Disturbance and climate effects on carbon stocks and fluxes across Western Oregon USA

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Abstract

We used a spatially nested hierarchy of field and remote-sensing observations and a process model, Biome-BGC, to produce a carbon budget for the forested region of Oregon, and to determine the relative influence of differences in climate and disturbance among the ecoregions on carbon stocks and fluxes. The simulations suggest that annual net uptake (net ecosystem production (NEP)) for the whole forested region (8.2 million hectares) was 13.8 Tg C (168 g C m⁻² yr⁻¹), with the highest mean uptake in the Coast Range ecoregion (226 g C m⁻² yr⁻¹), and the lowest mean NEP in the East Cascades (EC) ecoregion (88 g C m⁻² yr⁻¹). Carbon stocks totaled $2765 \,\mathrm{Tg}\,\mathrm{C}$ (33 $700 \,\mathrm{g}\,\mathrm{C}\,\mathrm{m}^{-2}$), with wide variability among ecoregions in the mean stock and in the partitioning above- and belowground. The flux of carbon from the land to the atmosphere that is driven by wildfire was relatively low during the late 1990s ($\sim 0.1\,\mathrm{Tg}\,\mathrm{C}\,\mathrm{yr}^{-1}$), however, wildfires in 2002 generated a much larger C source ($\sim 4.1\,\mathrm{Tg}\,\mathrm{C}$). Annual harvest removals from the study area over the period 1995–2000 were $\sim 5.5\,\mathrm{Tg}\,\mathrm{C}\,\mathrm{yr}^{-1}$. The removals were disproportionately from the Coast Range, which is heavily managed for timber production (approximately 50% of all of Oregon's forest land has been managed for timber in the past 5 years). The estimate for the annual increase in C stored in long-lived forest products and land fills was 1.4 Tg Cyr⁻¹. Net biome production (NBP) on the land, the net effect of NEP, harvest removals, and wildfire emissions indicates that the study area was a sink (8.2 Tg C yr⁻¹). NBP of the study area, which is the more heavily forested half of the state, compensated for \sim 52% of Oregon's fossil carbon dioxide emissions of 15.6 Tg Cyr⁻¹ in 2000. The Biscuit Fire in 2002 reduced NBP dramatically, exacerbating net emissions that year. The regional total reflects the strong east-west gradient in potential productivity associated with the climatic gradient, and a disturbance regime that has been dominated in recent decades by commercial forestry.

Keywords: carbon balance, carbon flux, respiration, net primary production, carbon stocks, soil carbon, carbon allocation, conifer forests

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Introduction

Interest in quantifying carbon flux over large geographical areas has increased in recent years in relation to science questions concerning the changing global carbon cycle and policy issues associated with the United Nations Framework Convention on Climate Change and the Kyoto Protocol (US Carbon Cycle Science Plan, 1999; IPCC, 2001). The North American Carbon Program emphasizes the need for both 'bottomup' approaches that use various levels of observations

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and ecosystem models, and 'top-down' approaches that use atmospheric data and inverse models to resolve carbon stocks and fluxes across North America. In the latter, spatial and temporal patterns in the atmospheric CO₂ concentration have been used to infer continental carbon fluxes (Denning *et al.*, 1996; Bosquet *et al.*, 2000), and methods are being developed to perform higher resolution inversions of atmospheric data collected during regional campaigns (Denning *et al.*, 2003). In contrast, bottom-up approaches to large area flux estimation take advantage of information from remote sensing, distributed meteorology, and terrestrial ecosystem observations. Carbon flux scaling is achieved by

application of a spatially distributed ecosystem process model, thus the mechanisms accounting for fluxes are generally discernable.

Understanding the complexity of the carbon cycle and the linkages to physical, biogeochemical, and ecological processes and human influences requires a comprehensive research strategy and a new level of scientific integration (USCCSP, 1999). Efforts are underway to compare bottom-up and top-down approaches to minimize uncertainty in estimates through improvements in methods and structure of both approaches. In this study, we describe results of a bottom-up C flux scaling approach applied in Western Oregon.

The iterative model development and testing required for model-based scaling of carbon pools and flux has often been limited to one type of data set (e.g. inventory aboveground wood production), but a spatially nested hierarchy of observations (Wu, 1999) provides the opportunity for building data-derived parameterization into models, and to test various levels of complexity in model output (e.g. seasonality). Each measurement has its strengths and weaknesses, but the combination of multiple measurements and modeling has the potential for refining estimates of carbon stocks and fluxes across regions.

Historically, experiments on leaf-level physiology and soil processes have provided information to develop mechanistic understanding that is incorporated into simulation models used for scaling carbon fluxes. However, there was generally no way to test model integration of processes. Recently, micrometeorological techniques and instrumentation have improved such that near continuous measurements allow quantification of net ecosystem exchange (NEE) of carbon dioxide, water vapor, and energy from vegetated surfaces. The measurements represent longitudinal length scales of 100-2000 m (Schmid, 1994), and they are useful for quantifying fluxes at daily, weekly, and monthly time scales, for example, to test model logic in photosynthesis, and respiration and the integrated flux, NEE.

Intensive chronosequence studies have proved useful for understanding forest dynamics over longer time frames (Gholz *et al.*, 1985; Acker *et al.*, 2002). A notable observation with regard to many even-aged temperate zone forests is a decline in aboveground wood production (net primary production (NPP)_{Aw}) in late succession (Gower *et al.*, 1996; Ryan *et al.*, 1997, 2004). Incorporating this understanding into dynamic simulation models means special attention to carbon allocation during stand development and to stand-level properties such as mortality (Thornton *et al.*, 2002; Bachelet *et al.*, 2003; Law *et al.*, 2003).

At a much broader scale, forest inventories at the stand level provide information on stemwood biomass and species composition at many locations, which can also be used to test simulated changes in wood mass over the inventory cycle (typically 5–10 years). There are many plots (e.g. thousands in a state), but the suite of measurements is small. A level of sampling intensity that has been missing from regional analyses is intermediate between intensive sites and inventories, where key parameters are measured such as foliar and soil C and N, coarse woody debris (CWD), and litter mass. Some of the data are needed to initialize models, and other data such as NPP and necromass are needed to test model output at many locations.

The Pacific Northwest US has a strong climatic gradient from the Pacific coast to coastal and Cascade mountain ranges and the Great Basin on the east side of the mountains. Precipitation ranges from 2500 at the Coast to 300 mm in the dry interior over a relatively short distance of about 250 km. The inland region typically experiences drought during the growing season, which limits carbon uptake and respiration (Irvine & Law, 2002). The productivity gradient in the region is large; forests in Oregon cover a range of productivity that is representative of the range observed in the rest of the US (Waring & Running, 1998), from the highest biomass and productivity forests on the west side of the mountains to the semi-arid woodlands and shrublands on the east side of the mountains. The forests are noted for the age that they can attain, and there has been intense political interest in forest management activities (FEMAT, 1993; USDA & USDI, 1994). These characteristics, combined with different disturbance regimes such as logging intensities east and west of the Cascade Mountains, provide an interesting laboratory for examining the range of carbon stocks and fluxes that exist in the region. Thus, the region is a high priority politically and scientifically.

The objectives of this paper are to use a spatially nested hierarchy of observations to initialize, test, and apply a biogeochemistry model, Biome-BGC across the forested region of Oregon, and to determine the relative influence of ecoregional differences in climate and disturbance regime on carbon stocks and fluxes of these forests.

Methods

Overview

The goal of our regional project, Terrestrial Ecosystem Research and Regional Analysis – Pacific Northwest (TERRA-PNW), is to quantify and understand the carbon budget of Oregon's forests. The study area is

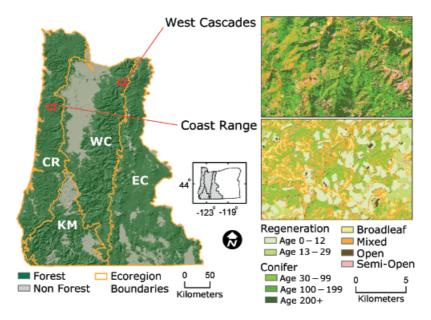


Fig. 1 Land cover of Western Oregon with expansion of areas showing conifer age class distributions, one heavily managed area as in the Coast Range ecoregion and one with less recent disturbance in the West Cascades ecoregion. CR, Coast Range; WC, West Cascades; KM, Klamath Mountains; EC, East Cascades.

10.9 million hectares (8.2 million forested) covering all of the state of Oregon west of the 120th meridian (Fig. 1). About 60% of the forest area is public and 40% is privately owned (Powell et al., 1993). The area consists of several ecoregions used for synthesis of results - the Coast Range to the west (CR), West Cascades (WC), Klamath Mountains to the south (KM), and EC.

The basic scaling approach is to develop a spatially nested hierarchy of field and remote-sensing observations (Fig. 2) that are used for parameterization and testing a biogeochemistry model, Biome-BGC, and ultimately applying the model in a spatially distributed mode. Field observations ranged from inventory data (many locations, few variables) to extensive sites, and intensive sites (chronosequences and tower flux sites, greater frequency and types of measurements, fewer locations). Some field measurements are relatively easy to make, and are needed for the wide range of vegetation types and environmental conditions. For example, the model parameters foliar C:N and specific leaf area (SLA) can be measured mid-season at many locations (extensive sites). More difficult measurements, such as maximum photosynthetic rates, were carried out at fewer intensive sites, or values were obtained from the literature. A large pool of field data is required to develop and test remote-sensing algorithms for vegetation mapping, so field observations were needed at many locations to cover the domain of application (e.g. forest type and age at inventory plots).

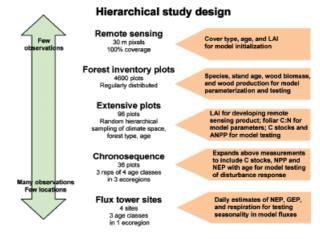


Fig. 2 Hierarchical study design where a combination of field and remote-sensing observations are used to parameterize, test, and constrain the Biome-BGC model.

Details of our approach to estimating and evaluating modeled fluxes are in the following sections.

Model implementation

The primary scaling tool in our approach to estimating area wide net ecosystem production (NEP) is the Biome-BGC carbon cycle process model (Law et al., 2001a; Thornton et al., 2002). The NEP scaling methods and initial validation results for their application in Oregon have been reported previously (Turner et al., 2003, 2004; Law *et al.*, 2004). The model has a daily time step and is run over multiple years to simulate primary and secondary succession. Simulated carbon cycle processes include photosynthesis, plant respiration, heterotrophic respiration, plant carbon allocation, and plant mortality.

Information from remote sensing that is used in our spatial mode model runs includes land cover type, approximate stand age, and leaf area index (LAI) (spatial resolution 25 m). Land cover determines the set of ecophysiological and allometric constants used in the model (the EPC file); stand age determines the age to which the model simulation is run after a simulated stand initiating disturbance; and LAI strongly regulates rates of mass flux.

The meteorological inputs to the model are daily minimum temperature, maximum temperature, precipitation, humidity, and solar radiation. For this application, an 18 years (1980–1997) time series at the 1 km resolution over Western Oregon was developed with the DAYMET model (Thornton *et al.*, 1997, 2000; Thornton & Running, 1999). These data are based on interpolations of meteorological station observations using a digital elevation model and general meteorological principles. The 18-year record is long enough to include multiple El Nino-Southern Oscillation (ENSO) cycles, and thus captures one of the dominant sources on interannual climate variation in the region (Greenland, 1994).

Once the input data sets are assembled for a given point, a model 'spin-up' is conducted for 1000 + years to generate the slow turnover soil carbon pools and bring them into near steady state. For the spin-up, the 18-year climate record is repeated as needed. To account for the effects of wood residues from previous disturbances on NEP, a disturbance regime is imposed in the model runs after the spin-up such that two clearcut harvests precede the final secondary succession. In these disturbances, a specified proportion of tree carbon is transferred off site and the remainder (33%) is assumed to stay on site to decompose. The final secondary succession is run forward to the age specified by the remote sensing. The 18-year climate sequence is manipulated such that all simulations end in the last year of the time series.

Because of the computational demands of the model spin-ups, it is not possible to make an individual model run for each 25 m resolution grid cell in the study area. The 1 km resolution of the climate data is adequate to capture the effects of the major climatic gradients but our earlier studies in this region have shown that the scale of the spatial heterogeneity associated with land management (logging) is significantly less that 1 km (Turner *et al.*, 2000). Thus, for the CR, WC, and KM

ecoregions, the model was run once for each combination of cover type and age class that was present. For the EC ecoregion, where age class beyond 30 years could not be resolved, remote-sensing-based LAI values within each 1 km cell were aggregated into bins of one LAI unit, and the model was run for each bin that was present.

Remote-sensing observations of land cover, stand age

The land cover analysis resolved five primary vegetation classes. The conifer, broadleaf, and mixed classes were all >85% cover, whereas the semi-open class was 31–84% cover, and the open class <30% cover. EPC files were created for each cover type based on White *et al.* (2000) and field data collected in this and other studies (Law *et al.*, 2004).

We used remote-sensing data to estimate age classes, rather than the inventory data, to obtain complete spatial coverage for the modeling. Age classes from the inventory data were used to determine uncertainty in the remote-sensing estimates in Law *et al.* (2004). For all stands <30 years of age, the year of stand origin was based on analysis of current imagery from the Landsat Thematic Mapper + sensor and change detection analysis using additional Landsat Thematic Mapper + and Multispectral Scanner imagery from the last 30 years (Cohen *et al.*, 1995, 2002). The stands were aggregated into two classes, Regeneration 1–13 and Regeneration 14–29 and were treated as conifer for the purposes of model parameterization.

For conifer stands >29 years, the remote-sensing analysis was able to resolve three age classes for the WC, CR, and KM ecoregions - young (30-99 years), mature (100-200 years), and old (>200 years). Age classes from the inventory data were used to determine uncertainty in the remote-sensing estimates in Law et al. (2004). In the EC ecoregion, conifer stands are often composed of trees covering a range of ages and distinct age classes were not detectable with optical remote sensing. Thus all stands older than 29 years were assigned an age of 150 years. Our chronosequence study (see the section Chronosequences) suggested that NEP is relatively stable in the older age classes in the EC ecoregion. For the other cover types, a reference age of 45 years was used that reflected the limited knowledge from forest inventory data (see the section Inventory data) and the knowledge that they were >29 years old based on the change detection analysis.

Remote-sensing observations of LAI

LAI cannot be prescribed directly in the Biome-BGC model because the model is self-regulating with respect

to LAI. However, the relatively dry summers in the Pacific Northwest mean that the soil depth and associated water storage capacity along with the elevation gradients in precipitation strongly influences the maximum LAI that can be supported (Grier & Running, 1977; Waring et al., 1978). We took advantage of these close relationships by using remotely sensed LAI to estimate soil depth. Thus, an initial set of model runs was made for each cover class within each 1km grid cell (or each LAI class in the case of the EC ecoregion) using different soil depths. The relationship of increasing equilibrium LAI to increasing soil depth was used to prescribe a soil depth that resulted in an LAI matching the LAI from remote sensing (Turner et al., 2003).

To produce maps of LAI, spectral regressions of remote-sensing reflectances to field measured LAIs were developed using the 36 chronosequence plots and 60 additional extensive plots (details in the following sections). Polygons were digitized around each of the plots in reference to 2001 Landsat ETM + scenes to ensure that a homogenous region was being referenced. Both the tasseled-cap indices and the normalized difference vegetation index (NDVI) were calculated from the ETM + mosaic and stepwise multiple regressions were used to determine the best set of variables for predicting LAI. For the western side of the study area, the resulting equation using the brightness and wetness indices raised explained 80% of variance (RMSE 1.67). For the East Cascades ecoregion, the resulting equation using only wetness explained 82% of variance (RMSE 0.74).

Model evaluation

Model performance was compared with observations at multiple scales. Daily and weekly fluxes were evaluated with flux tower observations. Annual estimates of NPP or stemwood production were compared with a variety of field observations including data from 36 chronosequence plots, 60 extensive plots, and 4600 inventory plots in Western Oregon. Annual model output for NEP was compared with estimates using a biometric approach at the 36 chronosequence plots.

Flux tower data. Carbon dioxide, water vapor, and energy fluxes were estimated from micrometeorological measurements using the eddy covariance technique at the Metolius ponderosa pine old (OS) and initiation stage (YS) flux sites in 2000–2001 (Anthoni et al., 2002; Law et al., 2003). Flux systems were comprised of threeaxis sonic anemometers that measured wind speed and virtual temperature (Solent model 1012 R2, Gill instruments, Lymington, UK; CSAT-3 Campbell Scientific Inc., Logan, UT, USA), open-path infrared gas analyzers that measured concentrations of water vapor and CO₂ (LI-7500, LI-COR, Lincoln, NE, USA), and a suite of software data processing. Fluxes were averaged half-hourly, and the records in the database were evaluated for data quality. Details on the instrumentation, flux correction methods, calculations were reported in Anthoni et al. (2002). Half-hourly measurements of climatic variables made at the top of the flux towers included air temperature $(T_{\rm air}),$ vapor pressure deficit (D),incident photosynthetically active radiation (PAR), and rainfall. The continuous meteorological measurements were used in Biome-BGC simulations with the same parameterization used in the regional runs to determine how well the model integrated processes seasonally.

Chronosequences. Biometric methods were used to quantify NPP and NEP at 36 independent forest plots arranged as three replicates of four age classes in each of three climatically distinct forest types, hemlock-Sitka spruce in the CR, Douglas-fir in the WC, and ponderosa pine in the EC ecoregions. Forest ages ranged from 10 to 800 years.

We measured tree and shrub dimensions, age and growth increment from wood cores, LAI, herbaceous plant biomass, coarse and fine woody detritus, forest floor fine litter mass, soil C and N, and annual fine litter fall. On four 10 m radius subplots within each 100 m × 100 m plot, height and diameter were measured on all trees >5 cm DBH. The smaller trees were included in the shrub survey. Increment cores from five trees per subplot were used to determine 5year mean growth increment, stand age, and wood density. Shrub dimensions and herbaceous plant biomass were measured on 1-2 m radius microplots at each subplot center in all stands. In the youngest stands, dimensions were measured on all trees and shrubs on the subplots.

LAI was determined with optical measurements made with an LAI-2000 at 39 points regularly stratified throughout each plot, and corrected for wood interception and clumping within shoot and scales larger than shoot using our own or published shoot clumping factors by species, and TRAC measurements of gap-fraction along two 100 m transects within each plot (3rd Wave Engineering, Ontario, Canada). Details of calculations are in Law et al. (2001b).

Carbon stocks in live and dead biomass pools were calculated using local or site-specific allometric equations for above- and belowground components, including stumps, coarse roots, and standing dead trees. These observations were used to characterize variation in carbon stocks with stand age and position along the climatic gradient. Wood NPP was calculated as the change in biomass and foliar NPP was from litter fall measurements. Fine root production was calculated for each plot as fine root mass multiplied by fine root turnover, which was measured with minirhizotrons in pine stands (0.60 year⁻¹, Law *et al.*, 2001a) and obtained from the literature for other forest types within each ecoregion. NEP was calculated following the methods described in Law *et al.* (2003):

$$NEP = (ANPP - R_w) + (\Delta C_{FR} + \Delta C_{CR} + \Delta C_S - L), (1)$$

where ANPP is the aboveground NPP (foliage and wood of understory vegetation and overstory trees), $R_{\rm w}$ is the respiration from woody debris (decomposition of coarse and fine woody debris (FWD), stumps, and snags), $\Delta C_{\rm FR}$ is the net change in fine root C (not different from zero in this study), $\Delta C_{\rm CR}$ is the difference between the net growth of live coarse roots and the decomposition of coarse roots attached to stumps, $\Delta C_{\rm S}$ is the net change in mineral soil C (not different from zero), and L is the annual litter fall. Measurement uncertainty associated with each component was propagated through to NEP with Monte Carlo stochastic uncertainty estimation (Law *et al.*, 2003; M. Harmon, Oregon State University, personal communication).

Interannual variation in stemwood production (NPP_{Aw}) was estimated for the period of 1981–2000 at the chronosequence plots to determine the effect of interannual variation in climate on wood production in stands of three contrasting age classes (young, mature, and old), and to evaluate simulated variation in wood production. The estimates were based on the annual radial increment and wood density of the increment cores. The radial growth of remaining trees on each plot was estimated allometrically based on plot-specific relationship between radial growth and tree DBH. Stemwood NPP and carbon mass were computed based on the plot-specific wood density and site- and speciesspecific allometric relationships between stemwood volume, total tree height, and DBH (Law et al., 2003, 2004).

Extensive plots. To characterize variation in key characteristics across Oregon's forests that are not measured in forest inventories, we established 60 additional plots using a hierarchical random sampling design that allowed maximum representation of forest types that exist in the region, the age classes present, and the climate space. This resulted in the selection of 10 areas with six stands of different ages in each area. A single visit to the plots provided data on soil C and N and texture to 1 m depth, canopy C and N (at least six shoots per species per plot), litter mass, CWD and

FWD, maximum LAI, live biomass, and aboveground productivity for the range of environmental conditions and forest types. LAI, age, and forest type were used to develop and test remote-sensing algorithms, foliar C:N, and SLA were used for model input, and ANPP and biomass were used to test model output.

Inventory data. We used data from the Forest Inventory and Analysis program (900 FIA plots; http://www. fs.fed.us\fia, USDA, 2001) on non-federal lands and Current Vegetation Survey data (3700 CVS plots; http://www.fs.fed.us\r6\survey) from federal forest lands. Both inventory programs use a systematic sampling design. Basic forest characteristics (species, diameter, height, age) are remeasured on approximately 10-year intervals. We determined biomass from species and ecoregion-specific volume equations and wood density from our 96 plots and published data (USDA Forest Service, 1965; Maeglin & Wahlgren, 1972; Forest Products Laboratory, 1974), where some of the data were from 850 of the FIA plots. Biomass values were converted to carbon using 50% carbon content. Within each plot, trees with measured radial growth were split into DBH quartiles and a mean radial growth for each quartile was assigned to trees without increment measurements. NPPAw was computed from the difference between biomass of the previous and most recent measurement cycle (CVS plots measured 1993 and 1997, FIA plots measured 1995 and 1997). Inventory data were used to evaluate modeled biomass and NPP_{Aw}, and to develop and test remote-sensing algorithms for vegetation type and age. Note that only fuzzed locations ($\pm 1 \,\mathrm{km}$) were available for the inventory plots when doing comparisons with model outputs, so the model value used in a comparison was that representative of the 1km grid cell in which the specified location fell.

Regional C balance estimation

To develop a carbon budget for the study area, we determined the 5-year (1993–1997) mean NEP for each 25 m grid cell from the model simulations. Two small areas had to be estimated separately. In the Northwest corner of the CR ecoregion, an area of 1208 km² could not be modeled because persistent clouds prevented acquisition of an ETM+ image in 2001. This area represented 3% of the CR ecoregion and the forested area was assigned an NEP equivalent to the mean value of the forested land in the CR. A small area in the southeast corner of the EC ecoregion (7% of the total EC area) was also not modeled and was similarly assigned the mean value for the ecoregion.

The other terms in the carbon budget relate to logging and fire. For logging, we estimated carbon

removed from the landscape using harvest statistics from the Oregon Department of Forestry (ODF). ODF reports the volume harvested per year at the county level in terms of board feet (http://www.odf.state. or.us/DIVISIONS/resource_policy/resource_planning/ Annual Reports/). These data for the period 1995–2000 were converted to C using a factor of 4.3 board feet per cubic foot (Lettman & Campbell 1997) and 6818 g C ft⁻³ or $243.4 \,\mathrm{kg}\,\mathrm{C}\,\mathrm{m}^{-3}$ (Turner *et al.*, 1995a). For counties on the eastern edge of the study area that were not completely included in the study area, the area harvested per year was determined from the remotesensing-based change detection and that area was multiplied by the average C removed per unit area in that county (data from the ODF statistics).

To estimate the net gain in C stored in slow turnover pools we referred to the analysis of Harmon et al. (1996). That study accounted for C transfers during the manufacturing process, the proportion of the harvest going into specific products, the turnover time of those products, and the turnover time of the residues that ended up in land fills. The analysis covered the period from 1900 to 1990. They concluded that in the early 1990s there was a disequilibrium (i.e. a net accumulation) equivalent to about 25% of the contemporary harvest in Oregon and Washington. We applied this value to our harvest removals to estimate the C sink associated with forest products.

The flux of carbon from the land to the atmosphere that is driven by wildfire was relatively low during the late 1990s in our study area. Average area burned from 1995 to 2000 from the remote-sensing-based change detection analysis was 1116 ha yr⁻¹. In stark contrast, the Biscuit Fire in 2002 in Southwest Oregon covered 150 000 ha. We estimated C emissions associated with each of the seven fires between 1995 and 2000 by using the relevant ecoregional mean values for vegetation + litter C and assuming that an average of 50% of fuels were consumed and there was complete combustion (Hardy et al., 1996; Schuur et al., 2003). Fuel loads are the major source of variation in emissions (McKenzie et al., 2002), so the combustion estimate is highly uncertain. However, the contribution of 1995-2000 fire emissions to the regional C flux turned out to be relatively small in any case. A preliminary estimate of the amount of carbon released during the Biscuit Fire was made by multiplying age class-specific estimates of preburn carbon pools (proportioned by the age class distribution in the fire area) by estimates of burn severity-specific combustion efficiencies for each pool (proportioned by the distribution burn severity within the fire). Live preburn carbon pools (bole, branch, and foliage) were estimated from over 200 FIA plots that were in the burn area, while dead preburn carbon pools

(soil carbon, forest floor, FWD, and CWD) were estimated from six of our extensive plots located near the fire. Burn severity-specific combustion factors for each carbon pool were approximated from visual estimates and preliminary data from Bernard Bormann (USDA Forest Service Research, Long-Term Ecosystem Productivity Program; Gray, 1998; Homann et al., 1998). Of these, the most important factors were the near complete combustion of the forest floor, and live foliage, partial combustion of the soil A horizon, and a 1-10% combustion of bole wood and CWD, depending on fire severity. The frequency of burn severity within the Biscuit Fire was determined from the Burn Area Emergency Response (BAER; http://www.biscuitfire. com/facts.htm).

Results and discussion

Land cover and LAI

The total study area was about 10.9 million hectares, and about 75% of the land was forested (Fig. 1). Of the forested area, conifers dominate land cover at 77%, while 4% was deciduous, 12% mixed forest, 2% open area, and 5% semi-open (Fig. 3). In comparing land cover/land use in the WC, CR, and KM ecoregions, it is evident that there is a larger proportion of the area in young stands in the Coast Range and more old-growth forests in the West Cascades (Fig. 3). There is poor differentiation of age classes in the EC, largely due to past management practices (e.g. high-grade logging), disturbance history (fire exclusion), and the open nature of the forest canopies. The remote-sensing change detection analysis found 14% of forest land in the EC ecoregion to be <29-year old. The mixed age structure is confirmed with field observations at the chronosequence and extensive plots.

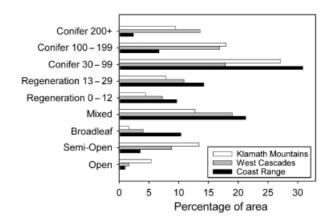


Fig. 3 Percent of land cover area by ecoregion and age class.

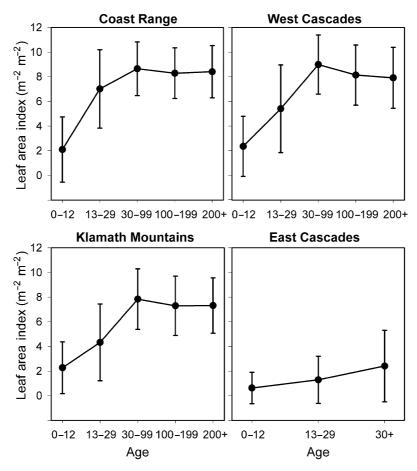


Fig. 4. Leaf area index (LAI; m² leaf m⁻² ground) by ecoregion and age class. Values are means and standard deviations from estimates based on remote sensing.

The remote-sensing estimates of LAI increased with stand age until maturity, averaging $8\,\text{m}^2\,\text{m}^{-2}$ (one-sided LAI) in mature stands of the more mesic ecoregions (CR, WC, KM), and $2\,\text{m}^2\,\text{m}^{-2}$ in the EC ecoregion (Fig. 4). The mean values within an age class did not differ much except in EC, which had a much broader age class definition (30 + years for oldest age class because of difficulty in identifying older stands in the open canopy).

Model evaluation

Comparison of modeled and measured daily fluxes. The modeled gross ecosystem production (GEP) and NEP were compared with daily fluxes from three sites in different age stands in the EC ecoregion to determine how well the model performed seasonally. The early analyses at the old pine site showed that the model was overestimating evapotranspiration, so the parameterization of stomatal conductance was adjusted to improve the comparisons with water vapor exchange. Subsequently, modeled daily GEP and NEP compared

well with measurements at the young pine site in 2002, with no apparent seasonal bias (Fig. 5). There, the model explained 87% of the seasonal variation in weekly GEP and 67% of the variation in weekly NEP.

Ecoregional differences in production. As noted, land cover in the study area is predominantly coniferous forest. The key features of the regional climate that favor the evergreen coniferous growth habit are mild wet winters and dry summers (Waring & Franklin, 1979). Deciduous species – notably red alder (Alnus rubra) – are common in the relatively mesic Coast Range ecoregion but are restricted to riparian areas in the other ecoregions. The dominant conifer tree species shifts from Douglas-fir west of the Cascade crest to Ponderosa Pine east of the crest.

Despite the uniform physiognomy of the forest cover in the region, strong environmental gradients generate significant variation in production potential (Gholz, 1982). In the FIA data and the Biome-BGC simulations, we found strong responses to the east–west climatic gradient (Fig. 6). Very negative leaf water potential

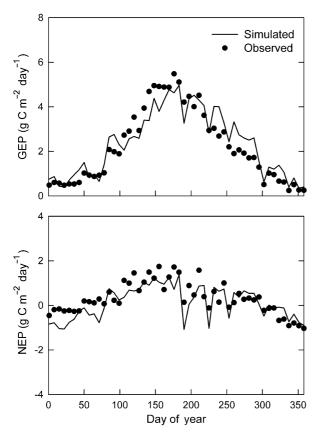


Fig. 5 Weekly eddy flux (points) vs. modeled (lines) gross ecosystem production (GEP) and net ecosystem production (NEP) at the Metolius young ponderosa pine site in 2002.

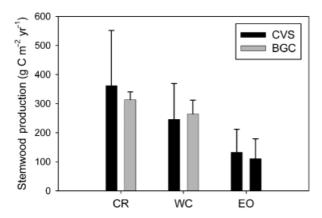


Fig. 6 Ecoregion differences in NPP $_{\!\mathrm{Aw}}$ for 100–200-year stands. Mean and standard deviation from inventory plots and comparable model simulations. Sample sizes are 266 for West Cascades (WC), 156 for Coast Range (CR), and 595 for the EC.

towards the end of the growing season in much of the area except the Coast Range suggests that water constraints are a primary driver of the production differences in these areas (Law & Waring, 1994; Runyon et al., 1994; Williams et al., 1997).

Besides the strong signals in the climate data and remotely sensed LAI, the model simulations were improved by incorporating results from our extensive plots. There were significant differences among the ecoregions in the foliar C:N ratio and SLA across the 96 plots (Law et al., 2004), so the foliar data were used to formulate unique ecophysiological parameterizations for the conifer class in each ecoregion. The relatively low foliar C: N ratio in the CR ecoregion is a function of the higher soil N there, and when used in the model, it helped to correctly simulate a relatively high NPP. For the complete set of extensive plots, the regression of simulated to measured ANPP values showed reasonably good agreement (y = 0.93x + 36, $R^2 = 0.82$, Law et al., 2004).

Age-specific changes in NEP and allocation. The chronosequence NEP data show a general pattern of a strong carbon sink in young to mature stands, and less of a sink or a small source in old stands (Fig. 7). In the WC, the old stands with relatively large CWD pools were sources. The C source expected in the youngest stands of the chronosequences was only apparent in the EC ecoregion; presumably the rapid recovery of LAI and NPP in the other ecoregions meant that the sampled stands had already passed through their postdisturbance period as a C source (the youngest stands in the chronosequences were 12 and 13-year old in the CR and WC, and 9-year old in the EC). Model results show the expected sequence for early development to mature stands, but the simulations predict that old stands are nearly carbon neutral over

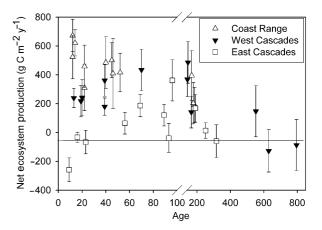


Fig. 7 Biometric estimates of net ecosystem production from chronosequences in three climatically distinct ecoregions. Error bars are 1 standard deviation from Monte Carlo simulations of uncertainty in net ecosystem production components.

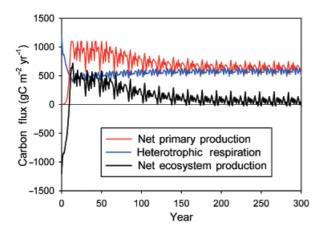
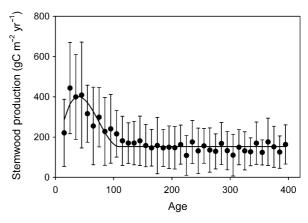


Fig. 8 The generic pattern for model simulations of net primary production, heterotrophic respiration, and net ecosystem production over succession.

the 18-year climate time series (Fig. 8). A mismatch between model and field estimates of NEP in older stands of the CR and EC ecoregions is consistent with previous studies (e.g. Law *et al.*, 2001a; Thornton *et al.*, 2002), and it suggests that model assumptions about stand structure are too simplistic. Patchy disturbances through stand development may result in a multi-age structure and stand dynamics that are not accounted for in the modeling, for example, changes in resource use efficiency and tree dominance (see Binkley, 2003). The agreement between measured and modeled NEP for the set of chronosequence plots was poor $(y = 0.55x + 99, R^2 = 0.37, Law \ et \ al., 2004)$ but it reflects relatively high uncertainty in both measured and modeled values.

A clear feature that emerges from the FIA estimates of NPP_{Aw} is a significantly lower wood production in late succession in the CR and WC ecoregions (Fig. 9). This trend is consistent with observations in a wide variety of forest types; however, the mechanisms accounting for the trend are unclear (Binkley *et al.*, 2002). Initial model simulations showed only a 10–20% decline in NPP_{Aw}, and to more closely approximate the FIA observations, it was necessary to introduce an algorithm to the Biome-BGC model that allowed for dynamic allocation (Law *et al.*, 2004). The new algorithm increased belowground allocation in late succession. There are several theories for why this trend in allocation might occur (e.g. Gower *et al.*, 1996; Ryan *et al.*, 2004).

The FIA data in the drier ecoregions, KM and EC, did not display the same decrease in NPP $_{\rm Aw}$ in late succession, hence the dynamic allocation algorithm was not implemented in those simulations. As noted, the relatively open nature of those stands permits multi-age class distributions, and belowground allocation is



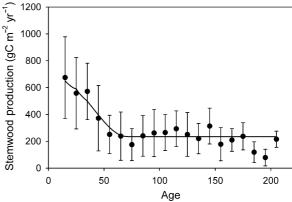


Fig. 9 Trends in above ground wood production (NPP $_{\rm Aw}$) with stand age for the Coast Range (top) and West Cascades (bottom) ecoregions.

relatively high in young stands compared with old stands in the dry regions, presumably to quickly develop roots for acquisition of the limited water (Law *et al.*, 2003).

Another feature evident in the FIA data but that did not correspond with the model assumptions was the treatment of mortality. In the conifer cover class, mortality was fixed at 1% of live tree biomass per year in the Biome-BGC modeling. Surveys of the FIA data and the literature (e.g. Waring & Schlesinger, 1985; DeBell & Franklin, 1987; Acker *et al.*, 2002) suggest that mortality varies with stand age and that these changes in mortality have a strong influence on C stocks and flux. These observations support the introduction of dynamically varying mortality into the model, something that was not done for this study but will be investigated in the future.

Interannual variation. Our 20-year tree ring analyses from the chronosequence plots indicate a 60% difference in bole wood production between years with low and high values (Fig. 10). The young stands show a similar pattern but it is overlain on a trend of

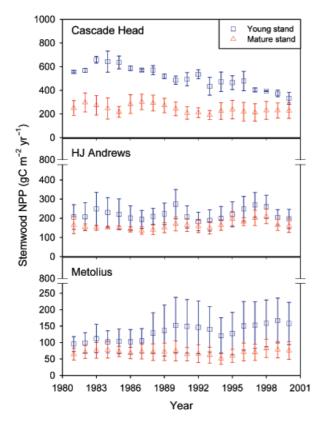


Fig. 10 Interannual differences in aboveground wood production (NPP_{Aw}) over the past 20 years for young and mature stands from the three chronosequences using wood increment cores.

increasing (semi-arid EC) or decreasing (mesic CR) NPP_{Aw}. Interannual variation in modeled NPP_{Aw} is as large as that of the observations (Fig. 8), but the modeled NPP_{Aw} anomalies are not well correlated with the observed NPPAw anomalies. The correlations of bolewood growth to obvious climate indices such as annual precipitation and growing degree days, whether direct or lagged, were weak. Studies of tree rings in western conifers at high elevation (Ettl & Peterson, 1995) have found more consistent relationships because of the strong influence of snow on the growing season. A regional study over a network of Douglas-fir plantations also found weak correlations of climate indices to stand growth (Peterson & Heath, 1990). Additional research on interannual variation in production is needed to gain the predictive power relevant to assessing potential climate change effects on regional NPP.

The interannual variation in modeled NEP over 18 years of our climate record was large, with NEP varying from -80 to $+190 \,\mathrm{g}\,\mathrm{C}\,\mathrm{m}^{-2}\,\mathrm{yr}^{-1}$ for a representative old-growth stand in the vicinity of the WC chronosequence (Turner et al., 2003). In that simulation, the NPP varied to a greater degree than

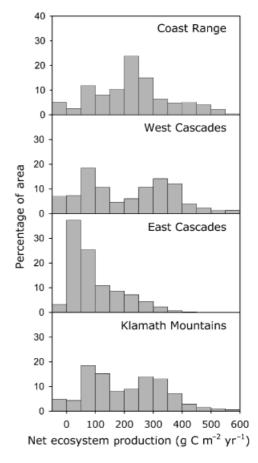


Fig. 11 Frequency distributions for 5 years mean net ecosystem production in each ecoregion.

the heterotrophic respiration (Fig. 8), the opposite of suggestions from some eddy covariance studies (e.g. Barford et al., 2001). Eddy covariance data from the Metolius old pine flux site in EC ecoregion indicated that NEP varied more than 100% over three climatically distinct years, and more of the variation was in respiration than GEP (Law et al., 2001a, this study).

NEP distributions among ecoregions

The distributions of NEP by ecoregion (Fig. 11) indicate that most of the land in Western Oregon was accumulating carbon in the late 1990s, a pattern consistent with observations in many forest regions (Law et al., 2002). For all ecoregions, less than 8% of the forested land was a C source. The highest mean NEP among the ecoregions was in the CR ecoregion $(226 \,\mathrm{g}\,\mathrm{C}\,\mathrm{m}^{-2}\,\mathrm{yr}^{-1})$, which also has a relatively high stemwood production rate (Fig. 6) and a high proportion of stands in the 30-99-year age class (Fig. 3). The mean NEP in the EC ecoregion was low $(88 \,\mathrm{g}\,\mathrm{C}\,\mathrm{m}^{-2}\,\mathrm{yr}^{-1})$ because of the semi-arid conditions

Table 1 Model estimates of carbon stocks and fluxes

| Ecoregion | Annual Rh $(g C m^{-2} yr^{-1})$ | Annual NPP (g C m ⁻² yr ⁻¹) | Annual NEP (g C m ⁻² yr ⁻¹) | Soil C (Mg C ha ⁻¹) | Necromass* (Mg C ha ⁻¹) | Live mass [†] (Mg C ha ⁻¹) | Total C stocks (Mg C ha ⁻¹) |
|-------------------|----------------------------------|---|---|------------------------------------|--|---|--|
| Coast Range | 445 | 672 | 226 | 118.0 315.1 (114) | 45.9 78.1 (52) | 164.1 180.5 (141) | 328.1 |
| West Cascades | 511 | 700 | 189 | 142.4 170.5 (78) | 48.8 58.7 (45) | 196.8 185.8 (129.6) | 388.1 |
| East Cascades | 275 | 356 | 88 | 111.9 70.6 (24) | 49.5 27.7 (20) | 128.6 66.2 (43.4) | 290.0 |
| Klamath Mountains | 450 | 640 | 190 | 128.0 119.6 (40) | 38.4 32.2 (17) | 181.8 172.6 (115.8) | 348.1 |

Values are means by ecoregion. Estimates of soil C to 1 m depth and aboveground necromass from extensive plots are shown as the second value, and the second value for live C stocks is based on inventory, extensive plot, and chronosequence data. Standard deviations are in parentheses.

*Sum of CWD and litter from model, and sum of CWD, FWD, standing dead, stumps, and litter from field observations at extensive plots (second value).

[†]Sum of live tree bole, branch, bark, coarse root, fine root, and foliage biomass. Field estimates (second value) are from forest inventory plots (FIA and CVS). Field estimates of bole, branch, bark, and coarse root biomass are based on allometric relationships applied at the tree level. Field estimates of fine root and foliage biomass are based on relationships with plot-level leaf area index developed from extensive plots and chronosequences.

NPP, net primary production; NEP, net ecosystem production; CWD, coarse woody debris; FWD, fine woody debris; FIA, Forest Inventory and Analysis; CVS, Current Vegetation Survey.

that limit growth and decomposition, and the large area in older, low NEP stands. WC and KM have mixed age class distributions and moderate climates, and thus had intermediate mean NEP values (189 and $190 \,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$, respectively).

Carbon budget for the region

Total carbon stocks in live and dead C pools was 2765 Tg $(1\,\mathrm{Tg}=10^{12}\,\mathrm{g})$ over the study area (Table 1), with a higher mean value in the WC ecoregion $(388\,\mathrm{Mg}\,\mathrm{C}\,\mathrm{ha}^{-1})$ and the lowest value in the EC ecoregion $(290\,\mathrm{Mg}\,\mathrm{C}\,\mathrm{ha}^{-1})$. Soil carbon accounted for 37% of the total. Mean live C was relatively high in the WC and KM ecoregions reflecting the larger proportion of those ecoregions in older age classes.

Comparisons of mean live tree C from the modeling and the field measurements showed good agreement (i.e. within 10%) except for the EC ecoregion. There, the assumed age of 150 years for all stands greater than the 30 years (as determined by change detection) led to an overestimate of live tree C. This was also the case for necromass. The low bias in the modeled necromass for the CR and WC ecoregions relates to the assumption in the modeling that two rotations occur before the run up to the specified stand age. The high CWD associated with the initial conversion from old growth to secondary forest tends to be reduced during these rotations. This assumption is more appropriate for private lands than for public lands and indeed the

Table 2 Mean land carbon budget for Western Oregon (1995–2000, 8.2 million forested hectares), where NEP is net ecosystem production, and NBP is net biome production on the land taking into account removals from harvest and fire

| Total NEP | 13.8 Tg C |
|------------------|-------------|
| Harvest removals | -5.5 |
| Fire | -0.1 (-4.1) |
| NBP | 8.2 (4.2) |
| | |

Values in parentheses are for 2002.

NEP, net ecosystem production; NBP, net biome production.

modeled estimate for mean CWD carbon in the CR and WC ecoregions (20.52 Mg ha⁻¹) was close to an estimate of 22.48 Mg C ha⁻¹ for 867 FIA plots in Douglas-fir stands on private land in Western Oregon (K. Waddell, USDA Forest Service, personal communication). The model results missed the relatively high soil C in the CR ecoregion (Homann *et al.*, 1998) but the mechanisms accounting for that spatial pattern are not well understood and thus are likely not included in the model algorithms.

Average NEP over the forested part of the study area was $168\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$, which is close to the Pacific Northwest regional value from Turner *et al.* (1995a), and the European-wide forest NEP estimate of $185\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ (Papale & Valentini, 2003). Total NEP over the forested part of the study area was $13.8\,\mathrm{Tg\,C\,yr^{-1}}$ (Table 2).

Approximately 50% of all of Oregon's forest land has been managed for timber in the past 5 years (Smith et al., 2001). The average annual harvest removals from the study area over the period 1995-2000 were 5.5 Tg C yr⁻¹. The removals were disproportionately from the Coast Range, which is heavily managed for timber production. The annual increase in C stored in longlived forest products and land fills was 1.4 Tg C yr Emissions from wildfire were very low over 1995-2000, only $0.1 \,\mathrm{Tg}\,\mathrm{C}\,\mathrm{yr}^{-1}$ from the burning of 6694 ha.

Net biome production (NBP) on the land (sensu Schulze et al., 2000) - the net effect of NEP, harvest removals, and fire emissions - indicates that the study area was a sink of 8.2 Tg C yr⁻¹ (Table 2), compensating for 52% of Oregon's fossil carbon dioxide emissions of 15.6 Tg C yr⁻¹ in 2000 (Oregon Department of Energy, 2003). Large areas of the EC are also forested but were not included in this analysis for logistical reasons. Once they have been treated, it will be possible to make the kind of state-wide analyses needed for state-level reports on greenhouse gas emissions (Oregon Department of Energy, 2003).

In the years following 2000, wildfires were a significant carbon source. The Biscuit Fire in the KM ecoregion in 2002, for example, covered over 150 000 ha (Sessions et al., 2003). Fire severity estimates for that fire have been made by the Burn Area Emergency Response (BAER; http://www.biscuitfire.com/facts.htm) but the proportion of aboveground biomass and litter that was combusted in different severity classes has not been fully characterized. Our preliminary estimate of carbon emissions from the Biscuit Fire was 4.1 Tg C. This reduced the net gain of carbon by Western Oregon forests to 4.2 Tg C, compensating for about 25% of Oregon's fossil CO₂ emissions that year. The fires add a significant amount of dead material (e.g. ~50% mortality area weighted average on the Biscuit Fire) for decomposition over decades. Throughout the western US, 100 years of fire suppression has resulted in relatively high fuel accumulations in dry coniferous forests and more large fires can be expected (Agee, 1993).

In the near future, the region will likely take up less carbon compared with years prior to the Biscuit Fire because wildfires often leave a large proportion of the tree stemwood carbon unburned and thus the burn areas can remain carbon sources for a decade or more. In addition, it is expected that because of the severity of the fire and low survival of the former old forests that developed in the cooler climate of the 1700s, the forests will likely be replaced with shrubs and invasive weeds with lower sequestration potential for a very long time (Sessions et al., 2003). If the proposed salvage logging follows wildfire, it will potentially impair ecosystem recovery (Lindenmayer et al., 2004) and

result in further removal of stored carbon in standing dead trees. Salvage could accelerate decomposition of wood depending on lifespan of the products and waste produced in manufacturing (Cohen et al., 1996).

Over a small area in the West Cascades, earlier studies that used an accounting model and remote sensing to estimate changes in the sum of live stocks, dead stocks and wood product stocks suggested a carbon source $(113 \,\mathrm{g}\,\mathrm{C}\,\mathrm{m}^{-2}\,\mathrm{yr}^{-1})$ in the Cascades from 1970 to 1985 (Cohen et al., 1996), and a transition to a small sink in the early 1990s (Wallin et al., in press). Our results support a continuation of this trend resulting in a stronger C sink in the late 1990s. The increase in sink strength is related to continued decreases in the area harvested on public lands and to the fact that the conversion of private lands to secondary forests is nearly complete. Much of the sustained C source in the 1900s was associated with converting the region from predominantly old-growth forests to Douglas-fir plantations (Harmon et al., 1990; Bolsinger & Waddell, 1993; Garman et al., 1999).

Analyses of regional NEP and NBP in the US, based primarily on forest inventories (Turner et al., 1995a; Birdsey & Heath, 1995), found that the Northeast region of the United States is also a significant carbon sink, largely because of carbon sequestration in trees on lands that were formerly agricultural. The carbon sinks in the Pacific Northwest and Northeast regions of the US are consistent with inverse modeling results that suggest a large North American terrestrial sink in the 1990s (Pacala et al., 2001; Bosquet et al., 2000).

The terrestrial sink in US forests is estimated to offset a significant proportion (10–30%) of the carbon source associated with US fossil fuel emissions (Houghton et al., 1999), more than the terrestrial offset for Europe (7–12%; Janssens et al., 2003). However, fossil fuel emissions grew at a rate of over 1% per year in the 1990s and continue to rise. Carbon stocks on private lands in the US are expected to decrease in coming decades with continued intensification of management (Turner et al., 1995b) but the current sink on public lands is likely to be maintained as the large areas clearcut in the 20th century move into high NEP age classes.

With the modeling infrastructure developed for this analysis, it will be possible to assimilate new land cover/land use data from remote sensing and updated distributed climate data from meteorological station interpolations. Thus, it will be possible to carefully monitor the regional forest carbon sink and to evaluate gradual responses to changing land use and climate variation or change. As this bottom-up approach to monitoring net carbon uptake comes to cover larger domains, it will help provide constraints on estimates from inverse modeling.

Conclusions

A hierarchy of observations including intensive flux sites, extensive sites with an intermediate level of variables (~ 100 sites), inventory sites with few measurement variables (1000s), and remote-sensing data can be used to improve process models and provide reliable estimates of carbon stocks in vegetation and soils, and annual carbon source and sink distributions in terrestrial ecosystems across a region. The mean distribution of stocks and fluxes in a recent five year period (1995–2000) shows the following patterns: (1) most of the land area in Western Oregon was accumulating carbon in the late 1990s, and the highest mean NEP among the ecoregions was in the more mesic Coast Range, which has relatively high stemwood production and a high proportion of stands in the 30-99-year age class, (2) the highest mean C stocks are in the West Cascades ecoregion, which is not managed primarily for timber production, (3) the NBP, accounting for losses from harvest and fire, indicated the study area in 1995-2000 was a sink that compensated for $\sim 50\%$ of Oregon's carbon dioxide emissions, and (4) large wildfires such as the Biscuit Fire in 2002 can significantly affect the forest C sink for specific years and reduce carbon uptake in subsequent years because of decomposition of the remaining debris; this would likely be exacerbated by salvage logging of remaining trees that store carbon and facilitate recovery from disturbance. These studies stress the importance of quantifying and understanding carbon stocks and fluxes over the long term, and the need to evaluate management options that take into account the consequences of carbon removals in harvests, wildfires, and fuels reduction activities including recovery following disturbance.

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References

- Acker SA, Halpern CB, Harmon ME *et al.* (2002) Trends in bole biomass accumulation, net primary production and tree mortality in *Psuedotsuga menziesii* forest of contrasting age. *Tree Physiology*, **22**, 213–217.
- Agee JK (1993) Fire Ecology of Pacific Northwest forests. Island Press, Washington, DC.
- Anthoni PM, Unsworth MH, Law BE et al. (2002) Seasonal differences in carbon and water vapor exchange in young and old-growth ponderosa pine ecosystems. Agricultural and Forest Meteorology, 111, 203–222.
- Bachelet D, Neilson RP, Hickler T *et al.* (2003) Simulating past and future dynamics of natural ecosystems in the United States. *Global Biogeochemical Cycles*, **17**, 1–21.
- Barford CC, Wofsy SC, Goulden ML et al. (2001) Factors controlling long- and short-term sequestration of atmospheric CO₂ in a mid-latitude forest. Science, 294, 1688–1691.
- Binkley D (2004) A hypothesis about the interaction of tree dominance and stand production through stand development. *Forest Ecology and Management*, **190**, 265–271.
- Binkley D, Stape JL, Ryan MG *et al.* (2002) Age-related decline in forest ecosystem growth: an individual tree, stand-structure hypothesis. *Ecosystems*, **5**, 58–67.
- Birdsey RA, Heath LS (1995) Carbon changes in U.S. forests. In: Climate Change and American Forests. USDA Forest Service, General Technical Report RM-GTR-271 (ed. Joyce L.A.), pp. 56–70. USDA Forest Service, Rocky Mountain Range and Experimental Station, Ft. Collins, CO.
- Bolsinger CL, Waddell KL (1993) Area of old-growth forests in California, Oregon and Washington. Resource Bulletin, PNW-RB-197.
- Bosquet P, Peylin P, Ciais P *et al.* (2000) Regional changes in carbon dioxide fluxes of land and oceans since 1980. *Science*, **290**, 1342–1346.
- Cohen WB, Harmon ME, Wallin DO et al. (1996) Two decades of carbon flux from forests of the Pacific Northwest. BioScience, 46, 836–844.
- Cohen WB, Spies TA, Alig RJ *et al.* (2002) Characterizing 23 years (1972–95) of stand replacement disturbance in Western Oregon forests with Landsat imagery. *Ecosystems*, **5**, 122–137.
- Cohen WB, Spies TA, Fiorella M (1995) Estimating the age and structure of forests in a multi-ownership landscape of Western Oregon, U.S.A. *International Journal of Remote Sensing*, 16, 721–746.
- DeBell DS, Franklin JF (1987) Old-growth Douglas-fir and western hemlock: a 36 years record of growth and mortality. Western Journal of Applied Forestry, 2, 111–114.
- Denning AS, Collatz JG, Zhang C *et al.* (1996) Simulations of terrestrial carbon metabolism and atmospheric CO₂ in a general circulation model. Part 1: surface carbon fluxes. *Tellus*, **48B**, 521–542.
- Denning S, Nichols M, Prihodko L *et al.* (2003) Simulated variations in atmospheric CO₂ over a Wisconsin forest using a couple ecosystem–atmosphere model. *Global Change Biology*, **9**, 1241–1250.

- Ettl GJ, Peterson DL (1995) Growth response of subalpine fir (Abies lasiocarpa) to climate in the Olympic Mountains, Washington, USA. Global Change Biology, 1, 213-230.
- Forest Ecosystem Management Assessment Team (FEMAT) (1993) Forest ecosystem management: an ecological, economic, and social assessment - report of the Forest Ecosystem Management Assessment Team. USDA, USDI, US Department of Commerce, and Environmental Protection Agency, Portland, OR.
- Forest Products Laboratory (1974) Wood handbook: wood as an engineering material. Forest Products Laboratory Report 72, Madison, WI.
- Garman SL, Swanson FJ, Spies TA (1999) Past, present, future landscape patterns in the Douglas-fir region of the Pacific Northwest. In: Forest Fragmentation: Wildlife and Management Implications (eds Rochelle JA, Lehmann LA, Wisniewski J), pp. 61-86. Brill Academic Publishing, the Netherlands.
- Gholz HL (1982) Environmental limits on aboveground net primary production, leaf area, and biomass in vegetation zones of the Pacific Northwest. Ecology, 63, 469-481.
- Gholz HL, Perry CS, Cropper WP et al. (1985) Litterfall, decomposition, and nitrogen and phosphorus dynamics in a chronosequence of slash pine (Pinus elliottii) plantations. Forest Science, 31, 463-478.
- Gower ST, McMurtrie RE, Murty D (1996) Above ground net primary production decline with stand age: potential causes. Trends in Ecology and Evolution, 11, 378-382.
- Gray J (1998) Testing two applications of image analysis for use in species-independent biomass equations for western Oregon forests. MS thesis, Oregon State University, Corvallis, OR.
- Greenland D (1994) The Pacific Northwest regional context of the climate of the HJ Andrews Experimental Forest. Northwest Science, 69, 81-95.
- Grier CC, Running SW (1977) Leaf area of mature northwestern coniferous forests: relation to site water balance. Ecology, 58, 893-899.
- Hardy CC, Burgan RE, Ottmar RD et al. (1996) A database for spatial assessments of fire characteristics, fuel profiles, and PM10 emissions. CRB Landscape Ecology Stars Report, Chapter 19B.
- Harmon ME, Ferrell WK, Franklin JF (1990) Effects on carbon storage of conversion of old-growth forests to young forests. Science, 247, 699-7002.
- Harmon ME, Harmon JM, Ferrell WK et al. (1996) Modeling carbon stores in Oregon and Washington forest products: 1900–1992. Climate Change, 33, 521–550.
- Homann PS, Sollins P, Fiorella M (1998) Regional soil organic carbon storage estimates for western Oregon by multiple approaches. Soil Science of America Journal, 62, 789-796.
- Houghton RA, Hackler JL, Lawrence KT (1999) The U.S. carbon budget: contribution from land use change. Science, **285**, 574–578.
- IPCC: Albritton DL, Meira Fillo LG, the WGI writing team (2001). WGI-Technical Summary. In: Climate Change 2001: Synthesis Report (ed Watson RT). Geneva, Switzerland (http:// www.ipcc.ch).
- Irvine J, Law BE (2002) Contrasting soil respiration in young and old-growth ponderosa pine forests. Global Change Biology, 8, 1183-1194.

- Janssens IA, Freibauer A, Ciais P et al. (2003) Europe's terrestrial biosphere absorbs 7 to 12% of European anthropogenic CO₂ emissions. Science, 300, 1538-1542.
- Law BE, Falge E, Baldocchi DD et al. (2002) Carbon dioxide and water vapor exchange of terrestrial vegetation in response to environment. Agricultural and Forest Meteorology, 113, 97-120.
- Law BE, Sun O, Campbell J et al. (2003) Changes in carbon storage and fluxes in a chronosequence of ponderosa pine. Global Change Biology, 9, 510-524.
- Law BE, Thornton P, Irvine J et al. (2001a) Carbon storage and fluxes in ponderosa pine forests at different developmental stages. Global Change Biology, 7, 755-777.
- Law BE, Turner DP, Lefsky M et al. (2004) Carbon fluxes across regions: observational constraints at multiple scales. In: Scaling and Uncertainty Analysis in Ecology: Methods and Applications (eds Wu J, Jones B, Li H, Loukes O), Columbia University Press, New York, USA.
- Law BE, Van Tuyl S, Cescatti A et al. (2001b) Estimation of leaf area index in open-canopy ponderosa pine forests at different successional stages and management regimes in Oregon. Agricultural and Forest Meteorology, 108, 1-14.
- Law BE, Waring RH (1994) Combining remote sensing and climatic data to estimate net primary production across Oregon. Ecological Applications, 4, 717–728.
- Lettman GJ, Campbell D (1997) Timber Harvesting Practices on Private Forest Land in Western Oregon. Oregon Department of Forestry, Salem, OR.
- Lindenmayer DB, Foster DR, Franklin JF et al. (2004) Salvage harvesting policies after natural disturbance. Science, 303, 1303
- Maeglin RR, Wahlgren HE (1972) Western wood density survey: report number 2. USDA Forest Service Research Paper FPL-183.
- McKenzie D, Larkin S, O'Neill S, Ferguson S, Sandberg D (2002) Carbon emissions from fire: effects of fuel loadings on variability. GOFC/GOLD-Fire Programmatic presentation, 17-19 July 2002, University of Maryland, College Park, MD.
- Oregon Department of Energy (2003) Report on reducing Oregon's greenhouse gas emissions. http://www.energy.state. or.us/climate/finalb-c.htm.
- Pacala SW, Hurtt GC, Baker D et al. (2001) Consistent land- and atmosphere-based U.S. carbon sink estimates. Science, 292,
- Papale D, Valentini R (2003) A new assessment of European forests carbon exchanges by eddy fluxes and artificial neural network spatialization. Global Change Biology, 9, 525-535.
- Peterson CE, Heath LS (1990) The influence of weather variation on regional growth of Douglas Fir stands in the U.S. Pacific Northwest. Water, Air, and Soil Pollution, 54, 295-305.
- Powell DS, Spanner MA, Running SW et al. (1993) Forest resources of the United States, 1992. United States Department of Agriculture Forest Service, Rocky Mountain Forest and Range Experiment Station, GTR RM-234.
- Runyon J, Waring RH, Goward SN et al. (1994) Environmental limits on net primary production and light use efficiency across the Oregon transect. Ecological Applications, 4, 226-237.
- Ryan MG, Binkley D, Fownes JH (1997) Age-related decline in forest productivity: pattern and process. Advances in Ecological Research, 27, 213-262.

- Ryan MG, Binkley D, Fownes JH *et al.* (2004) An experimental test of the causes of forest growth decline with stand age. *Ecological Monographs* (in press).
- Schmid HP (1994) Source areas for scalars and scalar fluxes. *Boundary Layer Meteorology*, **67**, 293–318.
- Schulze E-D, Wirth C, Heimann M (2000) Managing forests after Kyoto. Science, 289, 2058–2059.
- Schuur EAG, Trumbore SE, Mack MC et al. (2003) Isotropic composition of carbon dioxide from a boreal fire: inferring carbon loss from measurements and modeling. Global Biogeochemical Cycles, 17, 1001, doi:10.1029/2001GB001840.
- Sessions J, Buckman R, Newton M et al. (2003) The Biscuit Fire: management options for forest regeneration, fire, and insect risk reduction and timber salvage. College of Forestry, Oregon State University. http://www.cof.orst.edu/cof/admin/Biscuit% 20Fire%20Report.pdf.
- Smith WB, Vissage JS, Sheffield R et al. (2001) Forest resources of the United States, 1997. General Technical Report NC-219, US Department of Agriculture, Forest Service, North Central Research Station, St Paul, MN, 109 pp.
- Thornton PE, Hasenauer H, White MA (2000) Simultaneous estimation of daily solar radiation and humidity from observed temperature and precipitation: an application over complex terrain in Austria. Agricultural and Forest Meteorology, 104, 255–271.
- Thornton P, Law BE, Ellsworth DA et al. (2002) Modeling the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests. Agricultural and Forest Meteorology, 113, 185–222.
- Thornton PE, Running SW (1999) An improved algorithm for estimating incident daily solar radiation from measurements of temperature, humidity, and precipitation. *Agricultural and Forest Meteorology*, **93**, 211–228.
- Thornton PE, Running SW, White MA (1997) Generating surfaces of daily meteorological variables over large regions of complex terrain. *Journal of Hydrology*, **190**, 214–251.
- Turner DP, Cohen WB, Kennedy RE (2000) Alternative spatial resolutions and estimation of carbon flux over a managed forest landscape in western Oregon. *Landscape Ecology*, 15, 441–452.
- Turner DP, Guzy M, Lefsky M *et al.* (2003) Effects of land use and fine scale environmental heterogeneity on net ecosystem production over a temperate coniferous forest landscape. *Tellus*, **55B**, 657–668.
- Turner DP, Guzy M, Lefsky M *et al.* (2004) Monitoring forest carbon sequestration with remote sensing and carbon cycle modeling. *Environmental Management* (in press).

- Turner DP, Koerper GJ, Harmon ME et al. (1995a) A carbon budget for forests of the conterminous United States. Ecological Applications, 5, 421–436.
- Turner DP, Koerper GJ, Harmon ME *et al.* (1995b) Carbon sequestration by forests of the United States: current status and projections to the year 2040. *Tellus*, **47B**, 232–239.
- US Carbon Cycle Science Plan (1999) A report of the carbon and climate working group. (Co-chairs Sarmiento JL, Wofsy SC) http://www.carboncyclescience.gov
- USDA Forest Service (1965) Western wood density survey: report number 1. USDA Forest Service Research Paper FPL-27.
- USDA Forest Service (2001) Forest inventory and analysis national core field guide. Vol. 1: Field Data Collection Procedures for Phase 2 Plots, Version 1.5. US Department of Agriculture, Forest Service, Washington Office. Internal report. On file with: US Department of Agriculture, Forest Service, Forest Inventory and Analysis, Washington, DC.
- USDA and USDI (1994) Final supplemental environmental impact statement on management of habitat for late-successional and old-growth forest related species within the range of the northern spotted owl (Northwest Forest Plan). Portland, OR. http://www.fs.fed.us/r5/nwfp/plans/sus.shtml
- Wallin DO, Harmon ME, Cohen WB (2004) Modeling regionalscale carbon dynamics in Pacific Northwest forests: 1972–95. In: Carbon Dynamics of Two Forest Regions: Northwestern Russian and the Pacific Northwest (eds Krankina O, Harmon ME). Springer-Verlag, New York (in press).
- Waring RH, Emmingham WH, Gholz HL *et al.* (1978) Variation in maximum leaf area of coniferous forests in Oregon and its ecological significance. *Forest Science*, **24**, 131–139.
- Waring RH, Franklin JF (1979) Evergreen forests of the Pacific Northwest. Science, 204, 1380–1386.
- Waring RH, Running SW (1998) Forest Ecosystems Analysis at Multiple Scales. Academic Press, San Diego, CA, USA.
- Waring RH, Schlesinger WH (1985) Forest Ecosystems Concepts and Management. Academic Press, Orlando, USA.
- White JD, Thornton P, Running SW et al. (2000) Parameterization and sensitivity analysis of the Biome-BGC terrestrial ecosystem model: Net primary production controls. Earth Interactions 4, Paper No. 3. 85 pp.
- Williams ME, Rastetter EB, Fernandes DN et al. (1997) Predicting gross primary productivity in terrestrial ecosystems. Ecological Applications, 7, 882–894.
- Wu J (1999) Hierarch and scaling: extrapolation information along a scaling ladder. Canadian Journal of Remote Sensing, 25, 367–380.