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Effects of land use and fine-scale environmental heterogeneity on net ecosystem production over a temperate coniferous forest landscape

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ABSTRACT

In temperate coniferous forests, spatial variation in net ecosystem production (NEP) is often associated with variation in stand age and heterogeneity in environmental factors such as soil depth. However, coarse spatial resolution analyses used to evaluate the terrestrial contribution to global NEP do not generally incorporate these effects. In this study, a fine-scale (25 m grid) analysis of NEP over a 164-km^2 area of productive coniferous forests in the Pacific Northwest region of the United States was made to evaluate the effects of including fine scale information in landscape-scale NEP assessments. The Enhanced Thematic Mapper (ETM+) sensor resolved five cover classes in the study area and further differentiated between young, mature and old-growth conifer stands. ETM+ was also used to map current leaf area index (LAI) based on an empirical relationship of observed LAI to spectral vegetation indices. A daily time step climatology, based on 18 years of meteorological observations, was distributed (1 km resolution) over the mountainous terrain of the study area using the DAYMET model. Estimates of carbon pools and flux associated with soil, litter, coarse woody debris and live trees were then generated by running a carbon cycle model (Biome-BGC) to a state that reflected the current successional status and LAI of each grid cell, as indicated by the remote sensing observations. Estimated annual NEP for 1997 over the complete study area averaged 230 g C m^{-2}, with most of the area acting as a carbon sink. The area-wide NEP is strongly positive because of reduced harvesting in the last decade and the recovery of areas harvested between 1940 and 1990. The average value was greater than would be indicated if the entire area was assumed to be a mature conifer stand, as in a coarse-scale analysis. The mean NEP varied interannually by over a factor of two. This variation was 38% less than the interannual variation for a single point. The integration of process models with ground surface information provided by remote sensing provides a framework for investigating mechanisms regulating NEP and evaluating coarse resolution globally applied NEP scaling efforts.

1. Introduction

Mid-latitude forests of the northern hemisphere are currently a significant carbon sink, but the geographic distribution of the sink and the mechanisms generating it are uncertain (Fan et al., 1998; Ciais et al., 2000). The principal factors contributing to this sink include (1) those associated with land use, notably reversion of marginal agricultural lands to forestland, regrowth of harvested forests, reversion of rangeland to woodland, and fire suppression on forestland, and (2) those associated with environmental factors, including nitrogen deposition, rising atmospheric CO_2 and climate warming (Pacala et al., 2001). The northern hemisphere terrestrial sink is also subject to considerable interannual variation, the mechanisms of which are likewise poorly understood (Bousquet et al., 2000). From both policy and science perspectives, there is a need to develop improved approaches to scaling carbon cycle

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processes such that the mechanisms accounting for the terrestrial carbon sources and sinks in different regions, and their interannual variation, are understood.

A critical variable for understanding the terrestrial carbon flux is net ecosystem production (NEP), the balance of gross photosynthesis and ecosystem respiration (often calculated from biological measurements as the net primary production minus the heterotrophic respiration). NEP is sensitive to stand age, climate and local factors such as soil depth. Forest stands typically exhibit a negative NEP, i.e. act as a source of CO_2 to the atmosphere, early in succession when residues from the recent disturbance are rapidly decomposing and vegetation NPP has not recovered from the disturbance (Sprugel, 1985; Schulze et al., 2000). NEP is expected to be highest in mid-succession and to decline in late succession as the carbon pools approach a steady state. In addition to stand age effects on NEP, local environmental heterogeneity and interannual climate variation can affect NEP by disproportionately changing net primary production (NPP) and heterotrophic respiration (Rh).

Process-based biogeochemistry models represent working hypotheses about the important mechanisms regulating NEP (Ryan et al., 1996). Both prognostic models (e.g. Kicklighter et al., 1999), which are typically driven by distributed climate data, and diagnostic models (e.g. Potter et al., 1993), which employ remote sensing to characterize solar radiation absorbed by the canopy, provide insights into potential causes of the spatial and temporal patterns of terrestrial NEP inferred by inverse modeling (Fan et al., 1998). However, these analyses have generally been made at relatively coarse spatial resolutions (grid cells 10–100 km on a side) that do not account for land use and environmental heterogeneity likely influencing NEP in many forested areas (White and Running, 1994; Turner et al., 2000).

In this study, the Landsat Enhanced Thematic Mapper sensor (ETM+) with a spatial resolution of $\sim$30 m was employed to initialize a process-based carbon cycle model and examine the sensitivity of simulated landscape-scale NEP to the inclusion of high spatial resolution satellite data. Relatively high spatial resolution climate and soils data were used in the simulation as well. The study was conducted in the Pacific Northwest region of the US, which is of particular interest with regard to the carbon cycle because of the large pools of carbon in biomass, the high productivity of the forests and the large impacts of management in recent decades (Cohen et al., 1996). Earlier work has suggested that spatial resolution of $\leq$250 m is desirable for assessing spatial patterns in land cover and NEP in this region (Cohen et al., 1995; Turner et al., 2000).

2. Methods

2.1. Overview

A biogeochemistry process model (Biome-BGC) was applied over a 25 m grid covering a 164-km^2 area of managed coniferous forests in western Oregon. Model initiation required land cover classification, stand age and a reference leaf area index (LAI), all of which were provided by satellite remote sensing. The model was driven with a distributed daily climatology. Model outputs included NPP, Rh and NEP.

2.2. Study area

The study area surrounds the H.J. Andrews Experimental Forest (HJA) within the Willamette National Forest in the state of Oregon. The climate is temperate, with wet winters and dry summers. Mean annual precipitation at the Headquarters meteorological station is 227 cm and mean annual temperature is 8.2 °C. The dominant conifer species are Douglas fir (*Psuedotsuga menziesii*) western hemlock (*Tsuga heterophylla*) and western redcedar (*Thuja plicata*).

2.3. Land cover

Land cover for the study area was determined by updating a previously published land cover map for 1988 (Cohen et al., 1998; 2001; 2002). In the creation of the 1988 map, satellite imagery was first used to develop continuous (0–100%) data layers for total foliage cover and conifer cover. These data layers were the basis for creating five forest classes (Open: total cover $<$30%; Semi-open: 30% $<$ total cover $<$ 70%; Deciduous: total cover $>$ 70% and conifer cover $<$ 30%; Mixed: total cover $>$ 70% and 30% $<$ conifer cover $<$ 70%; Conifer: total cover and conifer cover $>$ 70%). There were also non-forest (primarily urban and agricultural lands) and water classes based on information from National Land Cover coverages (Vogelmann, 1998). In all, land cover mapping was performed over an area that included much of western Oregon; the area around HJA was subset for this study.

In the initial phase of the updating procedure, an analysis of changes associated with stand replacement disturbance was performed using Landsat ETM+ imagery from the years 1988 and 2000. With the year 2000 imagery, the reflectances in each of the seven individual Landsat scenes covering the area of interest (Rows 28, 29 and 30 for Paths 45 and 46, and Row 28 for Path 47) were first transformed using the "tasseled-cap" method of Crist and Cicone (1984). The tasseled-cap transformation is a series of three indices, specifically designed for use with Landsat images, which summarizes spectral variation. It is intended to enhance the vegetation components of imagery, generally by contrasting them against soil and background components. The corresponding tasseled-cap image for 1988 was then obtained from the LARSE (Laboratory for Applications of Remote Sensing in Ecology, Oregon State University) archive, to create a difference image. As in Cohen et al. (1998), iterative unsupervised classification was used to define change and no-change classes by visual inspection.

To apply the original 1988 classification to the areas that had changed, the 2000 imagery was first radiometrically normalized to the 1988 image employing the ridge regression procedure (Song et al., 2001), using only those areas that had been classified, in the previous analysis step, as "no-change". Ridge regression is a technique used to match the spectral qualities of two scenes by comparing their values in the area in which they overlap. Before land cover could be classified, the 2000 data had to be further transformed to duplicate the underlying variables used in creating the 1988 classification, namely green cover and conifer cover. To ensure that 2000 values for these variables matched those for 1988, new regressions between the three tasseled cap spectral vegetation indices (brightness, greenness and wetness) from the 1988 images and the 1988 estimates of green cover and conifer cover (percent) were performed for each scene. The resulting equations were then applied to the year 2000 tasseled-cap images and changed areas were classified. Results from an independent verification of the final cover map (using aerial photography) indicate better than 80% accuracy in predicting the five forest cover classes.

For the purposes of initializing the biogeochemistry model (see below) a representative stand age was needed. Cohen et al. (2001) concluded that Landsat-TM could only estimate age accurately in the conifer class, and had created continuous estimates of conifer age for the 1988 land cover map (Cohen et al., 2001).

Table 1. *Landsat ETM+ cover types in the study area*

Cover type	Area (km^2)	Representative age
Open	2.2	8
Semi-open	28.3	20
Conifer, Young	15.5	65
Conifer, Mature	37.2	150
Conifer, Old growth	41.4	400
Closed mixed forest	34.7	30
Deciduous forest	4.0	50
Other	0.7	–
Total	164	

These were aggregated to three conifer age classes [young (30–100 yr), mature (101–200 yr) and old (>200 yr)], and this information was carried over to the year 2000 land-cover map. Representative ages for these classes were set to the mid-points of their age ranges. Representative ages for the open, semi-open, mixed and deciduous classes (Table 1) were approximated from aged reference stands (Cohen et al., 1995; Turner et al., 2000).

2.4. *Leaf area index*

Leaf area index (LAI, half total leaf surface area) values were measured on 76 plots, each 100 × 100 m, at 13 locations broadly distributed throughout western Oregon (hierarchical random sampling design). All plots were georeferenced using a high-resolution Global Positioning System instrument (Trimble Navigation Ltd, Sunnyvale, CA). The measurements of LAI were made with a LAI-2000 (LICOR, Lincoln, NE) in diffuse light conditions, and corrected for leaf clumping within shoots, clumping at scales larger than shoot, and wood interception (Chen, 1996; Law et al., 2001a). Clumping within shoots was determined by taking into consideration the species composition of the stand and the clumping factors for individual conifer species found in the literature (Law et al., 2001a; Gower et al., 1999; Frazer et al., 2000). Clumping at scales larger than shoot was determined from optical measurements with a TRAC device (3rd Wave Engineering, Ontario, Canada) along two 100 m transects on each plot (Law et al., 2001a). Wood interception was calculated as half total surface area of stems and branches.

A single mosaic of Landsat ETM+ was created from six scenes using the ridge regression procedure

(Song et al., 2001). After the images were assembled, a dark-object subtraction was performed to remove atmospheric effects, following the conclusions of Turner et al. (1999). Polygons were hand-digitized around each of the plots in the Landsat ETM+ imagery to ensure that a homogenous region was used in the comparison of spectral characteristics and LAI. Both the tasseled-cap indices and the normalized difference vegetation index (NDVI) were calculated from the resulting mosaic and stepwise multiple regressions were used to determine the best set of variables for predicting LAI. The same equation was then used across all cover types to generate a LAI data layer.

2.5. *Meteorological data*

The distributed meteorological data used to drive the model was from 18 yr (1980–1997) of daily meteorological observations at a network of sites around the conterminous United States. The meteorological station data were interpolated to a 1 km grid using the DAYMET program (Thornton et al., 1997; Thornton and Running, 1999; Thornton et al., 2000). The resulting database included daily maximum and minimum temperature, precipitation, daytime average solar radiation and daytime average vapor pressure deficit. The gridded data were compared with meteorological observations made near the H.J. Andrews Headquarters (HJA, 2001).

2.6. *Model application*

Biome-BGC is a daily time-step biogeochemistry model with physiologically based algorithms for photosynthesis, autotrophic respiration and heterotrophic respiration (Running and Hunt, 1993; Thornton, 1998; Thornton et al., 2002). A set of ecophysiological constants, e.g. maximum stomatal conductance, is prescribed for each forest cover type (White et al., 2000). In this study, all cover types except the deciduous class were run as conifer. The major carbon compartments, or pools, include leaves and fine roots as well as bole, coarse roots, coarse woody debris (CWD), litter and two classes of soil organic matter.

To establish the initial conditions for those pools, a model "spin-up" is run. The soil carbon pools are brought into approximate equilibrium with the local climate during this thousand-year model run. In the spin-up, the 18-yr climate time series was run repeatedly.

Because most stands in the PNW region originated from catastrophic disturbances (Wallin et al., 1996), two successive disturbances were simulated at the end of each spin-up such that 1/3 of the live tree carbon was transferred to the CWD pool at each disturbance (Turner et al., 1995). The disturbances were 90 yr apart for all forest classes except the shorter-lived deciduous forest, where the interval was 60 yr. The model was then run forward in a final "succession run" to the representative stand age indicated by the remote sensing classification (Table 1). This brought the simulated live tree, CWD, litter and soil carbon pools into agreement with the stand age.

To bring simulated LAI into agreement with the reference remote sensing-based LAI, spin-ups were run at a range of soil depths. Potential LAI in PNW conifer forests is closely related to water availability (Grier and Running, 1977) and hence to soil depth (which influences soil water holding capacity). The model is self-regulating with respect to LAI, so increasing soil depth tends to result in an increase in the maximum achievable LAI. Thus, by running the spin-up process at a series of soil depths in each cell of the climate grid, a range of potential LAIs was generated (Fig. 1). Soil texture was first specified from Kern et al. (1997), where data layers for % sand, silt and clay were developed from the State Soil Geographic (STATSGO) database and the US National Soil Characterization Database. Soil depth was then assigned based on the best agreement between the simulated LAI and the remote sensing based reference LAI. To limit the number of computationally intensive spin-ups, a mean LAI per cover type (cover class by age class combination, Table 1) was determined for each 1 km cell and used as the reference LAI for that cover type and that cell. Then

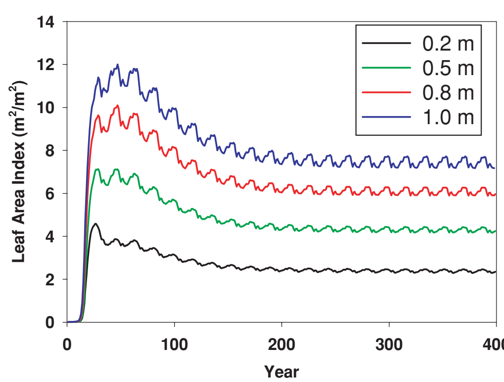

Fig. 1. Effect of alternative soil depths on simulated LAI.

all 25 m grid cells of that cover type were assigned the same soil depth based on the multiple spin-ups. In the case of the relatively young age classes (open and semi-open), which may not have reached their maximum LAI, soil depth was set to the value derived by Kern et al. (1997). The young stand age then limits the achieved LAI and tends to generate agreement with the remote sensing based reference LAI. The root mean square error for the reference LAI generated by remote sensing and the model generated LAI was 0.6 m^2 m^{-2} over the complete study area.

For development of the base year 1997 NEP data layer, the climate files were structured such that the year when the stand reached its representative age was the 1997 meteorological year. To examine interannual variation in NEP, while controlling for all vegetation factors, the meteorological data for each of the other 17 yr was successively substituted for the 1997 data at the end of the base year run.

3. Results

The land cover in the study area (Fig. 2a) is predominantly coniferous forest. Sixty-nine percent of the area is closed canopy conifer forest, and much of the remainder is land recovering from previous disturbance (Table 1). The land-cover map reveals distinct patchiness, with polygons corresponding primarily to areas clear-cut for timber harvest since 1940.

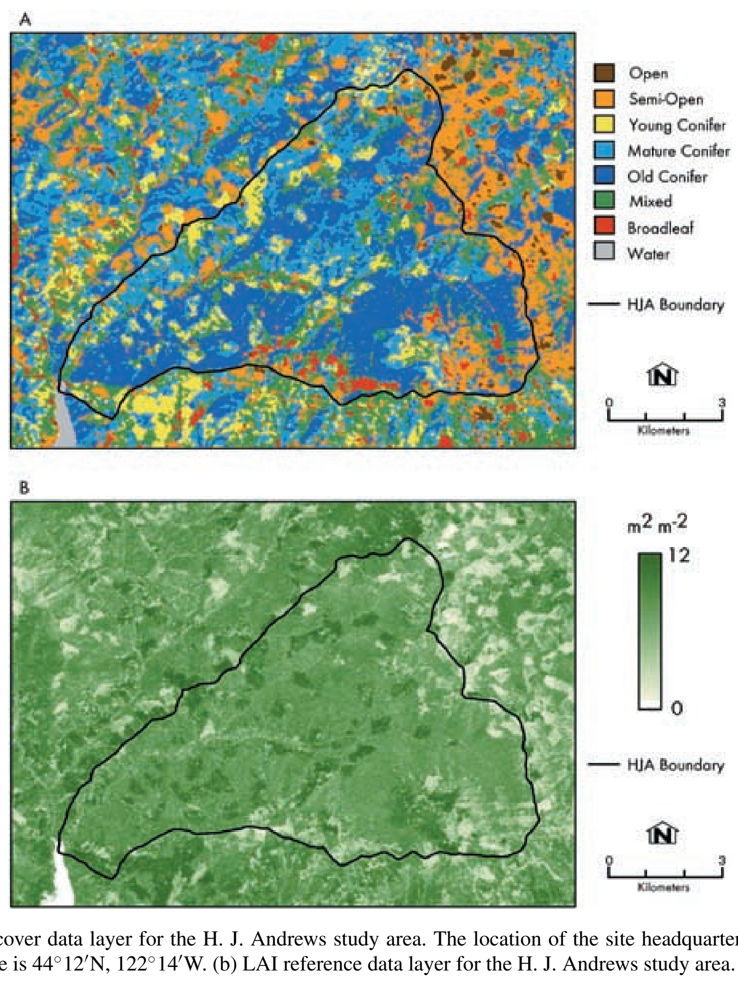

Fig. 2. (a) Land cover data layer for the H. J. Andrews study area. The location of the site headquarters in the lower left corner of the figure is 44°12′N, 122°14′W. (b) LAI reference data layer for the H. J. Andrews study area.

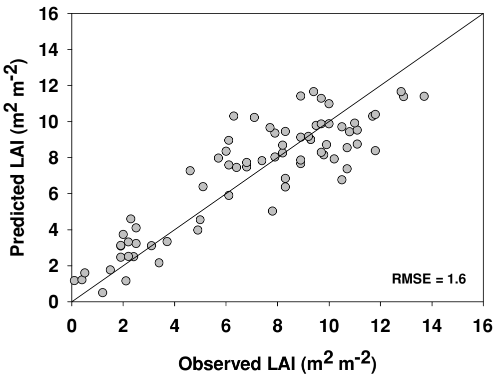

Fig. 3. Observed and predicted LAI for the LAI measurement plots. The one-to-one line is indicated.

Nineteen percent of the study area is in the open and semi-open classes, which are predominantly recent clear cuts. Twenty-seven percent of the land is old-growth conifer forest.

The optical measurements of LAI corrected for clumping and wood interception resulted in values ranging from 0.2 to 12.6 $m^2\ m^{-2}$. The best-fit equation relating measured LAI to ETM+ reflectances used the brightness and wetness indices and explained 80% of variance. Most of the error was at LAI > 5.0 (Fig. 3), where variation in LAI has little effect on simulated NEP. The range of LAI estimates extended to 12 $m^2\ m^{-2}$, in agreement with the optical measurements and with maximums recently measured in other Cascade forests (Thomas and Winner, 2000). Mean LAI within a cover type increased from Open, to Semi-open to Young Conifer then decreased in the oldest classes (Fig. 4). The remote sensing based LAI data

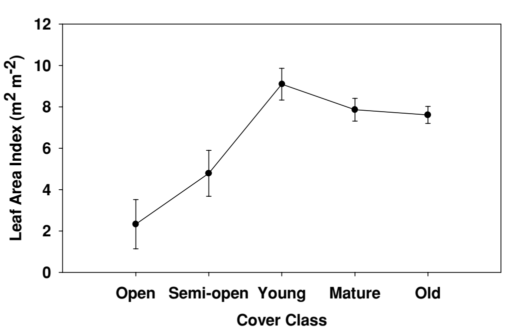

Fig. 4. Mean (and standard deviation) of leaf area index as determined from remote sensing by cover class. The Open and Semi-open classes are early stages in the conifer succession.

layer (Fig. 2b) revealed patchiness associated with previous clear cuts.

Meteorological observations at HJA (not used in creation of the gridded data) indicated a mean annual temperature over the 18 yr within 1 °C of the value from the interpolated meteorological data. Mean annual precipitation from the local measurements was 16% greater than that for the interpolated data.

Simulated successional trends in NPP and Rh for a mid-elevation (950 m) conifer stand indicated a large negative NEP predicted for early in succession, a cross-over from source to sink at a stand age of 10–20 yr, a maximum NEP at ages 30–50 yr, followed by a declining NEP until the old-growth stage which was nearly at carbon steady state (Fig. 5). The decline in NEP is primarily the result of a decline in NPP, which is driven by low nitrogen availability associated with decay of dead wood generated by an increasing input from mortality. The average NEP by age class over the study area was consistent with this temporal pattern (Fig. 6). For the complete study area, the average NEP for 1997 was 230 g C $m^{-2}\ yr^{-1}$ (Figs. 6 and 7).

For a mid-elevation grid cell classified as old conifer, there was a large interannual variation in NEP (Fig. 8). For the study area as a whole, the interannual variation in NEP was about a factor of two, but that range was only 62% of the range for the old conifer stand (Fig. 8). Interannual NEP values ranged from −70 to 183 gC $m^{-2}\ yr^{-1}$ at the old conifer stand, and 106 to 282 gC $m^{-2}\ yr^{-1}$ for the study area as a whole.

4. Discussion

4.1. Sensitivity of scaled NEP to fine spatial resolution input data

The large differences in mean NEP as a function of age class (Fig. 6) are indicative of the potential error if this area were modeled as one large cell with a single cover class. The prognostic NEP models are generally run to near steady state before perturbations (such as CO_2 increase) are imposed, thus their results would most likely resemble the behavior of the mid elevation old-growth stand. In that case, average NEP over the 18-yr climate time series was 56 gC $m^{-2}\ yr^{-1}$, considerably less that the 230 gC $m^{-2}\ yr^{-1}$ estimated over the study area when cover type and stand age were taken into account. Examination of coarse scale NEP estimates that do not account for land use generally

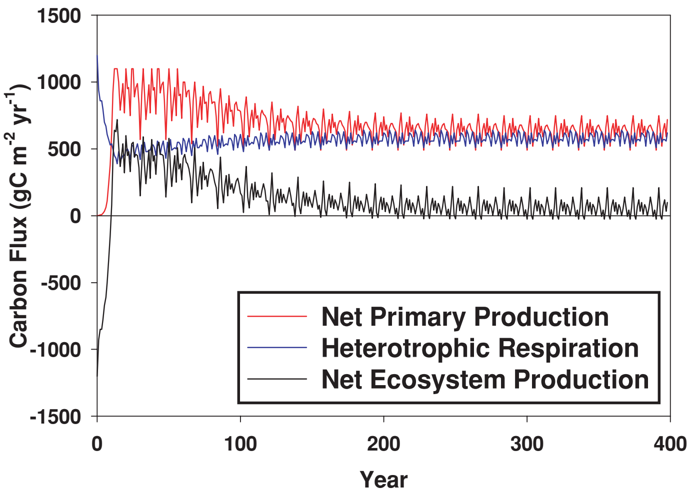

Fig. 5. Trends in net primary production, heterotrophic respiration and net ecosystem production during succession for a mid-elevation conifer stand.

show NEP values less than 50 gC m^{-2} yr^{-1} in the vicinity of the area studied here (e.g. Woodward et al., 2001).

NEP is notably high in this area because harvesting on public lands has slowed in recent decades (Fig. 9), leaving large areas in the young, high NEP, age classes (age 20–100 yr). During former periods of rapid cutting, a larger proportion of the landscape had been recently cut and was acting as a carbon source. The process of converting a landscape dominated by primary forests to one dominated by secondary forests results in a sustained carbon source to the atmosphere, even when the carbon sink associated with forest products is taken into account (Harmon et al., 1990; 1996). Federal lands in the study area are now in a phase of recovery from disturbance during the period 1940–1990, thus they are largely carbon sinks. Fire and logging need to be considered in a complete carbon budget (Turner et al., 1995; Schulze et al., 2000), but neither was significant in the 1997 reference year for the study area.

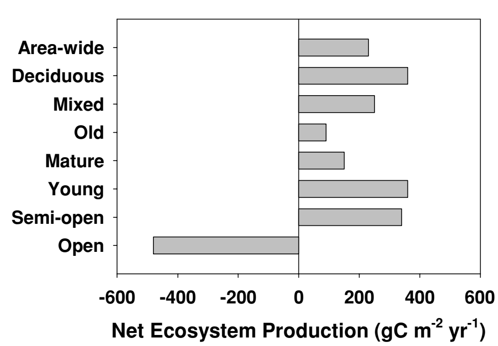

Fig. 6. Mean net ecosystem production by cover type in 1997.

The spatially explicit LAI extends the utility of the age-based land cover classification by providing information on within-class variation of a model variable that strongly influences NPP. For a variety of site quality or site history factors, many PNW forest stands are at less than full stocking. The less vigorous stands tend to have relatively low LAI (Gholz, 1982), which is likely to be detectable by remote sensing (Peterson et al., 1987).

The linkage of simulated LAI to remote sensing based LAI worked well in this study because of the strong influence of site water balance on LAI in the PNW region. In other regions, ecosystem attributes such as foliar nitrogen concentration and canopy nitrogen content [also potentially detectable by remote sensing (Martin and Aber, 1987)] are believed to be the dominant regulators of NPP. A major challenge in scaling studies is to incorporate information from remote sensing into a simulation modeling framework without compromising the model's capacity for self-regulation during simulation of stand development.

In this study, there was a tendency in the simulations to underestimate LAI in the Open class relative to the

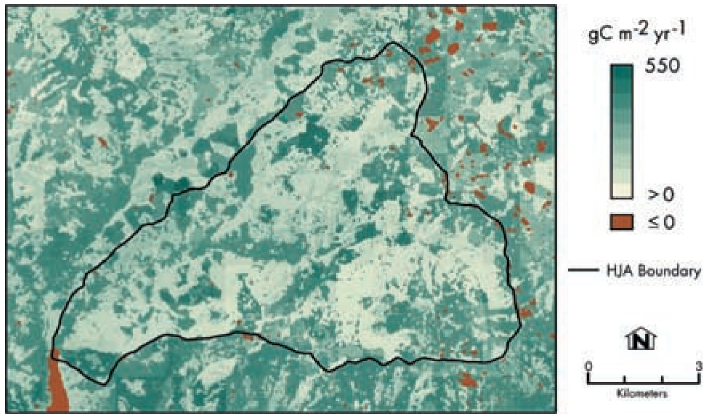

Fig. 7. Net ecosystem production for the H. J. Andrews study area in 1997.

remotely sensed reference LAI values. This discrepancy was related to a lag in simulated production after clearcuts. The heavy nitrogen demand associated with decomposition of the post-harvest residues restricted NPP and hence LAI in the model simulations. A potential approach to improving the simulations may be to assume significant nitrogen fixation early in succession, as has been widely observed in early successional PNW conifer forests (Binkley et al., 1992).

Besides the high-resolution land cover and LAI, the 1-km distributed meteorology was also beneficial to the analysis. The algorithms in Biome-BGC for photosynthesis, autotrophic respiration and heterotrophic respiration all employ non-linear temperature-based functions. Earlier analysis in this mountainous region has shown how spatial resolution influences interpolated temperatures (Turner et al., 1996). The more restricted range of temperatures at coarse resolution results in a lower range for respiration rates, with corresponding effects on NPP and NEP.

The difference in the NEP range over the 18-yr test period for a point and as an average over the study area (Fig. 8) suggests that incorporation of fine-scale data lowers sensitivity to climatic variation. The area-wide response is moderated to some degree because of counteracting responses to climate by different age classes and different locations on the environmental gradients.

4.2. *Prospects for validation of landscape-scale NEP estimates*

The 25 m spatial resolution of this analysis closely matches the plot size used in measurements of forest

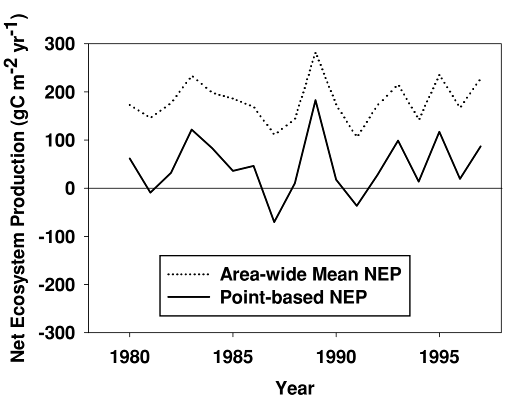

Fig. 8. Interannual variation in mean net ecosystem production for the complete study area and for a mid elevation cell classified as old conifer.

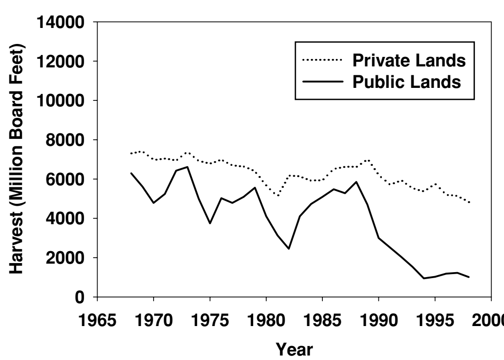

Fig. 9. Harvest volumes on public and private land in the Pacific Northwest region.

wood production and NPP (Gower et al., 1999). Wood production is usually a large component of NEP and provides a useful measure for partial model validation (Barford et al., 2001). Thus the network of permanent plots maintained by national forestry agencies, e.g. the US Forest Inventory and Analysis (FIA) Program (USDA, 1992), represents a potential source of validation data over large forested areas. However, the information on plot locations and volume increments may be poorly documented or unavailable. The locations of the FIA plots in the Pacific Northwest are not released and plot level data are not available except as raw diameter distributions. Because of the policy relevance of forests to national carbon accounting, increased attention should be paid to making locations and associated bolewood productions estimates available to carbon-cycle researchers. The FIA Program does report summary statistics on volume increment at the county and state levels, and these data will provide validation at an aggregate level as the spatial scale of the modeling grows to include complete political units.

Bolewood production estimates based on FIA data (non-georeferenced) for the Willamette National Forest, which surrounds the study area, decline significantly after age 50 (Fig. 10). The temporal trend in bole production simulated by Biome-BGC shows a similar pattern, lending confidence to the simulated trends in NPP and NEP. The large variation in bole production for a given stand age indicates the importance of accounting for site factors other than age class (e.g. LAI and climate data) in the simulations.

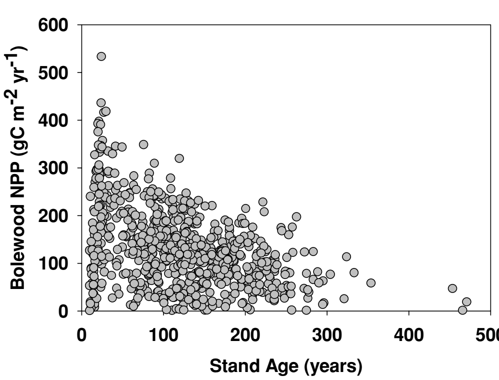

Fig. 10. Bole production estimates for all permanent plots in the Willamette National Forest. Data on diameter distributions and 5-yr increments by species (FIA, 2001) were converted to biomass and carbon using allometric relationships in BIOPAK (Means et al., 1994).

The heterotrophic respiration component of simulated NEP is more difficult to validate that the NPP component. Chronosequence studies give some indication of mass loss of CWD over time, and the FIA Program is beginning to include estimation of woody debris mass at a subset of the permanent plot network (Waddell, 2002). Chamber-based studies of soil respiration (e.g. Davidson et al., 1998) are helping to quantify litter and soil organic matter decomposition rates, but it remains problematic to isolate heterotrophic from autotrophic respiration (Hanson et al., 2000).

Eddy covariance flux towers can be used to verify simulated NEP. At tower sites, aggregated half-hourly measurements of net ecosystem exchange can be compared to simulated daily carbon flux values to reveal model effectiveness with regard to day-to-day variation in site meteorology (Aber et al., 1996). In the PNW region, there are flux towers at three conifer sites (Law et al., 2001b; Chen et al., 2002). Initial comparison of flux site data with simulations from Biome-BGC indicate that model estimates of major carbon flux components agree with budget-based observations to within ±20%, with larger differences for NEP and for several storage terms (Law et al., 2001b). Annual NEP values at tower sites require filling in missing data (Goulden et al., 1996a), but coherent patterns in interannual variation in NEP are beginning to emerge from tower studies (Goulden et al., 1996b; 1998). Multiple-year observations of NEP may thus provide valuable checks on model sensitivity to interannual climate variation.

4.3. Relationship of fine-scale to coarse-scale analyses

Global NEP models run at coarse resolution are increasingly providing insights into spatial and temporal patterns in terrestrial carbon flux. These flux estimates are compared with results from global-scale inverse modeling studies, or interannual anomalies in the rate of CO_2 increase in the atmosphere (e.g. Ito and Oikawa, 2000). The modeled NEP estimates are rarely evaluated for individual cells because of the mismatch in scale between the 10–100 km cell size of the simulations and the much finer scale of carbon flux measurements. The high spatial resolution approach to scaling NEP used in this study provides a means to bridge the gap between the scale of the carbon flux measurements and the coarse resolution currently employed for global-scale NEP simulations. Comparisons of one or more cells in selected regions could greatly inform model development at the global scale.

The fine scale approach described in this paper could potentially be extended beyond the landscape scale to the regional domain. Areas of intensive management and land-use change, especially where carbon stocks and growth rates are large, are of greatest interest. This extension is not constrained by availability of satellite data. The ETM+ sensor and Moderate Imaging Spectroradiometer (MODIS) sensor are providing global coverage suitable for mapping land cover to relevant scales. Mesoscale climate models which use General Circulation Models, or observations, for boundary conditions are increasingly able to provide distributed meteorological data appropriate for fine-scale simulation modeling at the regional scale (e.g. Pielke et al., 1996). As noted, the logistical constraints on the number of field measurements that can be made in support of fine scale simulation modeling are significant, hence government-supported permanent plot networks and the flux tower networks must be increasingly relied upon. Implementation of the fine-scale approach over a regional domain opens the possibility of comparisons with fluxes inferred from inverse modeling.

5. Conclusions

Globally applied NEP simulations are necessarily restricted to spatial resolutions with cell sizes on the order of 10–100 km on a side. At those coarse scales, most information on land use and local environmental heterogeneity is omitted. Landscape to regional analyzes which rely on fine-resolution remote sensing ($\leq$250 m) to characterize land cover and LAI can supplement coarse scale analyses by examining effects of fine-scale heterogeneity on mean NEP and sensitivity of mean NEP to interannual climate variation.

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REFERENCES

Aber, J. D., Reich, P. B. and Goulden, M. L. 1996. Extrapolating leaf CO_2 exchange to the canopy: a generalized model of forest photosynthesis validated by eddy correlation. *Oecologia* **106**, 267–275.

Barford, C. C., Wofsy, S. C., Goulden, M. L., Munger, J. W., Pyle, E. H., Urbanski, S. P., Hutyra, L., Saleska, S. R., Fitzgarrald, D. and Moore, K. 2001. Factors controlling long- and short-term sequestration of atmospheric CO_2 in a mid-latitude forest. *Science* **294**, 1688–1691.

Binkley, D., Sollins, P., Bell, R., Sachs, D. and Myrold, D. 1992. Biogeochemistry of adjacent conifer and alder-conifer stands. *Ecology* **73**, 2022–2033.

Bousquet, P., Peylin, P., Ciais, P., Quere, C. L., Friedlingstein, P. and Tans, P. P. 2000. Regional changes in carbon dioxide fluxes of land oceans since 1980. *Science* **290**, 1342–1346.

Chen, J. M. 1996. Optically-based methods for measuring seasonal variation of leaf area index in boreal conifer stands. *Agric. For. Meteorol.* **80**, 135–163.

Chen, J., Falk, M., Euskirchen, E., PawU, K. T., Suchanek, T. H., Ustin, S. L., Bond, B. J., Brosofske, D. D., Phillips, N. and Bi, R. 2002. Biophysical controls of carbon flows in three successional Douglas-fir stands based on eddy-covariance measurements. *Tree Physiol.* **22**, 169–177.

Ciais, P., Peylin, P. and Bousquet, P. 2000. Regional biospheric carbon fluxes as inferred from atmospheric CO_2 measurements. *Ecol. Appl.* **10**, 1574–1589.

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

Cohen, W. B., Harmon, M. E., Wallin, D. O. and Fiorella, M. 1996. Two decades of carbon flux from forests of the Pacific Northwest. *BioScience* **46**, 836–844.

Cohen, W. B., Fiorella, M., Gray, J., Helmer, E. and Anderson, K. 1998. An efficient and accurate method for mapping forest clearcuts in the Pacific Northwest using Landsat imagery. *Photogram. Eng. Remote Sensing* **64**, 293–300.

Cohen, W., Maiersperger, T. K., Spies, T. A. and Oetter, D. R. 2001. Modeling forest cover attributes as continuous variables in a regional context with Thematic Mapper data. *Int. J. Remote Sensing* **22**, 2279–2310.

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

Crist, E. P. and Cicone, R. C. 1984. A physically-based transformation of Thematic Mapper data – the TM Tasseled Cap. *IEEE Trans. Geosci. Remote Sensing* **GE-22**, 256–263.

Davidson, E. A., Belk, E. and Boone, R. D. 1998. Soil water content and temperature as independent or confounding factors controlling soil respiration in a temperate mixed hardwood forest. *Glob. Change Biol.* **4**, 217–227.

Fan, S., Gloor, M., Mahlman, J., Pacala, S., Sarmiento, J., Takahashi, T. and Tans, P. 1998. A large terrestrial carbon sink in North America implied by atmospheric and oceanic carbon dioxide data and models. *Science* **282**, 442–446.

FIA. 2001. U.S. Forest Inventory and Analysis web site. http://www.fs.fed. us/r6/survey/.

Frazer, G. W., Trofymow, J. A. and Lertzman, K. P. 2000. Canopy openness and leaf area in chronosequences of coastal temperate rainforests. *Can. J. For. Res.* **30**, 239–256.

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

Goulden, M. L., Munger, J. W., Fan, S., Daube, B. C. and Wofsy, S. C. 1996a. Measurements of carbon sequestration by long-term eddy covariance: methods and a critical evaluation of accuracy. *Glob. Change Biol.* **2**, 169–182.

Goulden, M. L., Munger, J. W., Fan, S.-M., Daube, B. C. and Wofsy, S. C. 1996b. Exchange of carbon dioxide by a deciduous forest: response to interannual climate variability. *Science* **271**, 1576–1578.

Goulden, M. L., Wofsy, S. C., Harden, J. W., Trumbore, S. E., Crill, P. M., Gower, S. T., Fries, T., Daube, B. C., Fan, S.-M., Sutton, D. J., Bazzaz, A. and Munger, J. W. 1998. Sensitivity of boreal forest carbon balance to soil thaw. *Science* **279**, 214–217.

Gower, S. T., Kucharik, C. J. and Norman, J. M. 1999. Direct and indirect estimation of leaf area index, f_{APAR}, and net primary production of terrestrial ecosystems. *Remote Sens. Environ.* **70**, 29–51.

Grier, C. C. and Running, S. W. 1977. Leaf area of mature northwestern coniferous forests: relation to site water balance. *Ecology* **58**, 893–899.

Hanson, P. J., Edwards, N. T., Garten, C. T. Jr. and Andrews, J. A. 2000. Separating root and microbial contributions to soil respiration: A review of methods and results. *Biogeochem.* **48**, 115–146.

Harmon, M. E., Ferrell, W. K. and Franklin, J. F. 1990. Effects on carbon storage of conversion of old-growth forests to young forests. *Science* **247**, 699–7002.

Harmon, M. E., Harmon, J. M., Ferrell, W. K. and Brooks, D. 1996. Modeling carbon stores in Oregon and Washington forest products: 1900–1992. *Clim. Change* **33**, 521–550.

HJA. 2002. H.J. Andrews Long Term Ecological Research site web page. http://www.fsl.orst.edu/lter/homepage.htm.

Ito, A. and Oikawa, T. 2000. A model analysis of the relationship between climate perturbations and carbon budget anomalies in global terrestrial ecosystems: 1970–1997. *Clim. Res.* **15**, 161–183.

Kern, J. S., Turner, D. P. and Dodson, R. F. 1997. Spatial patterns in soil organic carbon pool size in the Northwestern United States. In: *Soil processes and the carbon cycle* (eds. R. Lal, J. M. Kimbal, R. Follett and B. A. Stewart). CRC Press, Boca Raton FL, 29–43.

Kicklighter, D. W., Bruno, M., Donges, S. et al. 1999. A first-order analysis of the potential role of CO_2 fertilization to affect the global carbon budget: a comparison of four terrestrial biosphere models. *Tellus* **51B**, 343–366.

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

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

Martin, M. E. and Aber, J. D. 1997. High spectral resolution remote sensing of forest canopy lignin, nitrogen and ecosystem processes. *Ecol. Appl.* **7**, 431–443.

Means, J. E., Hansen, H., Koerper, G., Alaback, P. B. and Klopsch, M. W. 1994. Software for computing plant biomass – BIOPAK users guide. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-340. 184 pp.

Pacala, S. W., Hurtt, G. C., Baker, D. and coauthors. 2001. Consistent land- and atmosphere-based U.S. carbon sink estimates. *Science* **292**, 2316–2322.

Peterson, D. L., Spanner, M. A., Running, S. W. and Teuber, K. B. 1987. Relationship of Thematic Mapper Simulator data to leaf area index of temperate coniferous forests. *Remote Sensing Environ.* **22**, 323–341.

Pielke, R. A., Baron, J., Chase, T., Copeland, J., Kittel, T. G. F., Lee, T. J., Walko, R. and Zeng, X. 1996. Use of mesoscale models for simulation of seasonal weather and climate change for the Rocky Mountain States. In: *GIS and environmental modeling: progress and research issues* (eds. M. F. Goodchild, L. T. Steyaert, B. O. Parks, C. Johnston, D. Maidment, M. Crane and S. Glendinning). GIS World, Inc., Ft. Collins, CO, 99–103.

Potter, C. S., Randerson, J. T., Field, C. B., Matson, P. A., Vitousek, P. M., Mooney, H. A. and Klooster, S. A. 1993. Terrestrial ecosystem production, a process model based on global satellite and surface data. *Glob. Biogeochem. Cycles* **7**, 811–841.

Running, S. W. and Hunt, E. R. Jr. 1993. Generalization of a forest ecosystem process model for other biomes, BIOME-BGC and an application for global scale models. In: *Scaling physiological processes: leaf to globe* (eds. J. R. Ehleringer and C. Fields). Academic Press, Orlando FL, 141–158.

Ryan, M. G., Hunt, E. R. Jr., McMurtrie, R. E. et al. 1996. Comparing models of ecosystem function for temperate conifer forests. I. Model description and validation. In: *Global climate change: effects on coniferous forests and grasslands* (eds. A. I. Breymeyer, D. O. Hall, J. M. Mellilo and G. I. Agren). John Wiley, New York, NY, 313–361.

Schulze, E.-D., Wirth, C. and Heimann, M. 2000. Managing forests after Kyoto. *Science* **289**, 2058–2059.

Song, C., Woodcock, C. E., Seto, K. C., Lenney, M. P. and Macomber, S. A. 2001. Classification and change detection using Landsat TM data: when and how to correct atmospheric effects? *Remote Sensing Environ.* **75**, 230–244.

Sprugel, D. G. 1985. Natural disturbances and ecosystem energetics. In: *The ecology of natural disturbances and patch dynamics* (eds. S. T. A. Pickett and P. S. White). Academic Press, New York, NY, 335–352.

Thomas, S. C. and Winner, W. E. 2000. Leaf area index of an old-growth Douglas-fir forest estimated from direct structural measurements in the canopy. *Can. J. For. Res.* **30**, 1–7.

Thornton, P. E. 1998. Regional ecosystem simulation: combining surface- and satellite-based observations to study linkages between terrestrial energy and mass budgets. PhD Dissertation. University of Montana, 280 pp.

Thornton, P. E., Running, S. W. and White, M. A. 1997. Generating surfaces of daily meteorological variables over large regions of complex terrain. *J. Hydrol.* **190**, 214–251.

Thornton, P. E. and Running, S. W. 1999. An improved algorithm for estimating incident daily solar radiation from measurements of temperature, humidity, and precipitation. *Agric. For. Meteorol.* **93**, 211–228.

Thornton, P. E., Hasenauer, H. and White, M. A. 2000. Simultaneous estimation of daily solar radiation and humidity from observed temperature and precipitation: an application over complex terrain in Austria. *Agric. For. Meteorol.* **104**, 255–271.

Thornton, P. E., Law, B. E., Gholz, H. L., Clark, K. L., Falge, E., Ellsworth, D. S., Goldstein, A. H., Monson, R. K., Hollinger, D., Falk, M., Chen, J. and Sparks, J. P. 2002. Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests. *Agric. For. Meteorol.*, in press.

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

Turner, D. P., Dodson, R. and Marks, D. 1996. Comparison of alternative spatial resolutions in the application of a spatially distributed biogeochemistry model over complex terrain. *Ecol. Model.* **90**, 53–67.

Turner, D. P., Cohen, W. B., Kennedy, R. E., Fassnacht, K. S. and Briggs, J. M. 1999. Relationships between leaf area index and TM spectral vegetation indices across three temperate zone sites. *Remote Sensing Environ.* **70**, 52–68.

Turner, D. P., Cohen, W. B. and Kennedy, R. E. 2000. Alternative spatial resolutions and estimation of carbon flux over a managed forest landscape in western Oregon. *Land. Ecol.* **15**, 441–452.

USDA. 1992. *Forest Service resource inventories: an overview.* USDA Forest Service, Forest Inventory, Economics and Recreation Research, Washington, D.C. USA.

Vogelmann, J., Sohl, T. and Howard, S. 1998. Regional Characterization of Land Cover Using Multiple Sources of Data. *Photogram. Eng. Remote Sensing* **64**, 45–57.

Waddell, K. L. 2002. Sampling coarse woody debris for multiple attributes in extensive resource inventories. *Ecol. Indicators* (in press).

Wallin, D. O., Swanson, F. J., Marks, B., Cissel, J. H. and Kertis, J. 1996. Comparison of managed and pre-settlement landscape dynamics in forests of the Pacific Northwest, USA. *For. Ecol. Manag.* **85**, 291–309.

White, J. D. and Running, S. W. 1994. Testing scale dependent assumptions in regional ecosystem simulations. *J. Veg. Sci.* **5**, 687–702.

White, M. A., Thornton, P. E., Running, S. W. and Nemani, R. R. 2000. Parameterization and sensitivity analysis of the BIOME-BGC terrestrial ecosystem model: net primary production controls. *Earth Interactions* **4**, 1–85.

Woodward, F. I., Lomas, M. R. and Lee, S. E. 2001. Predicting the future productivity and distribution of global terrestrial vegetation. In: *Terrestrial global productivity* (eds. J. Roy, B. Saugier and H. A. Mooney), Academic Press, San Diego CA, 521–541.