2.73±0.80	227±102	65	0.09
WC	0.41±0.02	1.85±0.48	133±32	55	0.07
Mortality	Maximum (A)	Rate (B)^2	Shape ©	Years to Max	

Table 4 Continued

BM	0.21±1.17	0.001±0.006	0.50±0.32	600^+	0.34
EC	0.07±0.00	0.011±0.006	0.95±0.51	240	0.33
KM	0.05±0.01	0.008±0.012	0.72±0.77	260	0.10
SN	0.08±0.01	0.023±0.016	1.76±1.71	130	0.20
WC	0.09±0.01	0.030±0.017	3.26±3.36	120	0.35
6: Hardwoods					
Live	Maximum (A)	Rate $(B)^2$	Shape ©	Years to Max	Adj. r^2
CR	30.0±6.3	0.004±0.003	0.67±0.23	500	0.58
KM	23.1±2.1	0.007±0.004	1.06±0.43	300	0.51
SN	13.8±0.8	0.035±0.014	9.71±10.71	130	0.50
WC	9.7±1.2	0.137±0.208	95±677	50	0.18
NPP	Maximum (A)	Rate (B)	Decline Age ©	Years to Max	
CR	0.98±0.67	2.48±0.78	355±265	115	0.28
EC	0.70±0.12	1.08±0.49	231±85	145	0.10
KM	0.90±0.03	1.94±0.38	294±87	125	0.27
SN	0.65±0.02	1.44±0.24	280±59	145	0.52
WC	0.72±0.07	1.00±0.16	90±13	55	0.45
Mortality	Maximum (A)	Rate (B)	Shape ©	Years to Max	
KM	0.11±0.01	0.010±0.007	0.92±0.57	230	0.26
SN	0.13±0.01	0.035±.018	6.51±8.10	120	0.35
7: Non-Stocked					
Live	Maximum (A)	Rate (B)	Shape ©	Years to Max	Adj. r^2
BM	2.8±0.4	0.007±0.004	1.16±0.51	350	0.65
EC	2.3±0.3	0.010±0.007	0.90±0.53	230	0.36
KM	3.4±2.8	0.004±0.015	0.67±0.89	490	0.24
SN	2.0±0.3	0.019±0.019	1.20±1.38	140	0.25

Table 4 Continued

NPP	Maximum (A)	Rate (B)	Decline Age (C)	Years to Max	
BM	0.13±0.01	1.59±0.32	231±44	125	0.27
EC	0.15±0.01	2.13±0.58	180±60	70	0.08
SN	0.14±0.01	1.82±0.38	128±29	55	0.22
Mortality	Maximum (A)	Rate (B)[2]	Shape (C)	Years to Max	
BM	0.37±0.01	0.007±0.006	1.34±0.887	370	0.46
EC	0.03±0.04	0.002±0.009	0.474±0.477	600^{+}	0.13
SN	.03±.01	0.058±0.050	19.07±53.55	230	0.24

[1] Equation Forms: Live Biomass = A*(1 - exp(-B*SA)^C, NPP = A*exp(-.5*(ln(SA/C)/B)^2),
Mortality = A*(1 – exp(-B*SA)^C where SA is stand age

[2] Equation solved for the stand age where A is 90% of maximum

Table 5. Ecoregion, owner, and forest type total estimates of biomass, NPP, and mortality.

Ecoregion	**Live Biomass Pg C**									
	Private	Public	1	2	3	4	5	6	7	Total
BM	0.035	0.126	0.092	0.008	0.002	0.007	0.067	0.000	0.003	0.181
CR	0.289	0.236	0.415	0.049	0.000	0.014	0.002	0.118	0.000	0.606
EC	0.059	0.135	0.083	0.000	0.003	0.000	0.115	0.003	0.003	0.209
KM	0.172	0.415	0.477	0.005	0.000	0.000	0.016	0.124	0.001	0.623
SN	0.088	0.238	0.256	0.000	0.003	0.000	0.054	0.033	0.002	0.348
WC	0.011	0.476	0.458	0.005	-	0.002	0.016	0.004	0.001	0.487
CB	0.000	0.008	0.001	-	-	-	0.006	-	0.000	0.008
CO	0.106	0.016	0.020	0.004	-	-	0.011	0.051	-	0.129
CP	0.001	0.000	-	-	-	-	0.001	-	-	0.001
NB	0.001	0.003	0.002	-	0.001	-	0.001	-	-	0.004
WV	0.057	0.009	0.060	-	-	-	-	0.011	0.001	0.072
All	0.880	1.580	1.900	0.076	0.009	0.023	0.285	0.350	0.012	2.710
Ecoregion	**Dead Biomass Pg C**									
	Private	Public	1	2	3	4	5	6	7	Total
BM	0.010	0.037	0.027	0.003	0.000	0.002	0.014	0.000	0.003	0.054
CR	0.068	0.039	0.072	0.010	0.000	0.002	0.000	0.024	0.000	0.115
EC	0.012	0.028	0.017	0.000	0.000	0.000	0.022	0.001	0.001	0.042
KM	0.026	0.056	0.065	0.001	0.000	0.000	0.003	0.014	0.000	0.085
SN	0.016	0.041	0.046	0.000	0.000	0.000	0.009	0.004	0.001	0.062
WC	0.020	0.087	0.099	0.001	0.000	0.001	0.003	0.001	0.002	0.115
CB	-	0.001	-	-	-	-	0.001	-	-	0.001
CO	0.008	0.001	0.002	0.001			0.001	0.002	-	0.010
CP	$2.0\text{x}10^{-5}$	-	$2.0\text{x}10^{-5}$	-	-	-	-	-	-	$2.0\text{x}10^{-5}$
NB	-	$4.0\text{x}10^{-4}$	0.001	-	0.001	-	0.001	-	-	0.004
WV	0.005	0.001	0.007	-	-	-	-	-	0.001	0.008

Table 5 Continued

All	0.167	0.292	0.344	0.016	0.001	0.005	0.051	0.048	0.008	0.492
Ecoregion	**NPP Pg C yr^{-1}**									
	Priv	Pub	1	2	3	4	5	6	7	Total
BM	.002	.005	.0035	.0003	.0002	.0002	.0036	.0000	.0002	.0080
CR	0.0180	0.0080	0.0148	0.0023	0.0000	0.0004	0.0001	0.0071	0.0000	0.0257
EC	0.0030	0.0060	0.0037	0.0000	0.0001	0.0000	0.0060	0.0002	0.0002	0.0100
KM	0.0100	0.0160	0.0166	0.0002	0.0000	0.0000	0.0009	0.0068	0.0000	0.0246
SN	0.0050	0.0090	0.0095	0.0000	0.0001	0.0000	0.0027	0.0016	0.0002	0.0141
WC	0.0040	0.0110	0.0126	0.0001	0.0000	0.0000	0.0007	0.0002	0.0000	0.0144
CB	1.0x10^{-5}	0.0003	-	-	-	-	-	-	-	0.0003
CO	0.0070	0.0010	-	-	-	-	-	-	-	0.0084
CP	6.0x10^{-5}	0.0080	-	-	-	-	-	-	-	7.0x10^{-5}
NB	6.0x10^{-5}	0.0001	-	-	-	-	-	-	-	0.0002
WV	0.0030	0.0003	-	-	-	-	-	-	-	0.0034
All	0.0528	0.0577	0.0606	0.0029	0.0004	0.0006	0.0140	0.0144	0.0008	0.1090
Ecoregion	**Mortality Pg C yr^{-1}**									
	Private	Public	1	2	3	4	5	6	7	Total
BM	0.0004	0.0018	0.0015	0.0001	0.0000	0.0001	0.0006	0.0000	0.0000	0.0025
CR	0.0017	0.0006	0.0011	0.0002	0.0000	0.0000	0.0000	0.0006	0.0000	0.0021
EC	0.0001	0.0016	0.0013	0.0000	0.0000	0.0000	0.0010	0.0000	0.0000	0.0024
KM	0.0010	0.0027	0.0033	0.0000	0.0000	0.0000	0.0001	0.0007	0.0000	0.0042
SN	0.0011	0.0029	0.0033	0.0000	0.0000	0.0000	0.0005	0.0003	0.0000	0.0042
WC	0.0000	0.0032	0.0031	0.0000	0.0000	0.0000	0.0001	0.0000	0.0000	0.0035
CB	5.0x10^{-6}	7.0x10^{-5}	-	-	-	-	-	-	-	8.0x10^{-5}
CO	0.0014	0.0002	-	-	-	-	-	-	-	0.0015
CP	1.0x10^{-5}	-	-	-	-	-	-	-	-	1.0x10^{-5}
NB	7.0x10^{-6}	7.0x10^{-5}	-	-	-	-	-	-	-	8.0x10^{-5}

Table 5 Continued

WV	0.0003	$3.0\text{x}10^{-5}$	-	-	-	-	-	-	-	0.0003
All	0.0068	0.0126	0.0136	0.0003	0.0000	0.0002	0.0020	0.0014	.0000	0.0207

Forest Types: 1 =Fir/Douglas fir/Hemlock, 2=Cedar/Larch/Sequoia/Redwood, 3=Juniper/Cypress, 4=Spruce, 5=Pine, 6=Hardwoods, 7=Non-Stocked

Table 6. Ecoregion, owner, and forest type mean estimates (± standard errors) of biomass, NPP, and mortality.

Ecoregion	**Live Biomass KgCm^{-2}**									
	Private	Public	1	2	3	4	5	6	7	Total
BM	3.6±0.3	6.7±0.1	7.7±0.2	8.5±.6	1.8±0.2	9.7±0.5	5.8±0.1	-	1.8±0.1	6.4±0.1
CR	13.0±0.6	22.0±0.6	21.0±0.7	21.0±2.0	-	26.0±4.0	5.1±1.0	14.0±0.6	2.3±0.8	19.0±0.5
EC	5.8±0.4	6.8±0.1	10.0±0.3	5.9±2.0	4.6±0.6	-	5.8±0.1	8.3±1.0	1.6±0.1	6.8±0.1
KM	12.0±0.6	16.0±0.3	17.0±0.4	10.0±3.0	-	-	5.4±0.5	14.0±0.5	1.7±0.2	15.0±0.3
SN	8.8±0.6	12.0±0.3	14.0±0.4	-	9.3±2.0	-	6.8±0.3	11.0±0.6	1.4±0.1	11.0±0.3
WC	9.8±0.8	18.0±0.3	19.0±0.3	20.0±3.0	-	15.0±2.0	7.5±0.4	8.1±1.0	2.0±0.2	18.0±0.3
CB	3.7±0.0	5.0±0.8	-	-	-	-	5.8±0.9	-	1.4±0.1	5.0±0.8
CO	6.2±0.6	6.4±0.8	8.9±1.0	-	-	-	4.6±0.7	7.1±0.6	-	6.2±0.5
CP	2.0±1.0		4.0±1.0	-	0.8±0.0	-	6.1±0.0	-	0.1±0.0	2.0±1.0
NB	2.7±1.0	2.8±0.8	7.9±4.0	-	2.1±0.4	-	4.2±1.0	-	0.9±0.7	2.8±0.6
WV	12.0±1.0	19.0±0.3	16.0±2.0	-	-	-	-	11.0±2.0	-	14.0±1.0
All	9.2±0.2	13.0±0.1	16.0±0.2	15.0±1.0	3.6±0.4	14.0±1.0	6.0±0.1	13.0±0.3	1.7±0.1	12.0±0.1
	Dead Biomass KgCm^{-2}									
BM	1.5±0.2	2.0±0.1	2.3±0.1	3.5±0.4	0.3±0.1	3.4±0.3	1.3±0.1	-	2.1±.4	2.0±0.1
CR	3.1±0.2	3.7±0.2	3.8±0.2	4.5±0.8	-	3.2±0.6	1.4±1.0	2.8±0.2	1.9±.4	3.6±0.1
EC	1.5±0.2	1.4±0.1	2.1±0.1	1.6±0.3	0.7±0.2	-	1.3±0.1	1.6±0.3	1.0±.1	1.4±0.1
KM	1.9±0.2	2.2±0.1	2.4±0.1	1.7±0.3	-	-	1.1±0.1	1.6±0.1	.9±.2	2.2±0.1
SN	1.8±0.2	2.2±0.1	2.6±0.1	-	1.4±0.5	-	1.3±0.1	1.5±0.2	.9±.1	2.2±0.1
WC	3.7±0.5	4.0±0.1	4.1±0.1	6.3±1.0	-	4.7±0.9	1.5±0.1	2.9±0.5	5.8±2	4.0±0.1
CB	-	0.9±0.2	-	-	-	-	0.9±0.2	-	-	0.9±0.2
CO	0.9±0.2	0.6±0.2	1.0±0.2	-	-	-	0.7±0.3	0.6±0.1	-	0.8±0.1
CP	0.2±0.1	-	-	-	-	-	-	0.2±0.1	-	0.2±.1
NB	-	1.6±0.7	2.7±1.0	-	0.1±0.0	-	0.8±0.5	-	-	1.6±0.7
WV	1.6±0.5	2.4±0.9	2.2±0.5	-	-	-	-	0.7±0.2	-	1.9±0.4
All	2.2±0.1	2.6±0.0	3.2±0.1	3.9±0.3	0.8±0.2	3.6±0.3	1.2±0.0	1.9±0.1	1.9±.3	2.6±0.1

Table 6 Continued

	NPP KgCm^{-2}y^{-1}									
BM	0.2±0.01	0.3±0.00	0.3±0.00	0.3±0.01	0.1±0.01	0.3±0.02	0.3±0.00	-	0.1±0.00	0.3±0.00
CR	0.8±0.02	0.8±0.01	0.8±0.01	.9±0.04	-	0.8±0.04	0.4±0.10	0.8±0.02	0.2±0.04	0.8±0.01
EC	0.3±0.02	0.3±0.00	0.5±0.01	0.3±0.04	0.2±0.02	-	0.3±0.00	0.5±0.10	0.1±0.00	0.3±0.00
KM	0.7±0.02	0.6±0.01	0.6±0.01	0.5±0.07	-	-	0.3±0.01	0.8±0.02	0.1±0.01	0.6±0.01
SN	0.5±0.02	0.5±0.01	0.5±0.01	-	0.3±0.05	-	0.3±0.01	0.6±0.02	0.1±0.00	0.5±0.00
WC	0.6±0.03	0.5±0.00	0.5±0.00	0.5±0.04	-	0.4±0.04	0.4±0.01	0.5±0.05	0.1±0.01	0.5±0.00
CB	0.2±0.00	0.2±0.02	-	-	-	-	0.2±0.02	-	0.1±0.01	0.2±0.02
CO	0.4±0.03	0.4±0.03	0.5±0.07	-	-	-	0.3±0.04	0.5±0.04	-	0.4±0.02
CP	0.2±.02	-	0.3±0.00	-	0.1±0.00	-	0.3±0.00	-	0.1±0.00	0.2±0.02
NB	0.1±0.04	0.2±0.03	0.4±0.11	-	0.1±0.01	-	0.2±0.03	-	0.1±0.01	0.2±0.02
WV	0.7±0.05	0.7±0.06	0.7±0.04	-	-	-	-	0.7±0.10	-	0.7±0.04
All	0.6±0.01	0.5±0.01	0.5±0.01	0.6±0.03	0.2±0.01	0.4±0.03	0.3±0.01	0.7±0.01	0.1±0.01	0.5±0.00
	Mortality KgCm^{-2}y^{-1}									
BM	0.04±0.0	0.09±0.0	0.13±0.0	0.12±0.0	0.02±0.0	0.14±0.0	0.06±0.0	-	0.02±0.0	0.09±0.0
CR	0.07±0.0	0.06±0.0	0.06±0.0	0.08±0.0	-	0.06±0.0	0.04±0.0	0.08±0.0	0.01±0.0	0.06±0.0
EC	0.06±0.0	0.08±0.0	0.16±0.0	0.04±0.0	0.03±0.0	-	0.05±0.0	0.07±0.0	0.01±0.0	0.08±0.0
KM	0.07±0.0	0.11±0.0	0.12±0.0	0.07±0.0	-	-	0.04±0.0	0.08±0.0	0.01±0.0	0.10±0.0
SN	0.11±0.0	0.14±0.0	0.18±0.0	-	0.07±0.0	-	0.06±0.0	0.11±0.0	0.02±0.0	0.14±0.0
WC	0.05±0.0	0.12±0.0	0.13±0.0	0.14±0.0	-	0.15±0.0	0.07±0.0	0.05±0.0	0.01±0.0	0.12±0.0
CB	-	0.05±0.0	-	-	-	-	0.05±0.0	-	0.01±0.0	0.05±0.01
CO	0.08±0.0	0.06±0.0	0.07±0.0	-	-	-	0.03±0.0	0.11±0.0	-	0.07±0.01
CP	0.02±0.0	-	0.04±0.0	-	0.01±0.0	-	0.06±0.0	-	0.05±0.0	0.02±0.0
NB	0.01±0.0	0.06±0.0	0.32±0.2	-	0.02±0.0	-	0.03±0.0	-	0.01±0.0	0.05±0.02

Table 6 Continued

WV	0.06±0.0	0.06±0.0	0.06±0.0	-	-	-	-	0.06±0.0	-	0.06±0.01
All	0.07±0.0	0.10±0.0	0.13±0.0	0.10±0.0	0.03±0.0	0.12±0.0	0.05±0.0	0.08±0.0	0.02±0.0	0.10±0.0

Forest Types: 1 =Fir, Douglas fir, Hemlock, 2=Cedar, Larch, Sequoia/Redwood, 3=Juniper, Cypress, 4=Spruce, 5=Pine, 6=Hardwoods, 7=Non-Stocked

Table 7. Top ranked explanatory variables (from model weights) across entire study region (ecoregion, ownership, or forest type) and within each ecoregion (ownership or forest type), after accounting for age.

Region	Live Biomass	Dead Biomass	NPP	Mortality*
Study Area	Forest Type	Ecoregion	Ecoregion	Forest Type
BM	Forest Type	Forest Type	Forest Type	Forest Type
CR	Forest Type	Forest Type	Forest Type	Owner
EC	Forest Type	Forest Type	Forest Type	Forest Type
KM	Forest Type	Forest Type	Forest Type	Forest Type
SN	Forest Type	Forest Type	Forest Type	Forest Type
WC	Forest Type	Forest Type	Forest Type	Forest Type

*Effects of each factor on mortality could only be assessed for stands <= 250 years because transformations failed to adjust for non-normal distribution of all data points