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Title: Carbon Storage and Fluxes in Forests of Western Oregon -- Successional Patterns and Environmental Controls

Abstract approved   Signature redacted for privacy.

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Beverly E. Law

In this study we use a combination of data from forest inventories, intensive chronosequences, extensive sites, and remote sensing, to make estimates of biomass and net primary production (NPP) for the forested region of Western Oregon. Plot-level forest inventory data were provided by the USDA Forest Service through their Forest Inventory and Analysis and Current Vegetation Survey programs. We also use the light use efficiency model 3-PGS to estimate net primary production (NPP) of the forests of western Oregon. We evaluate the performance of the model using the forest inventory NPP dataset as well as with estimates of productivity from eddy flux towers. We also evaluate the belowground carbon allocation scheme employed in the 3-PGS model.

The forest age distributions differ by geographic location with fewer old stands in the Coast Range and the East Cascades, and a relatively uniform distribution of ages from 0 to greater than 800 in the West Cascades. Age distributions also differ by land ownership, with fewer old stands on non-federal lands than on national forest lands (maximum ages ~ 250 and >800 respectively).

The timing and magnitude of maximum net primary production varies by ecoregion, with high-productivity sites reaching a maximum NPP of ~2 kg C m^{-2} y^{-1} at about 30 years of age, and low-productivity sites (East Cascades) reaching a maximum NPP ~0.8 kg C m^{-2} y^{-1} between 80 and 100 years.

Measurements of additional carbon budget components combined with inventory data provide estimates of carbon storage and fluxes that may be useful for forest management and validation of regional model simulations. A forest productivity model, 3-PGS, was evaluated with NPP data and used to quantify controls on NPP in each of the ecoregions. Overall the 3-PGS model tends to overestimate NPP at high productivity sites and underestimate productivity at moderate and low productivity sites. Overestimates of NPP in the Coast Range are partially a function of the model, in effect, using fPAR to detect successional changes in NPP. Belowground allocation as estimated by the model does not compare well with belowground allocation estimates from forest inventory data and intensive site measurements. The model suggests that NPP is most constrained by environmental factors in the East Cascades (~20% of potential NPP), less constrained in the West Cascades (~45% of potential NPP), and least

constrained in the Coast Range (~60% of potential NPP). Coastal Range forests tend to be most limited by temperatures sub-optimal for photosynthesis and summer VPD constraints. East Cascades forests are limited by soil fertility, temperature, VPD, and strong soil water deficits throughout much of the year.

Carbon cycle research has reached a point where both small and large scale datasets of carbon storage and fluxes are necessary. There is an increased interest in understanding carbon cycling at regional to global scales and the combined power of large and small scale studies of carbon cycling help us to improve our understanding of successional carbon dynamics. Calibration and evaluation of modelling at these scales could be aided by data collected at equivalent scales.

Carbon Storage and Fluxes in Forests of Western Oregon – Successional Patterns
and Environmental Controls

by

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APPROVED:

Signature redacted for privacy.

Major Professor, representing Forest Science

Signature redacted for privacy.

Head of the Department of Forest Science

Signature redacted for privacy.

Dean of the Graduate School

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Steven Van Tuyl, Author

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CONTRIBUTION OF AUTHORS

Drs. Beverly E. Law, David P. Turner, and Alix I. Gitelman guided the
conception, analysis, interpretation, and editing of the manuscripts in this thesis.

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CHAPTER 1

Introduction

Introduction

Carbon cycle research was thrust into the forefront of the ecological world when it was discovered that human activity was causing an increase in concentrations of atmospheric carbon dioxide (IPCC 2001). Carbon dioxide, along with other gasses, has physical properties that allow them to trap long wave radiation near the surface of the earth. This phenomenon, known as the greenhouse effect, is projected to heat the surface of the earth and alter climate regimes across the globe at untold ecological and economic expense.

Forests have been a focus of carbon cycle research as it relates to climate change in part because of their potential to store vast quantities of carbon relative to other terrestrial biomes. Forests across the globe have historically been disturbed both by natural disturbance regimes (e.g. fire, windthrow, etc.) and by anthropogenic regimes (e.g. deforestation, harvesting, afforestation, etc.). As

forests recover after disturbances, the flux rates into and out of different carbon pools in the forest system change. Though these changes in carbon fluxes after disturbance have been observed in many studies, little is known about how they vary among and within biomes of the globe and how the forest environment affects these fluxes.

Most studies conducted on flux rates have focused on net primary production (NPP) because of its ease of measurement. Early studies of carbon storage and fluxes in forests primarily acted to describe carbon or mass pools and in some cases NPP (Bormann et al. 1970, Turner and Long 1975, Whittaker and Niering 1975, Grier and Logan 1977). When it came to explaining environmental controls on productivity many of these early studies focused on educated conjecture based on the current understanding of physiological processes. Later, studies focused on trying to understand how environmental factors controlled productivity of forests by focusing on measuring meteorological, nutrient, and other components of the ecosystems (Runyon et al. 1994, Law and Waring 1994, Gholz 1982, Graumlich et al. 1989). Important among early and current studies are those that either cross many biomes or environmental conditions and those that study, with great intensity, a single site. Paralleling the studies focused on understanding environmental controls were studies focused on understanding disturbance and successional effects on carbon storage and fluxes (Pearson et al. 1987, Harcombe et al. 1990, Smith and Resh 1999, Janisch and Harmon 2002). Interestingly, until recently these two types of studies were rarely combined

possibly due to the logistical and financial constraints on conducting such a project.

Carbon cycle research has been moving towards making estimates at large spatial scales. Part of this push is related to the improvement of physiological process models used to estimate carbon fluxes. These improvements have allowed modelers to simulate carbon storage and fluxes at large spatial scales, a process that requires field estimates of ecophysiological components for model calibration and validation. In addition to the needs of modelers, datasets have recently come online that have allowed researchers to make estimates from field data at large spatial scales. Specifically, forest inventory datasets collected at regional to continental scales have been exploited by a few researchers for estimating carbon storage and fluxes. These datasets have proven to be useful both for modellers (Turner et al. 2002) and for understanding patterns of carbon storage and fluxes from the datasets themselves (Brown and Schroeder 1999, Jenkins et al. 2001, Ni et al 2001).

Estimates of carbon storage and fluxes at these large spatial scales could, however, be improved by combining the spatial breadth of forest inventories with the depth of understanding gleaned from smaller scale yet more intensive studies. For example, belowground biomass is particularly difficult to quantify and is typically assumed to be a fixed fraction of aboveground biomass and productivity (e.g., Jenkins et al. 2001) or ignored (e.g., Ni et al. 2001) for lack of better information.

Objectives and Chapter Layout

The study area for this project, Western Oregon, is an excellent venue for studying the effects of disturbance history and environment on biomass and NPP in forests. The study area contains a wide range of forest types that generally differ in biomass and productivity through stand succession. This range in biomass and productivity is partly a product of a strong climatic gradient across the study area from the maritime coastal region in the west to the semi-arid forests and woodlands in the east. The study area also has a range of historical disturbance, both natural and anthropogenic, which allows for exploration of successional patterns in biomass and NPP. Because of both the climatic and successional diversity present in the study area, it is an excellent choice for studying both of these effects at the regional scale.

The first objective of this thesis is to estimate biomass and net primary production (NPP) in the forests of western Oregon using forest inventory data. This will be accomplished by gathering data from literature sources and supplementing the forest inventories with data collected throughout the study area. The second objective is to determine the climatic and edaphic factors driving the observed patterns of NPP in the study area. This will be accomplished by using a physiological process model to estimate the effects of climate and soil fertility on productivity across a steep climatic gradient in the study area.

In Chapter 2, we estimate stand age, biomass, and NPP in the forests of western Oregon. We use forest inventory data, biomass and volume allometric equations, wood density, and supplementary data collected throughout the study area to make these estimates. We then explore how biomass and NPP change with stand age in major ecoregions within the study area and discuss the effects of disturbance history on biomass and NPP in each ecoregion.

In Chapter 3, we use the physiological process model 3-PGS to estimate NPP across the study area. We evaluate model performance with our database of NPP estimates from forest inventory data as well as with data from eddy flux sites within the study area. We then explore the seasonal cycle of the climatic and edpahic constraints on NPP across a steep climatic gradient that crosses the study area.

Finally, Chapter 4 closes the thesis with a review of the main findings of the studies conducted here as well as some closing comments on future directions for these types of studies.

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CHAPTER 2

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

S. Van Tuyl, B.E. Law, D.P. Turner, and A.I. Gitelman

Abstract

In this study we use a combination of data from forest inventories, intensive chronosequences, extensive sites, and remote sensing, to make estimates of biomass and net primary production (NPP) for the forested region of Western Oregon. Plot-level forest inventory data were provided by the USDA Forest Service through their Forest Inventory and Analysis and Current Vegetation Survey programs. In addition data from our carbon budget studies across Oregon provided supplementary information on forest components not measured on inventory plots.

The study area was divided into four ecoregions differing in climatic conditions and soil properties that influence growth. The forest age distributions differed by geographic location with fewer old stands in the Coast Range and the East Cascades, and a relatively uniform distribution of ages from 0 to 815 in the Cascade Mountains. Age distributions also differed by land ownership, with fewer old stands on non-federal lands than on national forest lands.

Biomass increased rapidly in early development with the trajectory leveling out at an age of about 250 years. Peak biomass was generally lower in the Eastern Cascades than in other ecoregions (median biomass at asymptote ~10 kg C m^{-2} and ~30 kg C m^{-2} respectively). The timing and magnitude of maximum net primary production varied by ecoregion, with high-productivity sites reaching a median NPP ~1 kg C m^{-2} y^{-1} at about 30 years of age, and low-productivity sites (East Cascades) reaching a median NPP ~0.25 kg C m^{-2} y^{-1} between 80 and 100

years. Productivity was lower in older stands in all areas except for the Eastern Cascades, contrary to the paradigm of age-related decline in forest growth. These patterns are partly a function of management and competition-related changes in stand structure and resource-use efficiency of individual trees. Soil resources rather than light are the primary limitations to growth in the East Cascades such that proportionately more carbon is allocated belowground in early stand development. Measurements of additional carbon budget components combined with inventory data provide estimates of carbon storage and fluxes that may be useful for forest management and validation of regional model simulations.

Introduction

Carbon cycle research has been moving towards improving estimates of carbon storage and fluxes, and deeper examination of variation across regions and continents using both measurements and simulation models. Large-scale model applications, however, require extensive field data for evaluating performance and for data assimilation techniques. Forest inventories cover a range of conditions and disturbance regimes, and they tend to include measurements of many of the basic components needed to estimate biomass and net primary production (NPP). In the US, inventory data has been used for making estimates of biomass and productivity at various scales from regional (Brown et al 1997, Brown et al. 1999, Jenkins et al. 2001) to continental (Turner et al. 1995, Ni et al. 2001). Estimates could, however, be improved by including data from research sites with more intensive measurement regimes stratified across representative forest types and conditions. For example, belowground biomass is particularly difficult to quantify and is typically assumed to be a fixed fraction of aboveground biomass and productivity (e.g., Jenkins et al. 2001) or ignored (e.g., Ni et al. 2001) for lack of better information. Were these and other studies to make use of supplementary data collected within the region their estimates of belowground pools might more accurately reflect observed patterns rather than fixed fractions.

In the present study we use forest inventory data, along with supplementary data from 96 plots in different age classes and forest types to estimate biomass and NPP in the forested region of western Oregon. We explore

patterns of biomass and NPP associated with stand age, ecoregion, and type of land-ownership. Finally we estimate the error associated with assumptions made in our methodology.

Methods

Study Area

The study area is a 120,000-km^2 area covering all of the state of Oregon west of the 120th meridian (Figure 1). Sixty-one percent of the study area is forested land, 60% of which is public and 40% is privately owned (Powell 1993). The remainder is considered non-forest (alpine, rock, etc.), woodland, agricultural, or urban, according to landscape classifications using Landsat Thematic Mapper data (ETM+) and 24 aerial photos for evaluating classification accuracy (accuracies average 82% with a range of 49% to 97%; Law et al. in review).

The study region crosses a steep climatic gradient, ranging from maritime coastal forests to semi-arid forests and woodlands within approximately 250 kilometers. Annual precipitation ranges from 2110 mm at the coast to 530 mm in the semi-arid ponderosa pine region on the east side of the Cascade Mountains. This range in climate in turn results in a large range in forest biomass and productivity, as determined from six study sites along the Oregon Transect (Runyon et al, 1994).
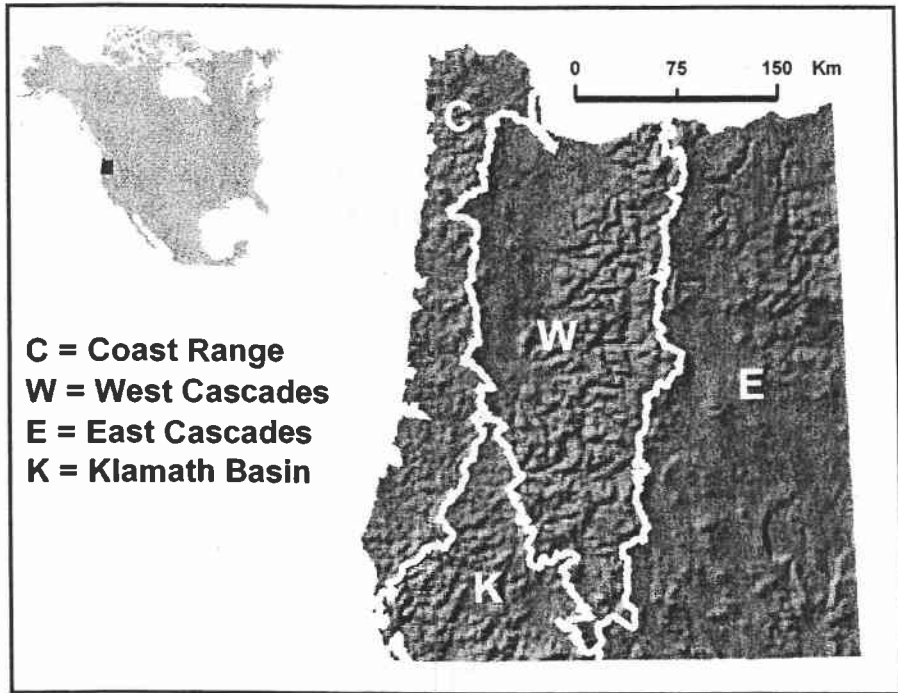
Figure 1: Study region with the boundaries of four ecoregions identified.

The study region includes long-term inventory plots as part of the Forest Inventory and Analysis program (FIA; www.fs.fed.us\fia) on non-federal lands and Current Vegetation Survey plots (CVS; www.fs.fed.us\r6\survey) on national forest lands. Both inventory programs use a systematic sampling design. Basic forest characteristics are remeasured on approximately 10-year intervals.

We developed our own sampling program to supplement the inventory plots with measurements of additional carbon budget components, with 96 plots selected within the study area using a hierarchical random sampling design based on forest type and climate zone (Law et al. in review). Thirty-six of the plots are in chronosequences in the coastal forest, the Cascade Mountains, and the semiarid east-side forests where more intensive measurements of carbon budget components are made (3 chronosequences, each with 4 age classes and three replications; Law et al. in review). The chronosequence plots are referred to as "intensive plots" and the carbon budget sampling that was intermediate to the inventory and intensive plots is referred to here as "extensive plots." Details of sampling methods and analysis are in Law et al. (in press) and Law et al. (in review).

Stand Age

Stand age was estimated on inventory plots by determining the average age of the oldest 10% of trees on a plot, similar to a method used by Spies and Franklin (1991; average age of dominant trees). In a separate analysis, the results

of a simple linear regression of predicted stand ages versus time since stand replacing disturbance for 15 plots resulted in an intercept coefficient that was not significantly different from zero (p = 0.58) and a slope coefficient close to 1 (p < 0.001, slope 0.95, standard error of slope 0.09, R^2=0.88). These results suggest that our estimates of age are representative of time since disturbance, although the range of ages tested here is smaller than in our full study (0-250 years versus 0-815 years).

Estimation of Biomass and Productivity

Both of the United States Forest Service inventory programs locate plots based on a systematic sampling design, though the style of sampling differs in two ways. First, the spatial sampling intensity of the CVS inventory is four times that of the FIA inventory, resulting in 3700 CVS plots and 900 FIA plots in the study area. Second, the FIA inventory excludes non-forested areas from its sampling while the CVS inventory locates plots in all cover types.

The sampling methods for the two inventories are generally the same. In both inventories components of data necessary for making broad estimates of biomass and productivity are collected (e.g., stem diameter, height, growth, etc.). A the plot-level the FIA program uses variable radius sampling plots (USDA Forest Service 2001) while the CVS program uses a series of concentric fixed radius sampling plots (Johnson 1998). This difference in sampling is not likely to result in differences in estimates of the components of biomass and NPP (Scott

and Alegria, 1990). Field crews visit the inventory plots and collect a set of tree-level measurements (e.g., species, diameter at breast height (DBH), increment cores, etc.) and the data are subsequently compiled by the inventory programs.

The method we used to estimate plot-level biomass and NPP from these inventories mirrors that commonly used for smaller scale estimates of plot-level carbon pools and fluxes (e.g., Law et al. 2001, Janisch and Harmon 2002).

Biomass

For each tree measured on the inventory plots, we estimate biomass for the following components: bole wood, branch wood, bark, foliage, and coarse roots.

Bole wood biomass is estimated as:

$$Biomass_b = Volume_b * Wood\ Density \qquad (1)$$

Where $Biomass_b$ is bole wood biomass (kg m^{-2} ground), $Volume_b$ is bole wood volume, and wood density is the dry density of wood. Bole wood, here, is defined as aboveground woody portion of the tree not including bark and branches. We convert biomass values to kilograms carbon per m^2 ground using 50% carbon content in wood, foliage, and roots. Values reported are the 10-year mean for CVS plots (measurements made between 1993 and 1997) and 8-12 year means for FIA plots (measurements made between 1995 and 1997).

We divide the study area into four ecoregions, each roughly corresponding to physiographic zones in Oregon: Coast Range, Western Cascades, Eastern Cascades, and Klamath Basin (following Franklin and Dyrness 1973). Where possible, we use species-specific volume equations developed in each of the four ecoregions in volume estimates (Appendix A). Where ecoregion and/or species-specific equations are not available, an equation from another ecoregion or similar species is chosen as a substitute. Of the approximately 400,000 trees in the CVS data 27% are subject to equation substitution and 34% of the approximately 23,000 trees in the FIA data are subject to substitution. The volume equations typically use diameter breast height (DBH – 1.37 meters) and tree height as predictor variables.

Wood density data were acquired for most of the major hardwood and softwood species of western Oregon through wood density surveys conducted by the U.S. Forest Service (USDA Forest Service 1965, Maeglin and Wahlgren 1972). The wood density data from these surveys is collected at 850 forest inventory plots throughout our study area, many of which are likely associated with the inventory plots used in this study, with a total of 5622 wood cores sampled. Where necessary, we acquired wood densities from another source (Forest Products Laboratory, 1974).

To refine our estimates of wood density, wood cores were collected at the 96 intensive sites and evaluated for relationships between wood density and species, diameter, height and stand age; however, no statistical model explained more than

five percent of the variability in wood density. This result is consistent with other regional studies of wood density (e.g., Western Wood Density Survey, USDA Forest Service 1965).

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

Foliage biomass was estimated from:

$$Biomass_f = LAI * LMA \qquad (2)$$

Where $Biomass_f$ is foliage biomass (grams foliage per m^2 ground), LAI is leaf area index (m^2 one-sided leaf area per m^2 ground), and LMA is leaf mass per unit leaf area (grams of leaf material per m^2 leaf) scaled to the plot level. Leaf area index (LAI) data were derived for the inventory plots by intersecting the plot locations with a continuous surface of remotely sensed LAI under the supervision of the FIA program. The LAI surface was derived from Landsat ETM+ data (Law et al. in review). Briefly, field measurements of LAI (LAI-2000, LICOR, Lincoln, NE) were corrected for clumping at multiple scales. LAI from half of the 96 intensive plots were used to develop spectral regression algorithms with the

ETM+ data, and the remaining plots were used for accuracy assessment (explained 82% of variance, RMSE 0.742; Law et al. in review).

LMA was sampled on the 96 intensive plots by removing between eight and twelve foliage samples from the dominant species on each plot. Leaf area of each sample was measured and then samples were dried 48 hours and weighed. Some species pairs differed in LMA ($p < 0.001$, Tukey's HSD). Only 10 of the 365 species pairs (3%) differed in LMA, so we used species-specific mean LMA. Species that were not sampled were assigned an average LMA by leaf/growth form groups (e.g., for unsampled *Abies* species we assigned an average LMA for the *Abies* species that were sampled). LMA was scaled to the plot-level by calculating a species basal-area weighted average.

Coarse root biomass equations were identified in a literature search that resulted in only three equations for species present in the study area: *Pseudotsuga menziesii* (Gholz et al. 1979), *Pinus ponderosa* (Omdal et al. 2001), and *Alnus rubra* (Zavitkovski and Stevens 1972). Coarse root biomass equations were converted to root volume equations by dividing the equation by a species specific wood density. We were unable to make comparisons among models to test for differences because the authors did not report sufficient regression statistics, however, an empirical analysis of the models suggested that results of using either the *Pseudotsuga menziesiii* or *Pinus ponderosa* yield similar results. The model form of the *Alnus rubra* equation yielded negative values at high tree diameters and was thus discarded.

To minimize errors associated with predicting outside of the range of values used to develop the allometric models equations, we chose to use the model with the greatest range in diameters in the original model population. The model selected was a *Pseudotsuga menziesii* equation (Gholz et al. 1979) for which the diameter range of the original model (2-135 cm DBH) would encompass greater than 95% of the trees in our study.

The coarse root biomass equation was converted to a volume equation by dividing by the wood density for *Pseudotsuga menzeisii* in western Oregon (USDA Forest Service 1965) in order to avoid errors associated with using *Pseudotsuga menzeisii* wood density for all species in our study. The resultant equation was then applied to all species in the study area and converted from coarse root volume back to biomass by multiplying by the wood density of the given species.

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

$$\exp(4.4179 + (0.3256 * LAI) - (0.0237 * LAI^2)) \tag{3}$$

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

Radial growth

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

Within each inventory plot, trees with measured radial growth were split into DBH quartiles and a mean radial growth for each quartile was calculated. The mean radial growth increment for the trees in each quartile was assigned to the unmeasured trees in the quartile, while trees with actual measurements of radial growth maintained their original values.

Bole, Branch, Bark, and Coarse Root NPP

Net primary production of the coarse woody components (bole, branch, bark, and coarse root) was estimated by difference method:

$$ANPP_w = Biomass_{w2} - Biomass_{w1} \qquad (4)$$

Where $ANPP_w$ is NPP of woody components and $Biomass_{w2}$ and

$Biomass_{w1}$ are biomass of woody components at current and previous time steps,

respectively. Previous height and current height for unmeasured trees was

modeled using height-diameter equations developed in the region from forest

inventory data (Garman et al. 1995).

Foliage NPP

Foliage NPP was estimated as:

$$NPP_f = Biomass_f / Foliage\ Retention \qquad (5)$$

Where NPP_f is foliage net primary production (kg m^{-2} y^{-1}), biomass$_f$ is foliage

biomass (kg m^{-2}), and foliage retention is the average number of years of foliage a

stand carries. The assumption in equation 5 is that foliage production is

uniformly distributed over the years of foliage is present, and may result in

underestimates of foliage production for evergreen coniferous stands in which

foliage retention is not in steady stasis (e.g., young stands). Because our

productivity estimates are ten-year means, variation in foliage retention with

climate should have little effect on our estimates (retention ranges from 3.5 to 5

years).

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

Fine Root NPP

Fine root NPP was estimated at the chronosequence plots by Law et al. (in review): fine root turnover rates were collected for the region (Santantonio and Hermann 1985, Chris Anderson, US EPA, pers. comm.) and multiplied by fine root mass at each plot to estimate fine root NPP.

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

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

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

Error Analysis

Due to the many assumptions and generalizations necessary for estimating

biomass and NPP at large spatial scales, we examine the potential for error

propagation through those estimates. We used bole biomass as a surrogate for the

remainder of the biomass error estimates because bole biomass accounts for

approximately 55% of total biomass on average, and because it allows us to

investigate the effects of errors in the volume and wood density components of

biomass. Bole volume equations were plotted for each species to estimate how

volume equations differ between ecoregions. Errors associated with using wood

density values from generic sources were estimated for 36 of our 96 intensive

plots by comparing biomass estimates from the generic sources used for the

inventory data with estimates from the plot-specific values.

Error in NPP estimates was determined in two ways. First, NPP estimates

for 36 plots at which plot-specific diameter to radial growth regressions have been

developed were compared with estimates using the method for determining radial

growth on the inventory plots. In addition, error estimates were made for each

inventory plot by defining the upper and lower 95% confidence interval for radial

growth estimates and carrying out NPP calculations at these upper and lower

intervals. This effectively gave us three estimates of NPP for each inventory plot:

a lower (using lower 95% CI for radial growth), middle (based on estimate of

radial growth), and upper estimate (using upper 95% CI for radial growth). While these methods we are not likely to account for all sources of error in our methods, we feel confident that the major sources are accounted for.

Results and Discussion

Stand Age

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

The patterns within ecoregions are generally the same, with lower means and standard deviations of stand ages on FIA plots than on CVS plots (Figure 2). The majority of the mature and old stands (>100 years) are on national forest lands in the West Cascades, Klamath Basin, and East Cascades ecoregions.

A series of large fires in the Coast Range between 1850 and 1960 burned approximately 710,000 hectares of forest (Miller 1982). These fire disturbances, coupled with insect infestations and a typical logging interval in the Western Oregon of 50-80 years are driving the distribution of stand ages in this ecoregion, resulting in 75-85% of the stands between the ages of 0 and 125 years (Figure 2).

In the West Cascades and Klamath Basin ecoregions, 75% of the stands on non-federal land are between 0 and 125 years of age while this same proportion of
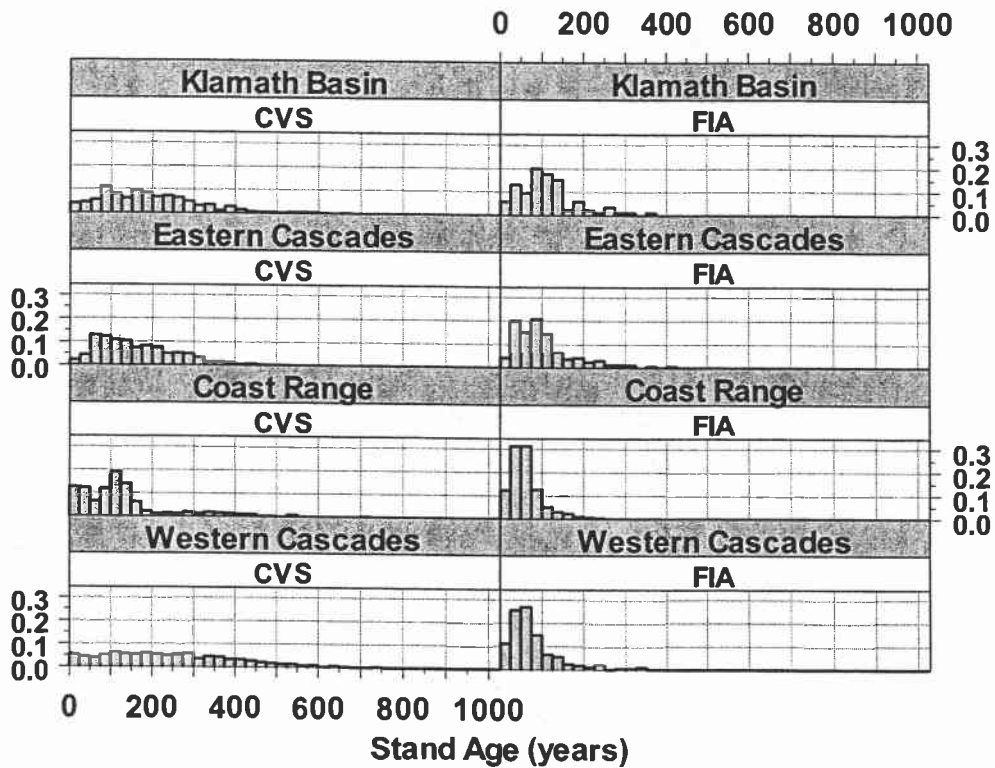
Figure 2: Frequency distributions of stand age by geographic and data type. Forests in western Oregon tend to have fewer old stands on non-federal (FIA) lands than on national forest (CVS) lands. This trend is apparent in all geographic areas and may reflect forest management practices on non-federal lands that tend to have short rotation periods of 50-100 years.

stands on national forest land is between 0 and 350 years. The uniform distribution of ages in the national forests of the West Cascades suggests a less punctuated and extreme historical disturbance regime in this ecoregion over the past 800 years compared with the Coast Range.

In the East Cascades, 65% of the stands on non-federal lands are between 50 and 125 years. The distinct peak in the distribution of stand ages in this region is the result of fire suppression as well as the removal of most of the old late-seral stands in eastern Oregon by early settlers (Everett et al. 1994). The CVS data are similarly clustered in this range of ages with 45% of the stands between 0 and 125 years. The typical age of harvest in Eastern Oregon is between 75 and 150 years (Lettman, 1995), implying that many stands are near harvest age if this rotation is continued. Both the CVS and FIA data for the East Cascades have relatively low frequencies of stands in the 0 to 25 year range. This is indicative of the difficulty in stand regeneration after disturbance in the water limited climate of Eastern Oregon (Coops et al. *in press*) as well as a general reduction in the number of young stands due to management (Everett et al. 1994). Stand history data indicate that it takes 8-10 years of favorable summer rainfall for re-establishment to occur in this region, and the region has experienced frequent severe drought over the past decade (Law et al. 2001).

Biomass

On average, stand biomass is higher on national forest lands than on non-federal lands in the study region (means: FIA plots 14.54 kg C m^{-2}, CVS plots 8.58 kg C m^{-2}), and variability follows the same trend (standard deviations: 12.42 and 6.92 kg C m^{-2} respectively). In all four ecoregions, the mean biomass and the variability in biomass is consistently higher on national forest lands than on non-federal lands. The difference in the distribution of ages appears to be primarily responsible for the overall difference in biomass between non-federal and national forest data. Because the national forest data tend to include more old stands and a wider range of stand ages, it follows that the mean biomass and the variance in biomass would be higher than for non-federal data.

We used a permutation test to determine whether there were differences between CVS and FIA data within each ecoregion. Traditional statistical methods for testing whether groups differ rely on sample size to determine the significance of differences. Because the sample size of our dataset is so large, traditional methods could lead to results suggesting significant differences where there are none. The permutation test does not rely on sample size for determining differences between groups and therefore is appropriate for large datasets such as ours.

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

a. Fit separate simple linear regression models to the FIA and CVS data.

b. Calculate a test statistic from these models:

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

Where β_0 and β_1 are the intercept and slope coefficients for the regression models.

c. Pool FIA and CVS data.

d. Randomly divide the pooled data into two groups with sizes corresponding to the original FIA and CVS sample sizes.

e. Refit the separate simple linear regression models to the two new groups.

f. Recalculate the test statistic (these are the permuted test statistics).

g. Repeat steps d through f one thousand times.

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

The permutation test results suggest that there is no difference between biomass on national forest and non-federal lands in the Western Cascades (p = 0.22). There is weak evidence to suggest that the model fit to the non-federal data

in the Eastern Cascades was significantly different from that fit to the national forest data (p = 0.03). There are differences between national forest and non-federal data in both the Klamath Basin and Coast Range (p < 0.001). The slopes of the models fit to the non-federal plots in the Eastern Cascades, Klamath Basin, and Coast Range are less than those of the national forest plots. One explanation for the difference between data types in the Eastern Cascades, Klamath Basin, and Coast Range might be that management on non-federal lands selects for lower biomass stands compared with the less intensively managed stands on the national forests i.e., thinning of forest stands or planting at low densities might cause a less biomass accumulation in managed stands, whereas minimal management or disturbance (e.g., fire) could result in more biomass accumulation on national forests.

Because the FIA data have a restricted range of stand ages we combine the two data types for our discussion of long-term trends in biomass accumulation. The biomass data in all four ecoregions show a pattern of rapid increase in biomass with stand development, then a gradual reduction in the rate of biomass accumulation to a point of little net gain in biomass in older stands (Figure 3). The age at which stands reach a maximum biomass differs by ecoregion, with stands in the East Cascades reaching a maximum earliest (at approximately 150 years) and stands in the West Cascades reaching a maximum latest (at approximately 250 years). The West Cascades and Klamath Basin ecoregions show similar patterns of biomass accumulation through stand development with
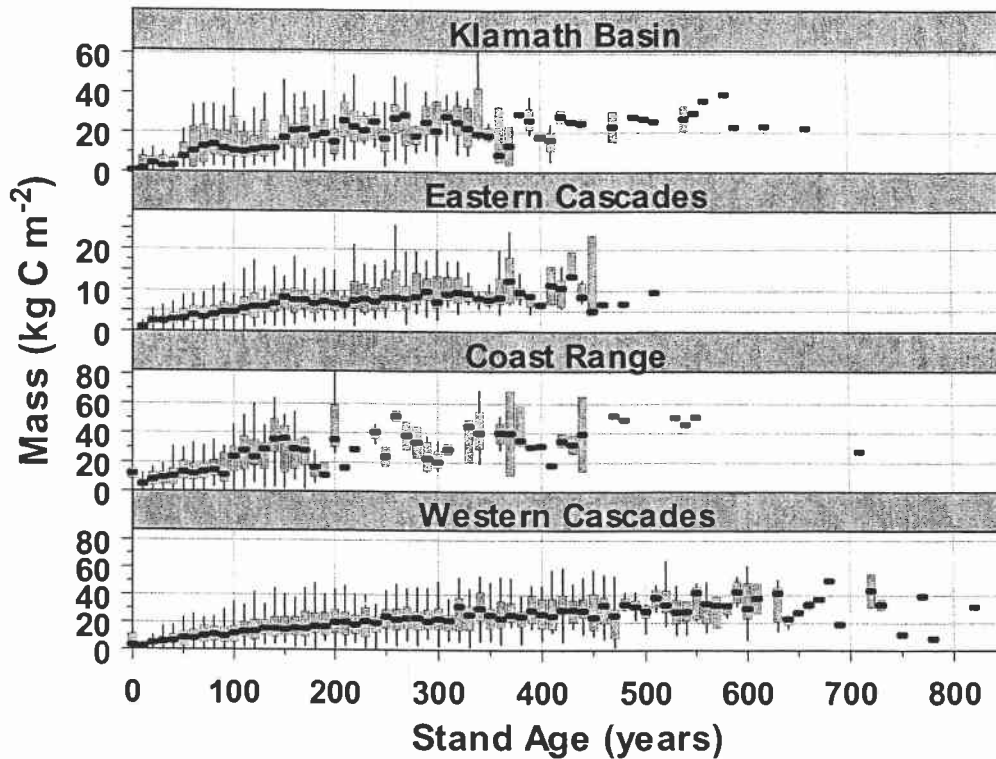
Figure 3: Trends in tree biomass accumulation with increase in stand age. Trajectories of biomass differ by ecoregion with biomass reaching an asymptote at different ages in different ecoregions. Plots are grouped into 10-year age classes and box plots were made for each age class. Bars represent the interquartile range (25th percentile to 75th percentile) and whiskers represent 0 to 25th and 75th to 100th percentile. The black bar indicates the median of each age class.

biomass increasing to a median of approximately 25-30 kg C m^{-2} and a maximum of 60 kg C m^{-2}. Biomass of stands in the East Cascades reaches a median value of about 10 kg C m^{-2} and a maximum of 20 kg C m^{-2}. Because the data for the Coast Range ecoregion is limited to a maximum age of about 200 years, it is difficult to determine whether Coast Range stands have reached a maximum biomass, however, by 175 years, the Coast Range forests reach a median biomass of 35 kg C m^{-2} and a maximum of 60 kg C m^{-2}. Thus maximum biomass values are similar in all ecoregions except for the East Cascades.

In all of the ecoregions the biomass values from existing studies in the Pacific Northwest tend to approach the upper limits of our estimates (figure 4). This result is not entirely surprising since the systematic sampling scheme allows inventory plots to be located in disturbed or otherwise heterogeneous stands while investigators in ecological studies typically select stands that represent relatively homogeneous forest conditions. An example of this effect is the difference between placing a study plot entirely in a forested area (as in many ecological studies) and placing a study plot on the edge of a clearcut and a forested area (an example of what can happen when employing a systematic sampling design).

This pattern has been previously observed in comparisons of forest inventory biomass data and data from ecological studies (Jenkins et al. 2001) and suggests that, when scaling plot-level estimate of biomass to larger spatial scales, the sampling design (systematic random vs. non-random) and original intent of the investigators should be considered. Because biomass data from ecological
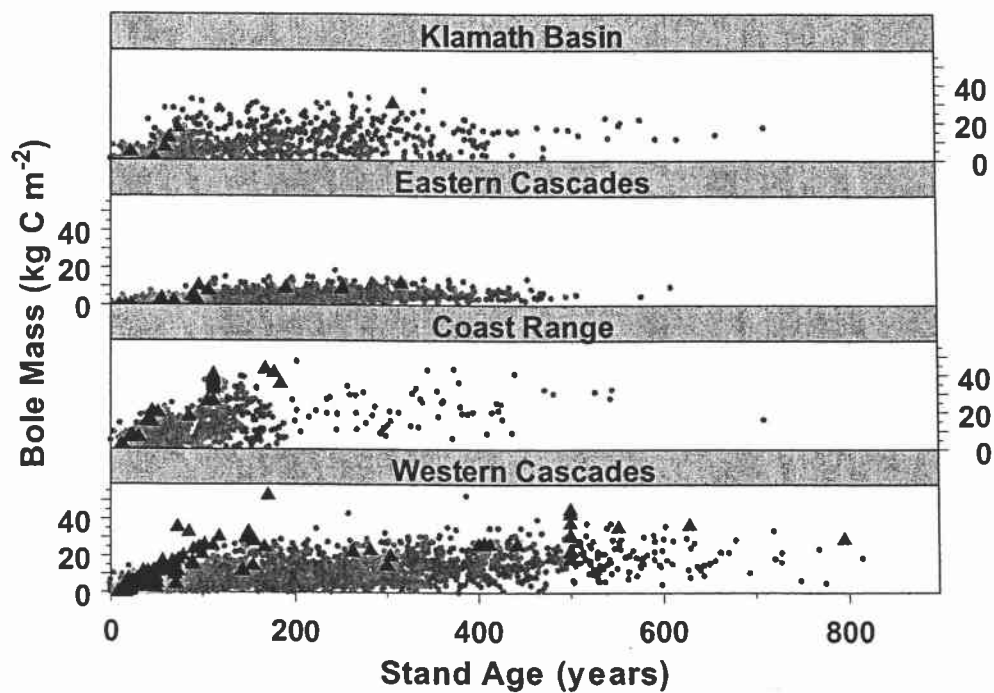
Figure 4: Change in tree bole mass with increase in stand age. Light dots are data from this study. Dark triangles are data from other studies in the Pacific Northwest: Acker et al. 2002, Janisch and Harmon 2002, Turner and Long 1975, Runyon et al. 1994, Gholz 1987, Harcombe et al. 1990, and Law et al. in review.

studies tends to be higher than data from inventories, it is likely that estimates of carbon storage that use only data from ecological studies will be biased upwards.

We estimate total carbon storage in live trees for our study area by weighting the total area of forest in each ecoregion by the frequency distribution of biomass. Our results suggest that the forests in our study area store 1.32 Pg C in live trees, representing most of the forested area of Oregon. This result is higher than the carbon storage in live trees reported by Turner et al. (1995) who estimate approximately 0.92 Pg C in Oregon, but is similar to total storage inferred from Smith et al. (2002) of 1.06 Pg C in live trees. The estimates in Turner et al. rely heavily on inventory data from non-federal lands to make their estimates and if we recalculate our estimates based on non-federal lands we get a total carbon storage in live that is trees more comparable (0.83 Pg C). Conversely, if we make estimates based on national forests only the total storage in live trees increases to 1.55 Pg C. This difference between storage in a national forest-like landscape compared with a non-federal-like landscape suggests that if disturbance regimes on national forests were more similar to those of non-federal lands, carbon storage in live trees could decrease considerably. Likewise, if forests on non-federal lands were managed for characteristics similar to those of national forests (e.g., more broad distribution of stand ages) the study area could store approximately 17% more carbon in live trees.

Net Primary Production

Mean NPP and variability about the mean is slightly higher for plots on non-federal than federal lands (0.69 kg C m^{-2} y^{-1} SD 0.37 versus 0.51 kg C m^{-2} y^{-1} SD 0.29 respectively).

Overall trends in NPP with age are similar for both ownerships, although the age at which maximum NPP is reached is slightly higher on non-federal lands. In the Klamath Basin and West Cascades, NPP increases to a maximum at a stand age of approximately 30 years (median 0.75 kg C m^{-2} y^{-1} – Figure 5). Coast Range forests reach a maximum NPP at 20 years (median 1 kg C m^{-2} y^{-1}). By contrast, forests in the East Cascades do not follow this pattern in that there is no distinct peak in NPP followed by a decline, rather, there is an increase in NPP from age 10 to 50 to a median NPP of 0.2 kg C m^{-2} y^{-1} followed by a gradual increase in NPP from age 50-200 reaching NPP of 0.3 kg C m^{-2} y^{-1}.

This unusual pattern in NPP in the East Cascades can be explained by differences in stand dynamics between Eastern Oregon and Western Oregon forests. It has been suggested that the theoretical NPP trajectory (peak then decline in NPP) can be explained as a function of stand community dynamics (Smith and Long, 2001) with canopy closure and the resultant self-thinning creating a decrease in stand-level NPP, or as a result of a decline in hydraulic conductivity in old trees that limits carbon uptake (Ryan et al. 2000). Law et al. (in press) report that LAI in a chronosequence of ponderosa pine in Eastern Oregon did not decline significantly between stand ages ~75 and ~300 years. This is contrary to succession theory that suggests old stands decline in
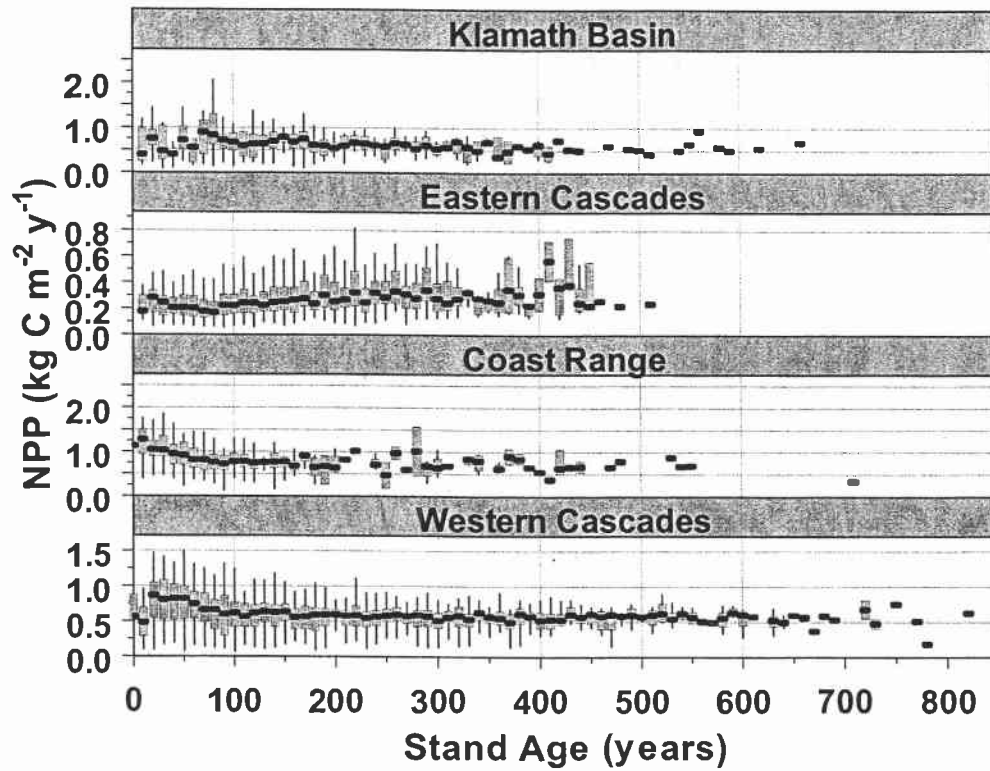
Figure 5: NPP change with stand development. Plots are grouped into 10-year age classes and box plots were made for each age class. NPP is an 8-12 year average.

productivity (Smith and Long 2001, Binkley et al. 2002). Forests in the Eastern

Cascades tend to grow at relatively low densities through stand development with

leaf area index typically reaching levels no higher than 4 $m^{-2} m^{-2}$. East Cascades

forests do not reach canopy closure in early development as is seen in Coast

Range and Western Cascades forests. Competition for light is minor compared

with competition for soil resources in contrast to competition-related structure in

the other ecoregions. This lends credence to the hypothesis that age-related

decline in forest growth is, at least in part, a product of stand structure and

community dynamics (Binkley et al. 2002).

A comparison of carbon allocation patterns show that relatively more

assimilated carbon is allocated belowground in young stands in the East Cascades,

and this becomes a smaller fraction as stands age (Figure 6). Earlier work has

shown that stand re-establishment is slow and young pines in the East Cascades

are severely drought stressed in summer, likely because of less developed roots

for accessing deep soil water compared with mature and old trees (Irvine et al.

2002). In the Coast Range and Western Cascades, stands exhibit the opposite

pattern with relatively high carbon allocation aboveground in early stand

development when there is competition for light resources. This is followed by a

shift to more carbon allocation belowground after as the dominant trees become

more efficient at acquiring resources (~50-60 years).

A comparison of NPP values estimated in our study with those of previous

studies in the region show that values are consistent with data across the climatic
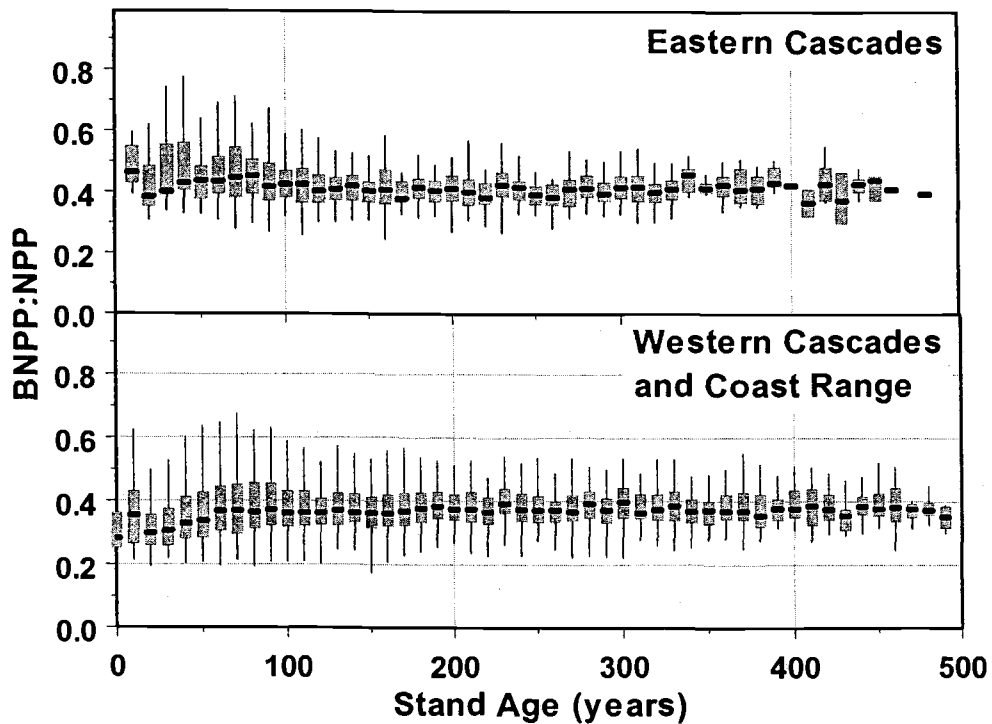
Figure 6: Ratio of belowground NPP to total NPP. Plots are grouped into 10-year age classes and box plots were made for each age class. Eastern Cascades plots are above and Western Cascades and Coast Range plots are below. Western Cascades and Coast Range plots were grouped because they show the same pattern of BNPP:NPP

gradient in Western Oregon where NPP ranges from 1.36-1.63 kg C m^{-2} y^{-1} at the

coast to 1.54-2.57 kg C m^{-2} y^{-1} in the West Cascades and 0.30-0.32 kg C m^{-2} y^{-1} in

the East Cascades (Runyon et al. 1994). The aboveground NPP estimates

presented in this study are high compared with those of deciduous and evergreen

forests in the mid-Atlantic U.S. where an analysis of FIA data showed

aboveground production ranged from ~0.35-0.46 kg C m^{-2} y^{-1} (Jenkins et al.

2001).

Environmental Effects on Biomass and NPP

Differences among ecoregions in biomass and NPP can be explained in

part by differences in climatic regimes among ecoregions. It is widely known that

as environmental conditions become harsher, the utilization of intercepted

radiation declines, and thus NPP decreases. For example, coniferous forests can

intercept sunlight through the year, but freezing temperatures in winter or summer

drought can limit photosynthetic carbon uptake. In previous studies in Oregon,

forests in the Eastern Cascades exhibit the lowest radiation-use efficiency due to

environmental limitations (Runyon et al. 1994, Law and Waring 1994). The

Western Cascades exhibit the next lowest energy-use efficiency followed by the

Coast Range. These patterns follow those we see in the inventory data with both

biomass and NPP lowest in the Eastern Cascades, moderate in the Western

Cascades and Klamath Basin, and highest in the Coast Range.

Error Analysis

Results of error analysis for biomass components suggest that using site-specific allometry and wood density can result in large reductions in errors. When we compare bole volume estimates among equations developed in our four ecoregions, differences in bole volume estimates could be as great as 40% for some species. While this level of error is unlikely to be the norm, we have no realistic way of testing appropriateness of each equation for the inventory plots. St.Clair et al. (1993) demonstrate the importance of using site-specific allometrics because of variation in equations developed within a region. This, however, was not feasible in our study and generally is not feasible for other large-scale studies of this sort due to the destructive and labor intensive nature of developing site-specific allometry at thousands of sites across a region.

Efforts to increase the specificity of wood density data could decrease error in biomass and NPP estimates. When generic wood densities were substituted for plot specific wood densities on 36 test plots, the average difference in biomass and NPP was 9% with a standard deviation of 13%. The errors associated with generalizing wood density were not systematic with stand age. The magnitude of the error associated with using generic wood densities suggests that it is important to use accurate estimates of wood density, although generic wood densities are usually the only data available at large spatial scales. The agencies collecting forest inventory data could improve carbon budget estimates by collecting wood cores for density estimates at the inventory plots.

Overall, the error associated with our method of estimating radial growth does not introduce a significant amount of error in our NPP estimates. Comparisons of NPP for the 36 test plots using plot-specific diameter to radial growth regressions and using our bin-averaging approach show only a 1% change in NPP estimates with a standard deviation of 4%. There appears to be no age or ecoregion related pattern associated with this error.

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

Conclusion

We found that, in Oregon, the distribution of stand ages on national forests versus non-federal lands is quite different. More old stands are present on national forest lands than on non-federal lands. This difference in stand age distributions results in lower mean storage of carbon in live trees on non-federal lands across the study area. Productivity generally peaks earlier and at a higher level in the Coast Range than in the Western Cascades and Klamath Basin. We

also found that productivity does not decline in older stands on the dry east side of the Cascade Mountains, possibly as a result of stand dynamics in the Eastern Cascades lacking a canopy closure/stem exclusion phase. Carbon allocation patterns differed between Western Cascades/Coast Range forests and Eastern Cascades forest with more carbon allocated belowground in Eastern Cascades forests early in stand development.

Integration of data from forest inventories, satellite remote sensing, and intensive sites across the vegetation types and age classes has allowed us to make reasonable estimates of biomass and NPP components of the regions forests, and to explore trends in biomass and NPP with disturbance and management. This integrative approach means fewer assumptions and generalizations have to be made regarding carbon allocation in forests – assumptions that are often not universally applicable. Our error analysis suggests that further refinements to this approach to making regional estimates of carbon fluxes and stocks should include more intensive measurement of certain key variables such as wood density and radial growth, and careful assessment of available equations. Investigation into the errors associated with allometric volume and biomass equations that are not specific to a site or species should be conducted when specific equations are not available. In addition to the patterns explored in this paper, this type of data might be useful in data assimilation and model evaluation of ecosystem carbon models (e.g., Turner et al. 2002).

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CHAPTER 3

Evaluating climatic and edaphic constraints on net primary production in

Oregon forests using a light use efficiency model – 3-PGS

S. Van Tuyl, B.E. Law, and D.P. Turner

Abstract

We use the spatial version of a light use efficiency model, 3-PGS, to estimate net primary production (NPP) of the forests of western Oregon and evaluate the seasonal cycle and spatial patterns of environmental constraints on NPP. The model is parameterized with data that include soil surveys, physiological constants, spatially modeled climate data, and remotely sensed fPAR. We evaluate the performance of the model using a dataset of NPP developed from forest inventories as well as with estimates of productivity from eddy flux towers. We also evaluate the belowground carbon allocation scheme employed in the 3-PGS model. Overall the model tends to overestimate NPP at high productivity sites and underestimate productivity at moderate and low productivity sites. Belowground allocation as estimated by the model does not compare well with belowground allocation estimates from field estimates which varies with age differently in the xeric versus mesic ecoregions.

The model suggests the NPP is constrained by environmental factors most in the xeric East Cascades (~20% of potential productivity), less constrained in the West Cascades (~45% of potential), and least constrained in the Coast Range (~60% of potential). Coastal Range forests tend to be most limited climatically by temperatures sub-optimal for photosynthesis and summer VPD. Productivity in the West Cascades is limited by temperatures that are sub-optimal for photosynthesis and freezing temperatures in the winter along with VPD and soil water constraints in the summer. Productivity in East Cascades forests is limited

by soil fertility, temperature, VPD, and soil water deficits throughout the year.

These patterns are consistent with previous studies conducted in the Pacific

Northwest. The 3-PGS model is well suited for evaluating climatic and edaphic

constraints on forest growth primarily because it isolates these effects and

translates them into commonly scaled and easy to understand metrics.

Introduction

Carbon cycle researchers have long sought to explain spatial and temporal patterns of carbon fluxes with climatic and edaphic information (Runyon et al. 1994, Law and Waring 1994, Gholz 1982, Graumlich et al. 1989, Emmingham and Waring 1976). An alternative approach has been the development of physiological process models ranging from relatively simple light-use efficiency models (Ruimy et al. 1994) to more complex models in which physiological processes are less aggregated (Thornton et al. 2002). The success of these models in predicting carbon fluxes has been difficult to evaluate. One critical issue is the lack of datasets suitable for model evaluation including datasets suitable for evaluating models at broad spatial scales, evaluating seasonal cycles of carbon fluxes and controls, and evaluating allocation patterns.

In the last decade there have been many efforts to make plot-level estimates of carbon fluxes at regional or continental scales (e.g. Van Tuyl et al. in review, Jenkins et al. 2001, Ni et al. 2001). These datasets have been used increasingly for the evaluation of spatial process models with some success (Turner et al. 2002, Coops et al. 2001b). The use of eddy-flux towers for the evaluation of the seasonal cycle of carbon fluxes in process models has show much promise in the past few years (Thornton et al. 2002). However, while eddy-flux systems are useful for evaluating carbon, water, and energy exchange, the evaluation of the seasonal cycle of environmental controls on carbon fluxes remains a difficulty. Finally, carbon allocation to above and belowground pools

is poorly understood in forests (Law et al 2003, Gower et al. 1994, Raich and Nadelhoffer 1989) and it follows that evaluation of allocation schemes in carbon flux models is lacking.

In the present study we use carbon flux estimates from regional forest inventory and intensive plot datasets to evaluate the ability of the 3-PGS model to estimate net primary production (NPP) of forests in western Oregon. We also evaluate the model's belowground allocation scheme and offer improvements on the model structure in this area. Finally, we use the 3-PGS model to evaluate the climatic and edaphic constraints on net primary production in this region.

Materials and Methods

In this study we run the light use efficiency model 3-PGS across western Oregon. Then, using an NPP dataset developed from forest inventory data, we evaluate the performance of the model across the study area. We also evaluate the seasonal cycle of modeled forest productivity with data from eddy flux sites in the study area. Finally, we use the output of the 3-PGS model to evaluate climatic and edaphic constraints on net primary production across a climate gradient within the study area.

Study Area

The study area is a 120,000-km^2 area covering all of the state of Oregon west of the 120th meridian (Figure 7). Sixty-one percent of the study area is

forested land, 60% of which is public and 40% is privately owned (Powell 1993).

The remainder is considered non-forest (alpine, rock, etc.), woodland,

agricultural, or urban, according to landscape classifications using Landsat

Thematic Mapper data (ETM+) and 24 aerial photos for evaluating classification

accuracy (accuracies average 82% with a range of 49% to 97%; Law et al. in

review).
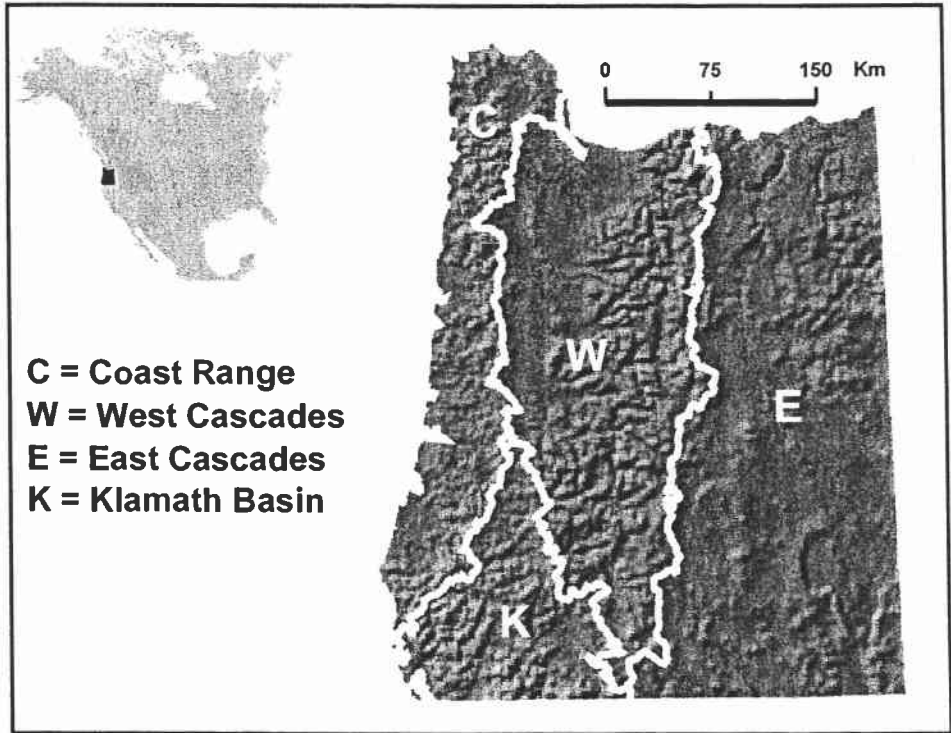
Figure 7: Study region with the boundaries of four ecoregions identified.

The study region crosses a steep climatic gradient, ranging from maritime coastal forests to semi-arid forests and woodlands within approximately 250 kilometers. Annual precipitation ranges from 2500 mm at the coast to 500 mm in the semi-arid ponderosa pine region on the east side of the Cascade Mountains. This range in climate, in turn, results in a large range in forest biomass and productivity (Law et al. 2003, Law and Waring 1994, Runyon et al. 1994, Gholz 1982).

3-PGS Model

The 3-PGS model (acronym stands for: Physiological Principles for Predicting Growth using Satellite data – Figure 8) is a simple light use efficiency model developed by Landsberg and Waring (1997) and altered for use with satellite data by Coops et al. (1998). 3-PGS runs on a monthly time-step using spatially modeled climate data and solar radiation, spatially referenced soil fertility and soil water holding capacity, and remotely sensed fraction of photosynthetically active radiation intercepted by the forest canopy (fPAR). Solar radiation and fPAR allow the model to calculate total photosynthetically active radiation absorbed by the canopy (APAR). We use version 2.54 of the model.

The climate and fertility data are used to define climatic and edaphic constraint modifiers that range in value from 1 (no constraint on production – production is at its maximum) to 0 (total constraint on production – production stops). These climate modifiers represent major constraints on productivity as
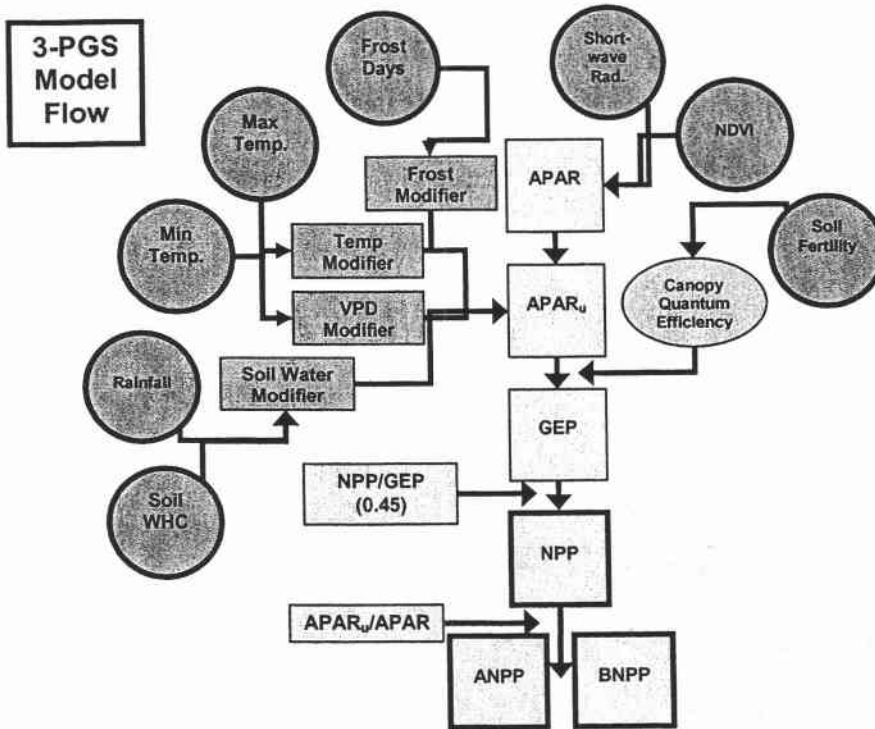
Figure 8: Diagrammatic representation of the 3-PGS model (adapted from Coops and Waring 2001c).

determined through principles of physiological processes and include constraints

due to soil water availability, freezing temperatures, sub-optimal leaf

temperatures, soil fertility, and high vapor pressure deficit (VPD). The soil water

balance is the difference between monthly precipitation plus remaining soil water

stored from the previous month and transpiration as estimated by the Penman-

Monteith equation.

Maximum canopy quantum efficiency (α) is defined and subsequently

reduced by the climatic and edaphic modifiers. The modified canopy quantum

efficiency (α_c) is then multiplied with APAR to estimate gross ecosystem

production (GEP). Net primary production is estimated as a constant fraction of

GEP (Waring et al. 1998), alleviating the need for the model to estimate

autotrophic respiration.

The fraction of total NPP allocated belowground is computed as the ratio

of utilized APAR (i.e. the APAR remaining after the modifier reductions) to total

APAR, which typically ranges from 0.2 to 0.8 (Coops et al. 1998, Coops et al.

2001a). Therefore, more environmental restrictions on production yield higher

allocation to belowground pools.

Climate and Radiation Data

Mean monthly maximum and minimum temperatures, number of days in a

month with freezing temperatures, monthly mean precipitation, and monthly

incoming shortwave radiation were acquired from the DAYMET climate model (Thornton et al. 1997; www.daymet.org) at a 1 km spatial resolution. The DAYMET model essentially interpolates between ground-based meteorological measurements, taking variation in terrain into account, resulting in a continuous surface for each climate variable. Eighteen-year monthly averages were used (years 1980 to 1997) because this corresponds approximately with the time period of the long-term average NPP represented in the forest inventory plot data used for model evaluation.

Soils Data

Soils data were acquired from the USDA NRCS STATSGO soil dataset (http://www.ftw.nrcs.usda.gov/stat_data.html) and converted from vector to raster format at a 1 km spatial resolution. We estimated soil water holding capacity with percent sand, silt, clay, and soil depth following the methods presented in Cosby et al. (1984).

Soil fertility was inferred from spatial coverages of soil nitrogen developed in the methodology of Kern et al. (1997). Soil nitrogen was then scaled log-linearly from 0 (low nitrogen) to 1 (high nitrogen) as required for input into the 3-PGS model.

Canopy Quantum Efficiency

Canopy quantum efficiency is typically scaled linearly with soil fertility in the 3-PGS model after defining potential upper and lower limits (Coops et al. 2001b, Landsberg et al. 2003). In this study we set these limits at a minimum of 0.2 mol C/mol photon (RH Waring, Oregon State University, personal communication) and the maximum set to 0.55 mol C/mol photon (Bond et al. 1999). This parameterization of 3-PGS is consistent with previous parameterizations in the Pacific Northwest (Coops et al. 2001b, Law et al. 2000, Waring and McDowell 2002).

fPAR

Mean monthly satellite predictions of the forest canopy density were available over the study area from the Numerical Terradynamic Simulation Group, University of Montana and provided to us by Nicholas Coops CSIRO Forestry and Forest Products, Australia. These data were calculated from monthly NOAA Advanced Very High Resolution Radiometer (AVHRR) 1 km^2 imagery based on the normalized difference vegetation index (NDVI) – the difference between reflectance measured in the near-infrared and the red wavelengths. This spectral vegetation index has been shown to be nearly linearly related to the fraction of photosynthetically active radiation (fPAR) absorbed by vegetation canopies (Sellers 1987, Goward et al. 1994, Law and Waring 1994).

Modeling Procedure

We used species-specific and ecoregion-specific parameter data from our intensive and extensive inventory plots (see below) or from previous publications from the study area when possible (e.g. Law et al. 2000, Law and Waring 1994, Coops et al. 2001b, Bond et al. 1999). Stock 3-PGS parameters were used where study area specific parameters were not available (e.g. maximum canopy conductance). We parameterized the model for the two dominant forest types in our study area: Douglas-fir (*Pseudotsuga menzeisii*) in the West Cascades, Coast Range, and Klamath Basin, and Ponderosa Pine (*Pinus ponderosa*) in the East Cascades.

We ran the model for 3 years, repeating the same climate and fPAR data each year, to bring the soil water into balance. We then used the final year of model run in our estimates of carbon fluxes, climatic, and edaphic constraints.

To evaluate the seasonal cycle of climate controls on productivity we examined the climate modifiers from the 3-PGS model runs across the west to east climatic gradient in the study area. Monthly climate modifiers were extracted for each of the inventory plot locations and then averaged for 10 kilometer wide north-south bands across a ~250 kilometer transect from the Oregon coast in the west to the East Cascades in the east. The climate modifiers are easily interpreted with respect to one another because they are all scaled from 0 to 1 and have physiological basis behind them.

Inventory Data

The USDA Forest Service conducts inventories of the forests of the United States at a periodic interval of approximately 10 years. As part of this inventory program in the Pacific Northwest, one-hectare forest stands are established on a systematic grid and sampled for basic forest mensuration characteristics (tree diameter, height, species, age, radial growth, etc.). In our study area there are approximately 4600 of these sample plots associated with two Forest Service sampling programs: Forest Inventory and Analysis (FIA; www.fs.fed.us\fia) on non-federal lands and Current Vegetation Survey (CVS; www.fs.fed.us\r6\survey) on national forests.

We developed our own sampling program to measure additional carbon budget components. Ninety-six plots were selected within the study area using a hierarchical random sampling design based on forest type and climate zone (Law et al. 2003, Law et al. in review). Thirty-six of the plots (hereafter – intensive plots) are in chronosequences in the maritime Coast Range, the montane West Cascades mountains, and the semiarid East Cascades forests. Intensive measurements of many carbon budget components were made at these stands including seasonal soil CO_2 fluxes and root biomass (3 chronosequences, each with 4 age classes and three replications; Law et al. in review). The remaining 60 plots (hereafter – extensive plots) were stratified across the study area and sampled for carbon budget components at an intensity intermediate to the forest inventory and intensive plots. Details of sampling methods and analysis are in Law et al. (2003) and Law et al. (in review).

We converted data from forest inventory plots to NPP using the methods described in Van Tuyl et al. (in review). Briefly, woody components of NPP (bole, branch, bark, coarse root) are estimated for each tree by differencing biomass at two points in time. These biomass values are estimated for each tree on a plot using species-specific volume and biomass equations. Radial growth is measured on a subset of trees on each inventory plot using increment borers and then estimated for the remainder of the trees based on plot-specific diameter-growth relationships. These values are then used to back-calculated previous tree dimensions for use in the volume and biomass equations. NPP estimates represent approximately 10 year averages depending on the return interval for each inventory plot (range of return interval is 8-12 years).

Foliage NPP was estimated using remotely sensed leaf area index (LAI; m^2m^{-2}) from Landsat ETM+, leaf mass per unit area (LMA; gm^{-2}), and foliage retention time (years; Turner et al. 2003, Law et al. in review). LMA and foliage retention data were collected at our 96 intensive and extensive plots and applied to the appropriate species across the study area (Van Tuyl et al. in review). Plot-level values of LMA and foliage retention were estimated by calculating a species basal-area weighted average.

Fine root NPP was estimated at the 36 intensive plots using fine root biomass and fine root turnover rates (Van Tuyl et al. in review and Law et al. 2003 for details). A regression model was then fit to the data using LAI as a

predictor of fine root production ($R^2 = 0.45$). This regression model was applied

across the study area to the forest inventory plots to estimate fine root production.

Stand age (time since stand replacing disturbance) was determined for

each inventory plot by averaging the ages of the oldest 10% of trees on the plot,

similar to a method used by Spies and Franklin (1991; average age of dominant

trees).

Model Evaluation

We chose to evaluate the performance of the 3-PGS model using the

traditional approach of building a regression model of inventory plot output on 3-

PGS output and examining the slope, intercept, and R^2. We use weighted

regression to help correct for a spatial scale mismatch between the forest

inventory data and the modeled data beacause the spatial resolution of the

inventory plot output is substantially less coarse (0.01 km^2) than that of the 3-PGS

output (1 km^2). Variability in NPP at the 0.01 km^2 scale within any 1km^2 pixel

affects how much confidence we have in the meaning of a direct comparison at

the two scales (i.e. direct comparison in a 1 km^2 pixel with high variability might

be less meaningful than direct comparison in a 1 km^2 pixel with low variability).

We use variability in leaf area index (LAI) as a surrogate for variability in

NPP within each 1 km^2 pixel because LAI data at the two resolutions in questions

is readily available from data collected in this project (AVHRR data at 1 km^2

resolution and ETM+ data at 0.01 km^2 resolution). We use the standard deviation

of LAI within each 1 km^2 pixel as our index of variability. The weighting procedure in effect lends more weight to pixels with a low standard deviation in LAI and less weight to pixels with low standard deviation in LAI.

We also evaluate the 3-PGS model's seasonal patterns of production by comparing the modeled monthly estimates of GEP with monthly summaries from flux towers at four sites in and around the study area. Three of the flux towers are in the Metolius River basin in the East Cascades ecoregion (www.fsl.orst.edu\terra; public.ornl.gov/ameriflux/Participants/Sites/Map/index.cfm). The fourth flux site is just north of the study area in the West Cascades ecoregion at the Wind River Canopy Crane research facility (http://depts.washington.edu/wrccrf; data gathered from Thornton et al. 2002). GEP is estimated at the flux sites by adding daytime ecosystem respiration to daytime net ecosystem production measured at the flux tower. Ecosystem respiration is estimated either by biometric measurement of soil, bole, and foliage respiration (Metolius sites; Law et al. 2001a) or derived from the relationship between air temperature and nighttime ecosystem respiration (Wind River sites; Thornton et al. 2002).

Results

We first report the results of the evaluation of modeled NPP and the estimated belowground allocation of NPP using the forest inventory data. We then report evaluation of seasonal cycles of carbon fluxes using data from eddy

flux sites in the study area. Finally, we report seasonal cycles of climatic constraints and how they affect productivity across the climatic transect in western Oregon.

Model Evaluation

Figure 9 shows the results of the weighted regression of forest inventory plot NPP on 3-PGS NPP. Overall the 3-PGS model tends to underestimate NPP in low and moderate productivity sites and overestimate NPP in high productivity sites (slope 0.73, standard error 0.01; intercept 172, standard error 6). Agreement between the model and field estimates was good with the model explaining 55% of the variability in field estimates. The weighting procedure brought the slope closer to 1 (from 0.64 to 0.73), brought the intercept closer to 0 (from 326 to 172), and increased the R^2 from 0.43 to 0.55. The 3-PGS model appears to perform slightly better in the East Cascades where fPAR is relatively low than in other ecoregions although the model generally underestimates NPP in this ecoregion.

The seasonal patterns of modeled and measured GEP at the flux sites in the East Cascades are similar, with minimum and maximum values occurring at approximately the same time. The 3-PGS model tends to underestimate GEP throughout the year, only reaching the same magnitude of GEP during the middle of the growing season (Figure 10). This result is consistent with previous studies using the parent model of 3-PGS, 3-PG, at two of the flux sites in the East Cascades (Law et al. 2000).

The flux data comparison for the West Cascades was made using data from the Wind River Canopy Crane flux site. The 3-PGS model shows the same overall pattern of fluxes with GEP peaking in July and the growing season extending throughout most months of the year. The model slightly underestimates fluxes in the early months but performs well from May through July. The model GEP declines rapidly in August and remains an underestimate of tower GEP through the rest of the year.
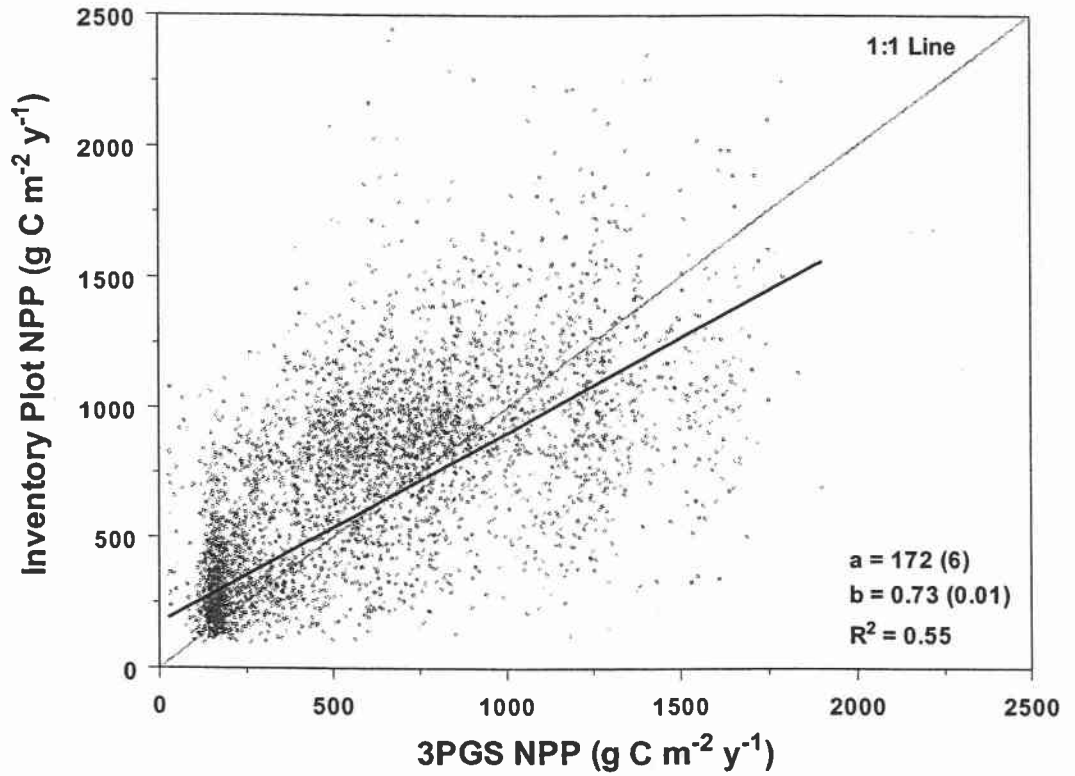
Figure 9: Linear regression of forest inventory plot estimated NPP on 3-PGS estimated NPP (g C m^{-2} y^{-1}). Intercept (a), slope (b), and R^2 values are noted in figure (n = 4293).

The 3-PGS model estimates of fraction of NPP allocated belowground show poor agreement with the field estimates of belowground allocation (figure 11). The belowground allocation scheme used in 3-PGS is a function of the ratio of utilized APAR to absorbed PAR ($APAR_u/APAR$), and is a modified version of the relationship described in Runyon et al. (1994).
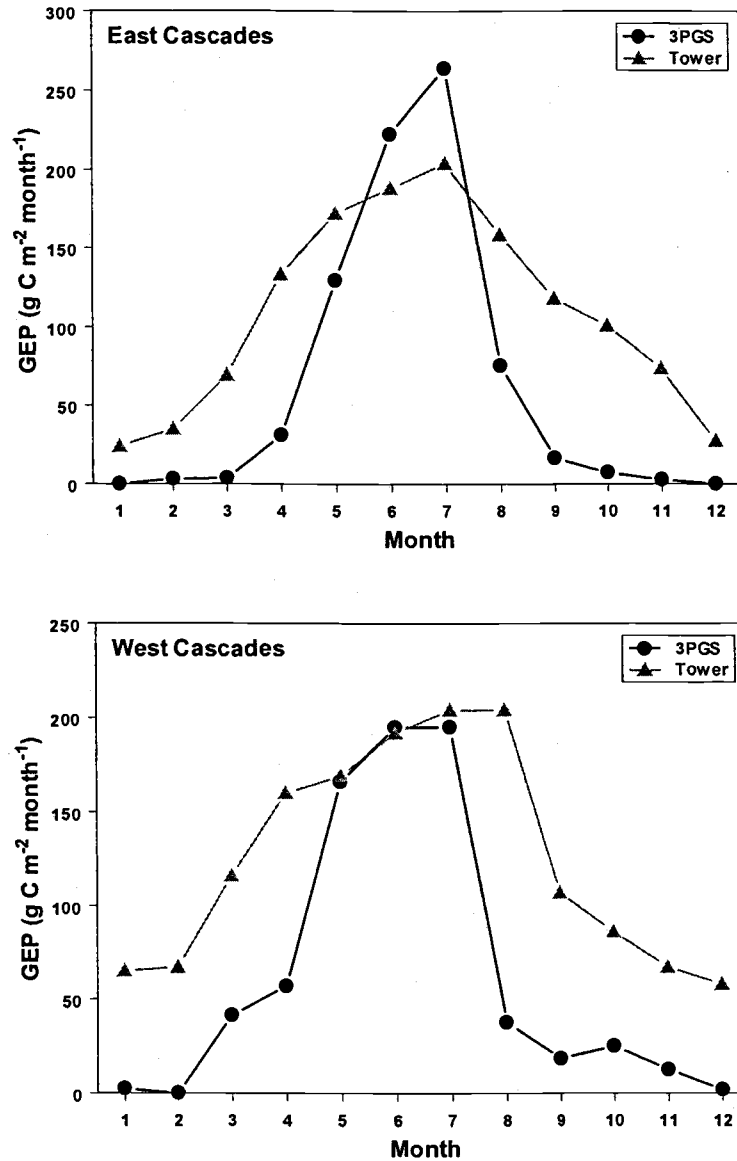
Figure 10: Comparison of seasonal cycles of 3-PGS GEP and GEP from a) the average of three flux towers and 3-PGS in the East Cascades and b) one flux tower in the West Cascades. East Cascades tower estimates are the average of three sites: young (~15 years), intermediate (~60 years), and old growth (~250 years) ponderosa pine at Metolius Oregon. West Cascades tower estimates are from a ~400 year old stand of primarily Douglas-fir/Hemlock at Wind River Washington.
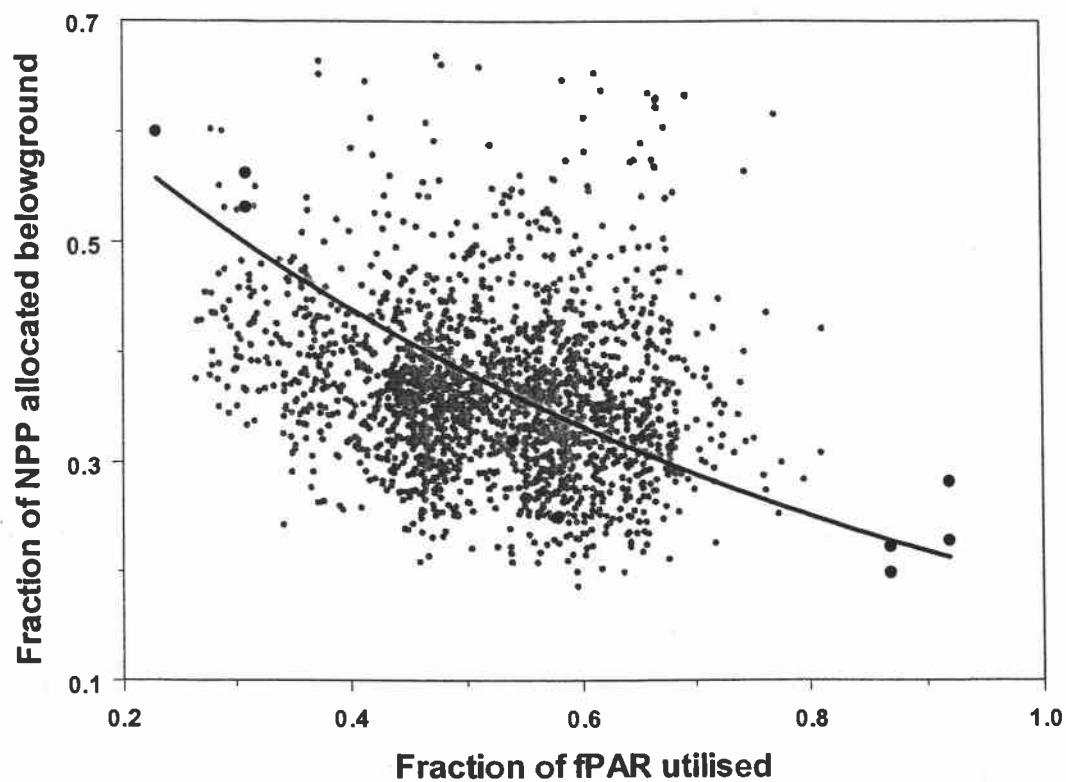
Figure 11: Relationship between percent of NPP allocated belowground and percent of intercepted PAR utilized. Grey dots are from forest inventory data. Black dots and line are from Runyon et al. (1994).

Climatic Constraints on NPP

The climate regime in western Oregon changes rapidly from the coastal region to the interior valleys, the West Cascades, and the semi-arid East Cascades. Precipitation decreases from an annual average of 2500 mm in the Coast Range to 900 mm in the West Cascades, and 500 mm in the East Cascades. Annual average temperature varies widely across the transect from 10 C on the coast to 4 C at high elevations in the Cascades.

The model estimated NPP ranging from 100 g C m^{-2} y^{-1} to 1900 g C m^{-2} y^{-1} in the Coast Range, 50 g C m^{-2} y^{-1} to 1250 g C m^{-2} y^{-1} in the West Cascades, and 50 g C m^{-2} y^{-1} to 800 g C m^{-2} y^{-1} in the East Cascades (means 1250 g C m^{-2} y^{-1}, 650 g C m^{-2} y^{-1}, and 200 g C m^{-2} y^{-1} respectively). These ranges and means are similar to our field estimates from forest inventories and intensive plot data.

Figure 12 shows monthly constraints of climatic factors and soil fertility on NPP west to east across the Oregon transect as predicted by the 3-PGS model illustrating the changing climate regime and its effect on NPP. The modifier values ranging from 0 to 1 are plotted with values approaching 0 indicating more constraint on productivity.

The first change in the 3-PGS climate modifiers when moving away from the coast into the Coast Range is that temperature and frost become more limiting in the early and late parts of the year. This is primarily the result of elevation effects on temperature as one approaches the crest of the Coast Range about 50 km east of the Oregon coast. From November through April sub-optimal leaf

temperatures and frost are the main constraints on productivity in the Coast Range. The constraint of VPD on productivity becomes somewhat constraining during the summer months and typically reaching a maximum constraint in August (30% reduction in productivity from the potential). The soil water balance modifier decreases below 1 in August and starts to constrain productivity in September and October then increases again in November due to increased precipitation. NPP is non-zero throughout most of year indicating a growing season extending from February through November. Productivity in the Coast Range is reduced to about 60% of its potential (i.e. utilized APAR/APAR) at low elevations and 50% at higher elevations.

The pattern of climatic constraints in the interior Willamette Valley is similar to that of the Coast Range with a few exceptions. Summer drought initiates about a month earlier in the growing season in the valley. The soil water modifier deviates from 1, though slightly, in July and drops quickly in August, reaching its lowest point of 0.45 in September and October. The increased soil water constraint is slightly stronger in the central portion of the Willamette Valley and is reduced in strength further east. This appears to be the effect of a minor rain-shadow created by the Coast Range, the effects of which are seen most readily in early and late season rainfall which is higher at the edges of the Willamette Valley than in the central portions of the valley.
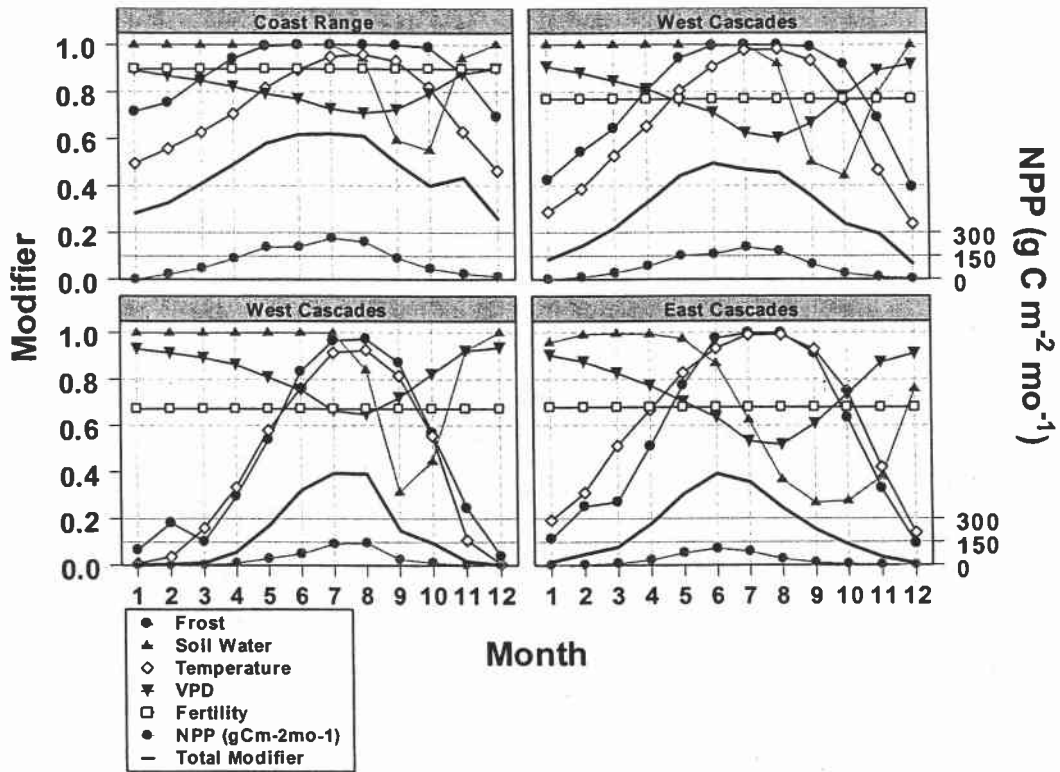
Figure 12: Monthly estimates of climate and fertility modifiers and NPP across the climatic gradient. Each panel represents a 10 km wide north-south swath of the study area. The title of each panel indicates the ecoregion. Climate and fertility modifiers are scaled from 0 (total constraint on productivity) to 1 (no constraint on productivity). The dark line represents the multiplicative effects of the modifiers and can be read as the fraction of potential productivity in each month. The grey line is monthly NPP (bottom of each panel with units on the right axis ranging from 0-300 g C m^{-2} month^{-1}).

As one moves into the West Cascades soil water becomes less constraining in November, with the modifier approaching 1 near the mid-elevations due to high late-season precipitation in October and November. Temperature and frost constraints become increasingly restrictive in the early and late months of the year and at high elevations (1000-1300 meters170-220 km from coast). The effect of these temperature constraints can be seen a reduction in the length of the growing season. At the base of the West Cascades the growing season begins in March and ends in October. By contrast, the growing season at the crest of the Cascades Range (190 km) begins in May and ends in August or September. Productivity is reduced to 50% of potential in low elevations and to 20% in the high elevations near the crest of the Cascades Range.

To the east of the crest of the Cascades Range another more prominent rain shadow is present. Precipitation in the East Cascades averages about 500 mm compared with about 900 mm just 30 km to the west in the West Cascades. There is a slight reduction in the frost and temperature constraints from January through May and again in November although the effects of this reduction are not reflected in the NPP estimates in those months. VPD constraints increase throughout the growing season in this ecoregion reaching a modifier value of 0.5 in some areas in July and August – the most constraining VPD seen across the entire transect. Soil water becomes constraining in July and remains constraining through November. Farther east, in the juniper/sagebrush of the high desert, soil

water becomes constraining as early as May and remains a constraint through December.

Climatic constraints are not solely responsible for the overall reduction in NPP in the East Cascades. The soil fertility rating in this ecoregion is quite low compared with that of the West Cascades and the Coast Range (0.3 in East Cascades, 0.6 in West Cascades, and 0.9 in Coast Range) and an abrupt decline in fertility can be seen just east of the Cascade Crest. The modifiers suggest that productivity ranges from about 25% of maximum potential to less than 10% of maximum potential in the juniper woodlands of the high desert.

Differences in incident shortwave radiation among the ecoregions are opposite the pattern of productivity – incident radiation in the Coast Range is generally lower than in the East Cascades. This suggests that productivity, based on incident radiation alone, should be higher in the East Cascades than the West Cascades and Coast Range. However, the level of climatic and edaphic constraint in the East Cascades is highlighted by the fact that, though the incident shortwave radiation in this ecoregion is higher, productivity is considerably lower.

Discussion

Evaluating 3-PGS

The performance of the 3-PGS model compared with field data in this study and others has been partly a function of the spatial resolution of the input data. Coops and Waring (2001b) also note that 3-PGS tended to underestimate

NPP in low and moderate productivity sites and overestimate NPP in high productivity sites in southwest Oregon. However, Coops et al. (1998) found the opposite pattern in that 3-PGS overestimated NPP at low productivity sites and underestimated NPP at high productivity sites in forests of New Zealand.

The scale mismatch between the estimates of NPP from 3-PGS and the forest inventory plots is an issue that should be explored in the future. As more field estimates of biomass and NPP become available across regions and continents (e.g. Van Tuyl et al. in review, Jenkins et al. 2001, Ni et al. 2001), modelers evaluating estimates carbon fluxes at these scales are likely to encounter the same issues. We have made an attempt to address the issue through our approach of weighting the evaluation by the variability in LAI within the 3-PGS output grid cells.

If fine-resolution model input variables (e.g. satellite NDVI or fPAR, climate, shortwave radiation, and soil fertility data) were available it would be more appropriate to make direct comparisons between the process model and field estimates of NPP. Using model input data at $1km^2$ might wash out fine resolution effects such as increased amplitude in temperatures in areas where vegetation has been removed, cold air drainage due to topography, and differences in incident radiation due to slope and aspect. Finer resolution fPAR data are available from Landsat (~30 meter resolution) and the Moderate Resolution Imaging Spectroradiometer (MODIS; ~250 meter resolution; http://modis.gsfc.nasa.gov)

sensor and some fine scale climate datasets are also becoming available (Smith 2002).

A previous study conducted with 3-PGS parameterized at the inventory plot scale (with the exception of fPAR) showed very close agreement between 3-PGS and inventory plot data when the model was run at six single points (Coops et al 2001d). This suggests that using fine resolution input data in the 3-PGS model data may help alleviate the scale-mismatch between modeled and field estimated of NPP. However, acquiring climate data of the same spatial scale as inventory plots may be a limiting factor in modeling at such fine scales. A more difficult task is improving the resolution of soils data used in these models, which is important given the sensitivity of many models to soil fertility.

In the comparison between tower flux and 3-PGS estimates of GEP, the 3-PGS model estimates of GEP are lower than observations in spring at the mesic and xeric flux sites, which could be due to too severe a penalty for frost events (currently 1 day of photosynthesis lost due to frost) plus a possible 'double counting' of this effect given that there is another temperature modifier working to limit productivity. During August and September when little to no rainfall occurs 3-PGS GEP tends to decrease sharply while tower flux estimates tend to show a more gradual decline. It is possible that the decline in modeled production in late summer is due to an inappropriate soil water holding capacity (too low) or an inappropriate parameterization of one of the canopy conductance terms (maximum canopy conductance, stomatal response to VPD, etc.) at these sites,

both of which could cause soil water limitation and both of which are difficult to measure accurately. This highlights the tradeoff between site-specificity of model parameterization and spatial extent of modeling.

While the 3-PGS model is intended to remain simplified, it may be difficult to maintain this level of simplification for a process as seemingly variable and complex as belowground carbon allocation. In the 3-PGS model a range of possible BNPP:NPP ratios is used to constrain the amount of carbon allocated belowground, but this range does not change with stand development. However, there is some evidence that the ratio changes as stands develop and that this pattern is not consistent among forest types or ecoregions. Van Tuyl et al. (in review) found that BNPP:NPP was most variable across western Oregon in the first 100 years of stand development with carbon allocation belowground amounting to between 25% and 80% of total NPP. After about 100 years the fraction of carbon allocated belowground ranged from about 30% to 50%. In addition, Van Tuyl et al. (in review) found that the pattern of BNPP:NPP through forest succession differed among ecoregions.

In the East Cascades, allocation belowground in the field estimates tends to remain constant or start high and gradually decrease to a steady state (from > 60% to about 40% of total NPP). However, the 3-PGS model predicts constant belowground allocation at about 60% of total NPP throughout stand succession (Figure 13). Allocation patterns in the field estimates in the West Cascades and Coast Range tended to start with low allocation belowground and gradually

increase to a steady state (from < 30% to 40% of total NPP). The 3-PGS model predicts a similar pattern of allocation though the model estimates generally show higher allocation belowground in these ecoregions. These differences in the field estimates and model predictions of belowground allocation patterns suggest that model improvement is necessary with respect to successional changes in carbon allocation and how these changes differ among ecoregions.
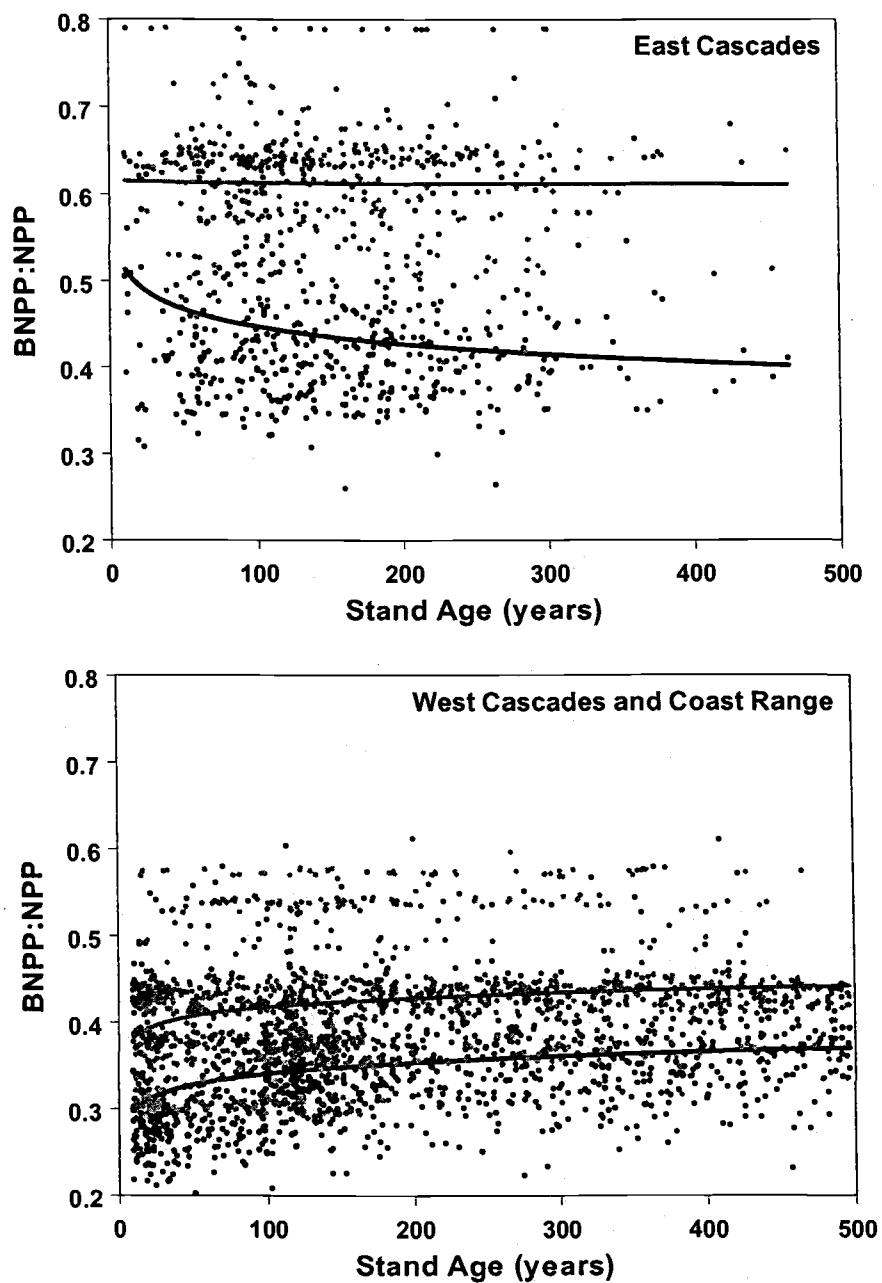
Figure 13: Relationship between BNPP:NPP ratio and stand age. Log linear regression models are fit to forest inventory data and 3-PGS model output. Black line and dots is the model fit to forest inventory data. Grey line and dots is the model fit to the standard 3-PGS belowground allocation scheme.

There are some other indications that climatic constraints on productivity may vary with stand age. For example, Irvine et al. (2002) show reduced canopy conductance in young forests in the East Cascades because of limited root development and access to deep soil water. The severe drought stress experienced by the young forest compared with deeper rooted mature forests in the East Cascades resulted in relatively less gross carbon uptake by the young forest. This pattern, while not well documented in many systems, may provide an argument for adding a component to models that takes into account changing soil resource availability as stands develop.

The spatial resolution of the input data, specifically the satellite derived fPAR, appears to create some problems for the 3-PGS model and presumably with other satellite driven light use efficiency models. First, there is a mixed pixel effect with respect to cover type at the 1 km^2 resolution. Due to patchiness across the forested landscape, there are many different vegetation types within a 1 km^2 area that have potentially different physiological characteristics. Because cover type is not a factor in the parameterization of 3-PGS, this may cause errors in estimates of NPP. An example of the differences in physiological characteristics is differences in canopy quantum efficiency between vegetation types. Law and Waring (1994) found that the shrubs common to early succession in the Pacific Northwest tend to have lower canopy quantum efficiency than trees. Turner et al. (2002) found that accounting for fine scale differences in quantum efficiency had a significant impact on estimates of NPP in crops.

There is a second mixed pixel effect with respect to successional differences in fPAR. Figure 14 shows the change in fPAR over the first 300 years of stand succession in three of the ecoregions. The fPAR estimates from the AVHRR at 1 km^2 resolution appear to show no successional pattern possibly due to an averaging effect at this coarse resolution. By contrast, estimates of fPAR from our 96 intensive and extensive plots show clear successional changes in the West Cascades and East Cascades. There is, however, no visible change in fPAR in the Coast Range field estimates. This brings up a third issue, that in forest systems where high leaf areas are reached early in succession, fPAR peaks early also. The result of this effect is that NPP as predicted by the light use efficiency model remains high throughout succession; even though there should be changes in NPP throughout succession.
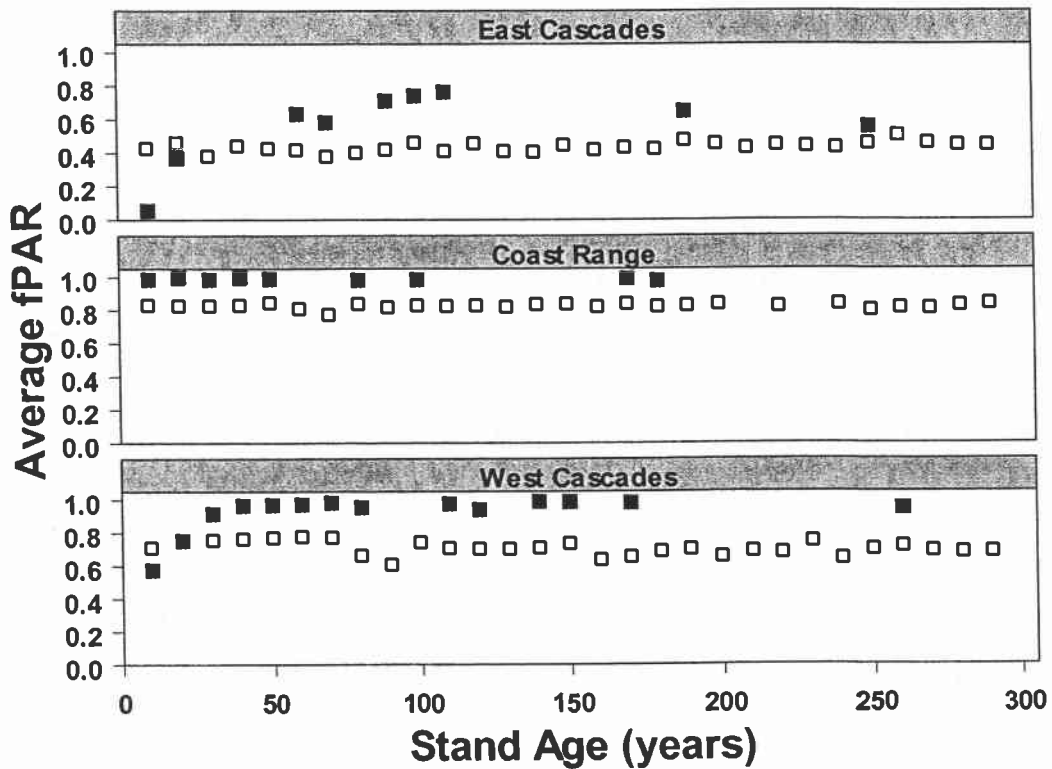
Figure 14: Successional differences between AVHRR estimated fPAR and field estimates of fPAR in three ecoregions of the study area. Grey boxes are mean values of AVHRR estimated fPAR for each 10 year age class. Black boxes are mean values of field estimated fPAR for each 10 year age class. Field estimates of fPAR are from the 96 intensive and extensive plots.

Climatic Constraints

In the past, forest ecologists have show the effects of climate on NPP by comparing annual or aggregated seasonal (e.g. average growing season precipitation) estimates of climate indices with NPP (e.g. Ni et al 2001) or by speculating on the effects (e.g. Hansen et al. 2000). While these exercises might be useful for gaining general insights into overall trends in production, a simple physiological process model such as 3-PGS is uniquely suited to help quantify the effects of climate on NPP and the season changes in these constraints.

Many of the patterns of climatic constraints on NPP predicted by 3-PGS have been observed in field studies conducted across the study area. Emmingham and Waring (1976) found that production was reduced below potential more in the interior Coast Range and West Cascades than on the coast. They also found that drought reduced production below its maximum at four sites from the Coast Range to the West Cascades. Runyon et al. (1994) estimate that productivity in the Coast Range is primarily constrained by VPD and frost and that as one travels east into the Willamette Valley and over the Cascades soil water stress and freezing temperatures become more important constraints. Law and Waring (1994) noted patterns in soil water stress similar to those seen in our study. Namely, soil water stress (measured as predawn water potential) was greatest in August and September in the Coast Range, greatest in August in the Willamette Valley, and greatest in October in the Juniper woodlands at the east end of the

transect. Likewise, leaf level measurements in mid-summer showed that VPD limited stomatal conductance most strongly in juniper followed by Douglas-fir in the Willamette Valley, and had a minor effect on trees in the coastal forests.

Many of the climate constraints described by the 3-PGS model are commonly observed at intensively studied sites across the globe. Some of these relationships are clear and easy to interpret. For example Hollinger et al. (1999) show a strong temperature/frost response at the beginning and end of the growing season in a boreal coniferous forest – a response similar to that seen at high elevations in our study area where temperature and frost restrict the growing season. Huxman et al. (2003) also show relatively clear seasonal patterns of temperature and VPD responses in a subalpine forest using path analysis.

In some cases, however, trends in seasonal environmental constraints on carbon fluxes are less clear. Typically relationships between environmental factors and productivity are not difficult to identify, but interpreting the seasonality and the magnitude of the constraint can be difficult. Reichstein et al. (2002) report strong drought effects on three Mediterranean evergreen forests though the seasonality of this trend is not readily apparent. Tchebakova et al. (2002) identified seasonal variability in water balance (precipitation – evaporation) through the growing season in a boreal forest, but conclude that there is no soil water constraint on canopy conductance. The parent model to 3-PGS (3-PG) has also been successfully employed in the past in a supplementary fashion. Law et al. (2001b) used 3-PG to aid in interpretation of climate effects

on young and old pine forests in California and Oregon, and found that milder

temperatures and more soil water availability in fall through spring at a young

California pine site offset severe climate limitations to productivity imposed by

summer drought. A model such as 3-PGS can be used to help understand climatic

constraints on productivity across disparate climate types as seen in this study.

Conclusion

The model used in this study is well suited for evaluating climatic and

edaphic constraints on forest growth primarily because it isolates these effects and

translates them into a commonly scaled and easy to understand metric making it

easy to interpret the output. There are, however, limitations in the behavior of the

model and significant improvements might be made to the model: adding stand

age effects to belowground allocation algorithms, allowing the model to restrict

soil resources in young stands, and using fine-resolution input data for modeling

at regional scales.

Environmental gradients such as those seen across the Oregon Transect

provide valuable data on the range of climatic constraints on productivity that

might be observed globally. Climatic and edaphic constraints on productivity

reduced photosynthesis throughout the year such that NPP was reduced to 60% of

its potential maximum in the coastal forests and up to 25% of its potential

maximum in the high desert. 3-PGS reveals seasonal patterns in climatic and

edaphic constraints – something difficult to detect with periodic field estimates

and in some cases even with detailed carbon flux and meteorological data.

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CHAPTER 4

Conclusions

Summary of Study Results

Integration of data from forest inventories, satellite remote sensing, and intensive sites across the vegetation types and age classes has allowed us to make reasonable estimates of biomass and NPP components of the regions forests, and to explore trends in biomass and NPP with disturbance and management. This integrative approach means fewer assumptions and generalizations have to be made regarding carbon allocation in forests – assumptions that are often not universally applicable.

In western Oregon, the distribution of stand ages on national forests versus non-federal lands is quite different. More old stands are present on national forest lands than on non-federal lands. The patterns of stand age also differ among ecoregions with a more uniform distribution of age occurring on the national forests of the West Cascades than anywhere else in the study area while the distribution of stand ages in the Coast Range is limited, for the most part, to stands less than 200 years old. These patterns are the result of both natural and anthropogenic disturbances occurring at varying time and space scales across the study area.

Mean biomass in all four ecoregions is higher on the national forests than on non-federal lands. This is primarily the result of the differences in age distributions between the two ownership types. Because the national forests tend to have more old stands, biomass, on average, tends to be higher. The trajectories of biomass accumulation were different in the East Cascades, Klamath Basin, and Coast Range where the rate of accumulation was less on non-federal lands than on national forests. This pattern could be the result of differences in management and disturbance between the ownerships. There was no difference between ownership types in the rate of biomass accumulation in the West Cascades.

The differences in stand age distributions results in lower mean storage of carbon in live trees on non-federal lands across the study area. This means that total storage in live biomass would be higher (1.55 Pg carbon) if the forests of western Oregon were managed for age distributions similar to those seen on national forests than for age distributions observed on non-federal lands (0.83 Pg carbon).

Mean NPP is slightly higher on non-federal lands than on national forest lands. This is a function of the differences in age distributions for the two ownership types. Because NPP peaks relatively early in stand development, and because the non-federal lands tend to have a higher frequency of young stands, we expect to see this pattern.

Productivity generally peaks earlier and at a higher level in the Coast Range than in the Western Cascades and Klamath Basin. We find that

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productivity does not decline in older stands on the dry east side of the Cascade

Mountains, possibly as a result of stand dynamics in the Eastern Cascades lacking

a significant canopy closure/stem exclusion phase. We also find that the pattern

of carbon allocation belowground changes differently through stand development

in the East Cascades than in the West Cascades and Coast Range. East Cascades

forests tend to allocate carbon belowground in early development compared with

high allocation aboveground in early development in the other ecoregions

possibly due to differences in resource competition between these forest systems.

When stands reach ~100 years carbon allocation stabilizes at an average of about

40% allocation belowground in all ecoregions.

Our uncertainty analysis suggests that further refinements to this approach

to making regional estimates of carbon fluxes and stocks should include more

intensive measurement of certain key variables such as wood density and radial

growth, and careful assessment of available allometric equations. Investigation

into the errors associated with allometric volume and biomass equations that are

not specific to a site or species should be conducted when specific equations are

not available. In addition to the patterns explored in this paper, this type of data

might be useful in data assimilation and model evaluation of ecosystem carbon

models.

Climatic and edaphic constraints on productivity reduced photosynthesis

throughout the year such that NPP was reduced to 60% of its potential maximum

in the coastal forests and to 25% of its potential maximum in the high desert. In

the Coast Range, soil water and VPD are most constraining throughout the

summer months although the growing season extends through all 12 months of

the year. Temperature and frost constraints become more noticeable in the early

and late months of the year in the West Cascades ecoregion, especially at high

elevations. These constraints, along with soil water constraints in the late

summer, reduce overall productivity in this ecoregion. Productivity in the East

Cascades is limited by reduced nutrition, early and late month temperature and

frost constraints, and extreme VPD and soil water constraints in the summer

months.

The physiological model used in this study is uniquely suited for

determining climatic and edaphic constraints on forest growth primarily because it

isolates these effects and translates them into a commonly scaled and easy to

understand metric making it easy to interpret the output. There are, however,

limitations in the behavior of the model and significant improvements might be

made to the model: adding stand age effects to belowground allocation

algorithms, allowing the model to restrict soil resources in young stands, and

using fine-resolution input data for modeling at regional scales.

Environmental gradients such as those observed across the Oregon

Transect provide valuable data on the range of climatic constraints on

productivity that might be observed globally. 3-PGS allows an investigator to see

seasonal patterns in climatic and edaphic constraints – something difficult to

detect with periodic field estimates and in some cases even with detailed carbon

flux and meteorological data. The model could be used in the future to estimate

constraints on forest productivity at large spatial scales for many sites where

carbon fluxes are measured in the absence of supporting meteorological data (e.g.

forest inventory programs) or as a supplement to studies that do not have detailed

meteorological data available (e.g. eddy flux sites).

Future Directions

Further improvements of the techniques used in this project fall into a few

main categories. First, we need to be able to better estimate the errors associated

with each component of biomass and productivity and cumulative errors. While

we have attempted to indicate the errors associated with individual components of

our estimates, we have not been able to provide robust estimates for many

components and certainly have not been able to provide a single estimate for total

biomass or productivity.

Second, because biomass and volume allometric equations are the primary

methods by which we estimate woody components of carbon storage and fluxes it

is important to understand the degree to which the use of species specific and

geographically explicit equations are necessary. Traditional thought on the

subject would suggest that species and site-specificity is important for accurately

estimating biomass and productivity, but few studies have actually investigated

this question explicitly and almost none have investigated the question at the scale

of this type of study. While our estimates of biomass and productivity have made use of our best understanding of how we should apply allometric equations, one must wonder if the process of making these estimates might be simplified by generalizing these equations when using them over such large spatial scales. Conversely, even in our attempts to make best estimates with the allometric equations available, we have missed the mark due to the extreme site or species specificity of these equations. I contend that the former is more likely than the latter and that investigating the viability of regionalizing biomass and volume allometry is a field of study worth investigating.

Third, the scaling of characteristics of forest canopies should be another point of interest for further studies. Our estimates of foliar biomass and production rely on the scaling from branches to trees to plots to regions tree-level characteristics such as leaf mass per unit area and foliar retention time. Our understanding of how these characteristics vary within trees and within stands may be much better than our understanding of variability across regions and between species.

Fourth, belowground pools and fluxes are difficult to estimate even at intensively studied sites, let alone across entire regions. Estimates of belowground pools and fluxes are, however, important to understanding the overall carbon cycle in ecosystems and how carbon is allocated to different pools at different points in succession. It is for this reason that further study of

belowground processes and further investigation into methods for estimating them is a necessity.

Finally, it is possible that studies like ours and the suggestions made for improvement could be used to help guide the future of forest inventory programs. The agencies administering forest inventory programs are interested in input from the community of data users, but until recently, carbon cycle researches have not used these datasets. The success of this study and others like it and our continued use of the data and participation in the process of delivering feedback to the administrators of inventory programs will ensure that the needs of carbon cycle researchers are in mind when changes are made to the inventory programs.

Conclusions

Carbon cycle research has reached a point where both small and large scale datasets of carbon storage and fluxes are necessary. There is an increased interest in understanding carbon cycling at regional to global scales and the combined power of large and small scale studies of carbon cycling help us to validate our understanding of successional carbon dynamics and to change these preconceptions where they are not supported by data. The datasets are also useful to investigators using physiological process models to estimate fluxes at regional to global scales. Calibration and evaluation of modelling at these scales could be aided by data collected at equivalent scales.

In this study we used a combination of many techniques that, up to this point, have generally been used singly for estimating carbon budgets and fluxes. This combination of techniques could use some improvement, but the success of this project should be encouraging to those who will investigate such improvements for the future. The amount of data that is accumulating in the area of carbon cycling research and related fields will help guide future attempts to use large scale forest inventories to estimate carbon storage and fluxes in forests and possibly other biomes.

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APPENDIX

Appendix A

Table of allometric equations used in this study. DBH.CM is diameter at breast height in centimeters, DBH.M is diameter at breast height in meters, DBH.IN is diameter at breast height in inches, HT.M is tree height in meters, and HT.FT is tree height in feet.

Bole Volume Scientific Name	Common Name	Ecoregion	Allometric Sources	Equation
Abies amabilis	Pacific Silver Fir	All	Browne 1962	(10^(-2.575642+1.806775*(log10(DBH.IN))+1.094665*(log10(HT.FT)))*0.0283)
Abies concolor	White Fir	East Cascades	Cochran 1985	(exp(-6.186+1.7533*(log(DBH.IN))+1.1684*(log(HT.FT)))*0.0283)
Abies concolor	White Fir	West Cascades	Cochran 1985	(exp(-6.186+1.7533*(log(DBH.IN))+1.1684*(log(HT.FT)))*0.0283)
Abies concolor	White Fir	Coast Range	Cochran 1985	(exp(-6.186+1.7533*(log(DBH.IN))+1.1684*(log(HT.FT)))*0.0283)
Abies concolor	White Fir	Klamath Basin	Walters et al. 1985	((0.00108*(HT.FT/DBH.IN)^0.3583*(DBH.IN^2*HT.FT))+((3.14159*(0.287414+0.828652*DBH.IN^1.082631)^2/175616)*((729+81*((0.904973*DBH.IN^0.287414)/(0.287414+0.828652*DBH.IN^1.082631))^(2/3))+(297*((0.904973*DBH.IN^0.287414)/(0.287414+0.828652*DBH.IN^1.082631))^(4/3))+(265*((0.904973*DBH.IN^0.287414)/(0.287414+0.828652*DBH.IN^1.082631))^(2)))))*0.0283

Abies grandis	Grand Fir	East Cascades	Cochran 1985	(exp(-6.186+1.7533*(log(DBH.IN))+1.1684*(log(HT.FT))))*0.0283
Abies grandis	Grand Fir	Coast Range	Walters et al. 1985	((0.00108*(HT.FT/DBH.IN)^0.3583*(DBH.IN^2*HT.FT))+((3.14159*(0.287414+0.828652*DBH.IN^1.082631)^2/175616)*((729+81*((0.904973*DBH.IN^0.287414)/(0.287414+0.828652*DBH.IN^1.082631))^(2/3))+(297*((0.904973*DBH.IN^0.287414)/(0.287414+0.828652*DBH.IN^1.082631))^(4/3))+(265*((0.904973*DBH.IN^0.287414)/(0.287414+0.828652*DBH.IN^1.082631))^(2)))))*0.0283
Abies grandis	Grand Fir	West Cascades	Walters et al. 1985	((0.00108*(HT.FT/DBH.IN)^0.3583*(DBH.IN^2*HT.FT))+((3.14159*(0.287414+0.828652*DBH.IN^1.082631)^2/175616)*((729+81*((0.904973*DBH.IN^0.287414)/(0.287414+0.828652*DBH.IN^1.082631))^(2/3))+(297*((0.904973*DBH.IN^0.287414)/(0.287414+0.828652*DBH.IN^1.082631))^(4/3))+(265*((0.904973*DBH.IN^0.287414)/(0.287414+0.828652*DBH.IN^1.082631))^(2)))))*0.0283
Abies grandis	Grand Fir	Klamath Basin	Walters et al. 1985	((0.00108*(HT.FT/DBH.IN)^0.3583*(DBH.IN^2*HT.FT))+((3.14159*(0.287414+0.828652*DBH.IN^1.082631)^2/175616)*((729+81*((0.904973*DBH.IN^0.287414)/(0.287414+0.828652*DBH.IN^1.082631))^(2/3))+(297*((0.904973*DBH.IN^0.287414)/(0.287414+0.828652*DBH.IN^1.082631))^(4/3))+(265*((0.904973*DBH.IN^0.287414)/(0.287414+0.828652*DBH.IN^1.082631))^(2)))))*0.0283

Species	Common Name		Reference	Equation
Abies lasiocarpa	Subalpine Fir	All	Browne 1962	10^(-2.502332+1.864963*(log10(DBH.IN))+1.004903*(log10(HT.FT)))*0.0283
Abies magnifica	California Red Fir	All	FSDB TV0098	0.2467*HT.M*DBH.M^2
Abies procera	Noble Fir	All	FSDB TV0098	0.2734*HT.M*DBH.M^2
Acer macrophyllum	Bigleaf Maple	All	Pillsbury and Kirkley 1984	0.0000718042*(DBH.CM^2.22462)*(HT.M^0.57561)
Alnus rubra	Red Alder	All	Snell and Little 1983	(exp(-2.9326+2.4999*(log(DBH.IN))))*0.0283
Arbutus menzeisii	Pacific Madrone	All	Pillsbury and Kirkley 1984	0.0000821921*(DBH.CM^1.96628)*(HT.M^0.83458)
Betula papyrifera	Western Paper Birch	All	Browne 1962	(10^(-2.757813+1.911681*(log10(DBH.IN))+1.105403*(log10(HT.FT)))*0.0283
Calocedrus decurrens	Incense Cedar	All	FSDB TV0098	0.2149*HT.M*DBH.M^2
Castanopsis chrysophylla	Golden Chinkapin	All	Snell and Little 1983	exp(-3.2199+2.5169*(log(DBH.IN))))*0.0283
Chamaecyparis lawsoniana	Port-Orford Cedar	All	see *Chamaecyparis nootkatensis*	(10^(-2.454348+1.741004*(log10(DBH.IN))+1.058437*(log10(HT.FT)))*0.0283)
Chamaecyparis nootkatensis	Alaska Cedar	All	Browne 1962	(10^(-2.454348+1.741004*(log10(DBH.IN))+1.058437*(log10(HT.FT)))*0.0283)
Cornus nuttallii	Pacific Dogwood	All	see *Alnus rubra*	(exp(-2.9326+2.4999*(log(DBH.IN))))*0.0283
Fraxinus latifoloia	Oregon Ash	All	see *Alnus rubra*	(exp(-2.9326+2.4999*(log(DBH.IN))))*0.0283
Ilex sp.	Holly	All	see *Alnus rubra*	(exp(-2.9326+2.4999*(log(DBH.IN))))*0.0283

Juniperus occidentalis	Western Juniper	All	Means et al. 1994	(0.005454154*DBH.IN^2*0.307+0.00086*HT.FT-0.0037*DBH.IN*HT.FT/(HT.FT-4.5)*HT.FT*HT.FT/(HT.FT-4.5)^2)*0.0283
Larix occidentalis	Western Larch	All	Cochran 1985	(exp(-6.9499+1.6782*(log(DBH.IN))+1.3287*(log(HT.FT))))*0.0283
Lithocarpus densiflorus	Tanoak	All	Pillsbury and Kirkley 1984	0.0000763045*(DBH.CM^2.14321)*(HT.M^0.7422)
Picea engelmannii	Engelmann Spruce	All	Cochran 1985	(exp(-5.77345+1.8507*(log(DBH.IN))+1.0182*(log(HT.FT))))*0.0283
Picea sitchensis	Sitka Spruce	All	FSDB TV0098	0.2286*HT.M*DBH.M^2
Pinus contorta	Lodgepole Pine	Coast Range	Browne 1962	(10^(-2.615591+1.847504*(log10(DBH.IN))+1.085772*(log10(HT.FT)))*0.0283)
Pinus contorta	Lodgepole Pine	West Cascades	FSDB TV0098	0.3782*HT.M*DBH.M^2
Pinus contorta	Lodgepole Pine	East Cascades	FSDB TV0098	0.3782*HT.M*DBH.M^2
Pinus contorta	Lodgepole Pine	Klamath Basin	FSDB TV0098	0.3782*HT.M*DBH.M^2
Pinus jeffreyi	Jeffery Pine	All	FSDB TV0098	0.2739*HT.M*DBH.M^2
Pinus lambertiana	Sugar Pine	All	Walters et al. 1985	((0.000887*(HT.FT/DBH.IN)^0.38394*(DBH.IN^2*HT.FT))+((3.14159*(0+1.03908*DBH.IN^1)^2/175616)*((729+81*((0.859045*DBH.IN^0)/(0+1.03908*DBH.IN^1))^(2/3))+(297*((0.859045*DBH.IN^0)/(0+1.03908*DBH.IN^1))^(4/3))+(265*((0.859045*DBH.IN^0)/(0+1.03908*DBH.IN^1))^(2)))))*0.0283
Pinus monticola	Western White Pine	All	Cochran 1985	(exp(-6.1498+1.7048*(log(DBH.IN))+1.1769*(log(HT.FT))))*0.0283
Pinus ponderosa	Ponderosa Pine	East Cascades	FSDB TV0098	0.2934*HT.M*DBH.M^2

Pinus ponderosa	Ponderosa Pine	West Cascades	Cochran 1985	(exp(-6.0336+1.8715*(log(DBH.IN))+1.1066*(log(HT.FT))))*0.0283
Pinus ponderosa	Ponderosa Pine	Coast Range	Cochran 1985	(exp(-6.0336+1.8715*(log(DBH.IN))+1.1066*(log(HT.FT))))*0.0283
Pinus ponderosa	Ponderosa Pine	Klamath Basin	Walters et al. 1985	((0.001265*(HT.FT/DBH.IN)^0.172813*(DBH.IN^2*HT.FT))+((3.14159*(0+1*DBH.IN^1)^2/175616)*((729+81*((0.809427*DBH.IN^0)/(0+1*DBH.IN^1))^(2/3))+(297*((0.809427*DBH.IN^0)/(0+1*DBH.IN^1))^(4/3))+(265*((0.809427*DBH.IN^0)/(0+1*DBH.IN^1))^(2)))))*0.0283
Populus tremuloides	Quaking Aspen	All	Browne 1962	(10^(-2.63536+1.946034*(log10(DBH.IN))+1.024793*(log10(HT.FT)))*0.0283)
Populus trichocarpa	Black Cottonwood	All	Browne 1962	(10^(-2.945047+1.803973*(log10(DBH.IN))+1.238853*(log10(HT.FT)))*0.0283)
Pseudotsuga menziesii	Douglas Fir	East Cascades	Cochran 1985	(exp(-5.8785+1.8357*(log(DBH.IN))+1.0279*(log(HT.FT))))*0.0283
Pseudotsuga menziesii	Douglas Fir	Coast Range	FSDB TV0098	0.2346*HT.M*DBH.M^2
Pseudotsuga menziesii	Douglas Fir	West Cascades	FSDB TV0098	0.2346*HT.M*DBH.M^2

Species	Common Name	Region	Source	Equation
Pseudotsuga menziesii	Douglas Fir	Klamath Basin	Walters et al. 1985	((0.001168*(HT.FT/DBH.IN)^0.26543*(DBH.IN^2*HT.FT))+((3.14159*(0+0.989819*DBH.IN^1)^2/175616)*((729+81*((0.903563*DBH.IN^0)/(0+0.989819*DBH.IN^1))^(2/3))+(297*((0.903563*DBH.IN^0)/(0+0.989819*DBH.IN^1))^(4/3))+(265*((0.903563*DBH.IN^0)/(0+0.989819*DBH.IN^1))^(2)))))*0.0283
Quercus agrifolia	Coast Live Oak	All	Pillsbury and Kirkley 1984	0.0000446992*(DBH.CM^2.31958)*(HT.M^0.62528)
Quercus chrysolepis	Canyon Live Oak	All	Pillsbury and Kirkley 1984	0.0000730718*(DBH.CM^2.20527)*(HT.M^0.6119)
Quercus douglasii	Blue Oak	All	Pillsbury and Kirkley 1984	0.0000697541*(DBH.CM^2.33089)*(HT.M^0.461)
Quercus emoryi	Engelmann Oak	All	Pillsbury and Kirkley 1984	0.0000805935*(DBH.CM^2.40248)*(HT.M^0.2806)
Quercus garryana	Oregon White Oak	All	Pillsbury and Kirkley 1984	0.0000674342*(DBH.CM^2.14321)*(HT.M^0.7422)
Quercus kelloggii	California Black Oak	All	Pillsbury and Kirkley 1984	0.0000870843*(DBH.CM^1.97437)*(HT.M^0.85034)
Quercus lobata	Valley Oak	All	Pillsbury and Kirkley 1984	0.000033475*(DBH.CM^2.33631)*(HT.M^0.74872)
Quercus wislinzeni	Interior Live Oak	All	Pillsbury and Kirkley 1984	0.0001238312*(DBH.CM^2.02989)*(HT.M^0.63257)
Robinia pseudoacacia	Black Locust	All	see *Alnus rubra*	(exp(-2.9326+2.4999*(log(DBH.IN))))*0.0283
Salix sp.	Willow Spp.	All	see *Alnus rubra*	(exp(-2.9326+2.4999*(log(DBH.IN))))*0.0283
Sequoia sepervirens	Redwood	All	see *Sequoiadendron gigantieum*	0.2267*HT.M*DBH.M^2
Sequoiadendron gigantieum	Giant Sequoia	All	FSDB TV0098	0.2267*HT.M*DBH.M^2

Scientific Name	Common Name	Ecoregion	Allometric Sources	
Taxus brevifolia	Pacific Yew	All	see *Tsuga mertensiana*	0.2921*HT.M*DBH.M^2
Thuja plicata	Western Redcedar	All	Browne 1962	(10^(-2.464614+1.701993*(log10(DBH.IN))+1.067038*(log10(HT.FT)))*0.0283)
Tsuga heterophylla	Western Hemlock	All	Chambers and Foltz 1979	(10^(-2.7217+2.00857*(log10(DBH.IN))+1.0862*(log10(HT.FT))-0.00568*(DBH.IN)))*0.0283
Tsuga mertensiana	Mountain Hemlock	All	FSDB TV0098	0.2921*HT.M*DBH.M^2
Ubellularia californica	California Laurel	All	Pillsbury and Kirkley 1984	0.0000763133*(DBH.CM^1.94553)*(HT.M^0.88389)

Branch Mass

Scientific Name	Common Name	Ecoregion	Allometric Sources	
Abies amabilis	Pacific Silver Fir	All	Gholz et al. 1979	(exp(-4.8287+2.5585*(log(DBH.CM))))*1000
Abies concolor	White Fir	All	see *Abies amabilis*	(exp(-4.8287+2.5585*(log(DBH.CM))))*1000
Abies grandis	Grand Fir	All	Means et al. 1994	(13000+0.0124*(DBH.CM)^2*(HT.M*100))
Abies lasiocarpa	Subalpine Fir	All	see *Abies amabilis*	(exp(-4.8287+2.5585*(log(DBH.CM))))*1000
Abies magnifica	California Red Fir	All	see *Abies amabilis*	(exp(-4.8287+2.5585*(log(DBH.CM))))*1000
Abies procera	Noble Fir	All	Gholz et al. 1979	(exp(-4.1817+2.3324*(log(DBH.CM))))*1000
Acer macrophyllum	Bigleaf Maple	All	included in bole volume equation	
Alnus rubra	Red Alder	All	Means et al. 1994	(8100+0.0285*(DBH.CM)^2*(HT.M*100))
Arbutus menzeisii	Pacific Madrone	All	included in bole volume equation	

Betula papyrifera	Western Paper Birch	All	Means et al. 1994	(-600+0.0451*(DBH.CM)^2*(HT.M*100))
Calocedrus decurrens	Incense Cedar	All	see *Chamaecyparis nootkatensis*	(exp(-3.2261+2.0877*(log(DBH.CM))))*1000
Castanopsis chrysophylla	Golden Chinkapin	All	Gholz et al. 1979	(exp(-4.579+2.576*(log(DBH.CM))))*1000
Chamaecyparis nootkatensis	Alaska Cedar	All	Gholz et al. 1979	(exp(-3.2261+2.0877*(log(DBH.CM))))*1000
Cornus nuttallii	Pacific Dogwood	All	see *Alnus rubra*	(8100+0.0285*(DBH.CM)^2*(HT.M*100))
Fraxinus latifoloia	Oregon Ash	All	see *Alnus rubra*	(8100+0.0285*(DBH.CM)^2*(HT.M*100))
Ilex sp.	Holly	All	see *Alnus rubra*	(8100+0.0285*(DBH.CM)^2*(HT.M*100))
Juniperus occidentalis	Western Juniper	All	see *Chamaecyparis nootkatensis*	(exp(-3.2261+2.0877*(log(DBH.CM))))*1000
Larix occidentalis	Western Larch	All	Means et al. 1994	(20400+0.0077*(DBH.CM)^2*(HT.M*100))
Lithocarpus densiflorus	Tanoak	All	included in bole volume equation	
Picea engelmannii	Engelmann Spruce	All	Means et al. 1994	(16800+0.0144*(DBH.CM)^2*(HT.M*100))
Picea sitchensis	Sitka Spruce	All	Means et al. 1994	(9700+0.022*(DBH.CM)^2*(HT.M*100))
Pinus contorta	Lodgepole Pine	All	Means et al. 1994	(7800+0.0123*(DBH.CM)^2*(HT.M*100))
Pinus jeffreyi	Jeffery Pine	All	see *Pinus ponderosa*	(exp(-5.3855+2.7185*(log(DBH.CM))))*1000
Pinus lambertiana	Sugar Pine	All	Gholz et al. 1979	(exp(-7.637+3.3648*(log(DBH.CM))))*1000
Pinus monticola	Western White Pine	All	Means et al. 1994	(9500+0.0168*(DBH.CM)^2*(HT.M*100))
Pinus ponderosa	Ponderosa Pine	All	Gholz et al. 1979	(exp(-5.3855+2.7185*(log(DBH.CM))))*1000
Populus trichocarpa	Black Cottonwood	All	Means et al. 1994	(1700+0.0262*(DBH.CM)^2*(HT.M*100))
Populus tremuloides	Quaking Aspen	All	Means et al. 1994	(2500+0.0368*(DBH.CM)^2*(HT.M*100))

Pseudotsuga menziesii	Douglas Fir	All	Gholz et al. 1979	(exp(-3.6941+2.1382*(log(DBH.CM))))*1000
Quercus agrifolia	Coast Live Oak	All	included in bole volume equation	
Quercus chrysolepis	Canyone Live Oak	All	included in bole volume equation	
Quercus douglasii	Blue Oak	All	included in bole volume equation	
Quercus emoryi	Engelmann Oak	All	included in bole volume equation	
Quercus garryana	Oregon White Oak	All	included in bole volume equation	
Quercus kelloggii	California Black Oak	All	included in bole volume equation	
Quercus lobata	Valley Oak	All	included in bole volume equation	
Quercus wislinzeni	Interior Live Oak	All	included in bole volume equation	
Robinia pseudoacacia	Black Locust	All	see *Alnus rubra*	(8100+0.0285*(DBH.CM)^2*(HT.M*100))
Salix sp.	Willow Spp.	All	see *Alnus rubra*	(8100+0.0285*(DBH.CM)^2*(HT.M*100))
Sequoia sepervirens	Redwood	All	see *Thuja plicata*	(exp(-3.2261+2.0877*(log(DBH.CM))))*1000
Sequoiadendron gigantieum	Giant Sequoia	All	see *Thuja plicata*	(exp(-3.2261+2.0877*(log(DBH.CM))))*1000
Taxus brevifolia	Pacific Yew	All	see *Tsuga mertensiana*	0.2921*HT.M*DBH.M^2
Thuja plicata	Western Redcedar	All	Gholz et al. 1979	(exp(-3.2261+2.0877*(log(DBH.CM))))*1000
Tsuga heterophylla	Western Hemlock	All	Gholz et al. 1979	(exp(-5.149+2.778*(log(DBH.CM))))*1000

Scientific Name	Common Name	Ecoregion	Allometric Sources	
Tsuga mertensiana	Mountain Hemlock	All	Gholz et al. 1979	(exp(-5.2581+2.6045*(log(DBH.CM))))*1000
Ubellularia californica	California Laurel	All	included in bole volume equation	

Bark Mass

Scientific Name	Common Name	Ecoregion	Allometric Sources	
Abies amabilis	Pacific Silver Fir	All	Gholz et al. 1979	(exp(-6.1166+2.8421*(log(DBH.CM))))*1000
Abies concolor	White Fir	All	FSDB TV0098	(0.0795*HT.M*DBH.M^2)*590000
Abies grandis	Grand Fir	All	Means et al. 1994	600+0.0164*(DBH.CM)^2*(HT.M*100)
Abies lasiocarpa	Subalpine Fir	All	FSDB TV0098	(0.018*HT.M*DBH.M^2)*570000
Abies magnifica	California Red Fir	All	FSDB TV0098	0.0635*HT.M*DBH.M^2*550000
Abies procera	Noble Fir	All	Gholz et al. 1979	(exp(-6.1+2.8943*(log(DBH.CM))))*1000
Acer macrophyllum	Bigleaf Maple	All	included in bole volume equation	
Alnus rubra	Red Alder	All	Means et al. 1994	(-1200+0.024*(DBH.CM)^2*(HT.M*100))
Arbutus menzeisii	Pacific Madrone	All	included in bole volume equation	
Betula papyrifera	Western Paper Birch	All	Means et al. 1994	(-1200+0.0291*(DBH.CM)^2*(HT.M*100))
Calocedrus decurrens	Incense Cedar	All	Means et al. 1994	(exp(0.500948+2.8594*log(DBH.CM)))
Castanopsis chrysophylla	Golden Chinkapin	All	Gholz et al. 1979	(exp(-5.923+2.989*(log(DBH.CM))))*1000
Chamaecyparis nootkatensis	Alaska Cedar	All	Gholz et al. 1979	(exp(-4.1934+2.1101*(log(DBH.CM))))*1000
Juniperus occidentalis	Western Juniper	All	see *Chamaecyparis nootkatensis*	(exp(-4.1934+2.1101*(log(DBH.CM))))*1000
Larix occidentalis	Western Larch	All	Means et al. 1994	(2400+0.0150*(DBH.CM)^2*(HT.M*100))
Lithocarpus densiflorus	Tanoak	All	included in bole volume equation	

Picea engelmannii	Engelmann Spruce	All	Means et al. 1994	(4500+0.0093*(DBH.CM)^2*(HT.M*100))
Picea sitchensis	Sitka Spruce	All	FSDB TV0098	(0.006*HT.M*DBH.M^2)*538000
Pinus contorta	Lodgepole Pine	All	Means et al. 1994	(3200+0.0091*(DBH.CM)^2*(HT.M*100))
Pinus jeffreyi	Jeffery Pine	All	FSDB TV0098	(0.0936*HT.M*DBH.M^2)*345000
Pinus lambertiana	Sugar Pine	All	Gholz et al. 1979	(exp(-5.295+2.6186*(log(DBH.CM))))*1000
Pinus monticola	Western White Pine	All	Means et al. 1994	(9500+0.0168*(DBH.CM)^2*(HT.M*100))
Pinus ponderosa	Ponderosa Pine	All	Gholz et al. 1979	(exp(-4.2063+2.2312*(log(DBH.CM))))*1000
Populus tremuloides	Quaking Aspen	All	Means et al. 1994	(1300+0.0276*(DBH.CM)^2*(HT.M*100))
Populus trichocarpa	Black Cottonwood	All	Means et al. 1994	(1200+0.0155*(DBH.CM)^2*(HT.M*100))
Pseudotsuga menziesii	Douglas Fir	All	Gholz et al. 1979	(exp(-4.3103+2.43*(log(DBH.CM))))*1000
Quercus agrifolia	Coast Live Oak	All	included in bole volume equation	
Quercus chrysolepis	Canyone Live Oak	All	included in bole volume equation	
Quercus douglasii	Blue Oak	All	included in bole volume equation	
Quercus emoryi	Engelmann Oak	All	included in bole volume equation	
Quercus garryana	Oregon White Oak	All	included in bole volume equation	
Quercus kelloggii	California Black Oak	All	included in bole volume equation	
Quercus lobata	Valley Oak	All	included in bole volume equation	
Quercus wislinzeni	Interior Live Oak	All	included in bole volume equation	

Sequoia sepervirens	Redwood	All	see *Sequoiadendron gigantieum*	(0.0293*HT.M*DBH.M^2)*430000
Sequoiadendron gigantieum	Giant Sequoia	All	FSDB TV0098	(0.0293*HT.M*DBH.M^2)*430000
Taxus brevifolia	Pacific Yew	All	see *Tsuga mertensiana*	(exp(-5.5868+2.7654*(log(DBH.CM))))*1000
Thuja plicata	Western Redcedar	All	Gholz et al. 1979	(exp(-4.1934+2.1101*(log(DBH.CM))))*1000
Tsuga heterophylla	Western Hemlock	All	Gholz et al. 1979	(exp(-4.373+2.258*(log(DBH.CM))))*1000
Tsuga mertensiana	Mountain Hemlock	All	Gholz et al. 1979	(exp(-5.5868+2.7654*(log(DBH.CM))))*1000
Ubellularia californica	California Laurel	All	included in bole volume equation	

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