

Ecological Modelling 164 (2003) 33-47

ECOLOGICAL MODELLING

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A regional forest ecosystem carbon budget model: impacts of forest age structure and landuse history

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Received 6 February 2002; received in revised form 5 November 2002; accepted 2 December 2002

Abstract

This study investigated the impacts of landuse history and forest age structure on regional carbon fluxes for the forests in the Pacific Northwest of the United States based on a two-stage modeling strategy. In the first stage, an individual-based forest ecosystem carbon flux model (IntCarb) at stand scale is developed. IntCarb combines components from the ZELIG and CENTURY models to simulate forest development and heterotrophic respiration, respectively. Stand scale carbon fluxes simulated by IntCarb strongly depend on stand age. A forest stand can be a carbon sink for up to 200 years old with a peak at 30–40 years old. Old-growth stands are carbon neutral to the atmosphere in the long term. For any particular year, an old-growth stand can be either a carbon sink or source. The interannual variation of Net Ecosystem Productivity (NEP) for an old-growth stand is primarily determined by heterotrophic respiration. Due to the high spatial variability of stand ages, forest age structure needs to be taken into account to improve estimation of carbon budgets of forest ecosystems over large areas. In the stand stage, a regional carbon budget model (RegCarb) is developed to estimate regional carbon fluxes over large areas based on forest age structure, adjusting for the nonrespiratory carbon losses (timber harvesting). Our initial estimate with RegCarb for the Pacific Northwest of the United States indicates that this region was a tremendous carbon source to the atmosphere from 1890 to 1990 due to extensive logging of old-growth forest. Projection for the role of forests in this region in global carbon cycle in the future strongly depend on the amount of timber to be harvested, i.e. how the age structure of forests in this region is to be altered.

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Keywords: Carbon budget; Terrestrial ecosystems; Landuse history; Forest age structure; Ecosystem modelling

1. Introduction

Forests cover nearly one-third of Earth's land area, containing up to 80% of the total above-ground terrestrial carbon and 40% of below-ground carbon, thus having a critical role in global carbon cycle (Dixon et al., 1994). However, accurate estimate of forest

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ecosystem contribution to the global carbon cycle remains a major challenge. Forest ecosystem absorbs carbon dioxide from the atmosphere through the process of photosynthesis in which green leaves produce carbohydrate. The total amount of carbohydrate produced by vegetation over a unit-ground area is referred to as the Gross Primary Productivity (GPP). A significant portion of GPP is consumed by the organism itself, a process which is called autotrophic respiration (R_a) through which the carbon dioxide fixed in carbohydrate during the photosynthesis is released back

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into the atmosphere. The amount of growth that a tree can realize is the amount of GPP after R_a is deducted, which is called the Net Primary Productivity (NPP). A forest ecosystem cannot accumulate all annual NPP through time. Due to litter fall and mortality, part of NPP is released into the atmosphere through decomposition of the detrital carbon, which is called the heterotrophic respiration (R_h) . The net carbon exchange for a stand with the atmosphere is the amount of NPP after R_h is deducted, which is called the Net Ecosystem Productivity (NEP). To estimate carbon budget for large areas over a long time, there is an additional carbon loss from the forest ecosystem that need to be accounted, the nonrespiratory carbon loss (R_n) including harvesting, wildfire, insect damage, etc. The total amount of carbon left from NEP after R_n is deducted is called the Net Biome Production (NBP) (Schulze et al., 2000). In essence, NBP is the difference between the total amount of carbon input into and output from the ecosystem, both of which are a magnitude larger than their difference. Reducing uncertainties in estimates of the various components of carbon cycle is critical to an enhanced understanding of global carbon cycle. Numerous studies suggest that stand age or successional stage is a critical factor determining ecosystem carbon storage and fluxes (Turner et al., 1995; Caspersen et al., 2000; Schulze et al., 2000; Law et al., 1999, 2001). However, the impacts of successional stages or stand age structure on ecosystem carbon budget over large areas are rarely unknown. In this study, we investigated the impacts of forest age structure and landuse history on carbon storage and fluxes for the 10 million ha of commercial forests in the US Pacific Northwest. Though this region sustains the world's most productive conifer forests, whether this region is a carbon sink or source is still under debate (Schimel et al., 2000; Cohen et al., 1996). Due to intensive timber harvesting over the last century, the stand age structure has been significantly modified in this region. A large fraction of the harvesting is clearcut, and these areas are under regeneration. The rapid change in stand age structure over the last century makes this region an interesting place to study the impacts of stand age structure and landuse history on regional carbon budget.

Numerous models have been developed in the literature to simulate forest ecosystem processes. Earlier models primarily focused on population dynamics (Botkin et al., 1972a,b; Shugart and West, 1977;

Urban, 1990). Forest population dynamics models are successful in predicting stand level population demographics, but stop short of addressing ecosystem biogeochemical processes. Recent developments focus more on the processes related to exchanges of water, carbon and nutrient cycles (Running and Coughlan, 1988; Running and Gower, 1991; Aber and Federer, 1992; Weinstein et al., 1991; Wang et al., 1998). These models are useful research tools at fine spatial/temporal scales. However, it is exceedingly difficult to use these sophisticated photosynthesis models to predict the amount of growth of forests for large areas over long time periods. It is not that the mechanisms of photosynthesis are not important, but that the phenomena involved in photosynthesis at leaf level are lost in the broader spatial and/or temporal scales (Jarvis and McNaughton, 1986).

A new generation of models have recently been developed in the literature to address terrestrial ecosystem biogeochemical processes, particularly in the context of global climate change. Among those, TEM (Raich et al., 1991), Biome-BGC (Running and Hunt, 1993), CENTURY (Parton et al., 1987, 1993) have significantly improved our understanding of the possible consequences and responses from the terrestrial ecosystem at different climatic scenarios, such as CO₂ fertilization (McGuire et al., 1997; Kicklighter et al., 1999), nitrogen deposition (Magill et al., 1997) and global warming (Schimel et al., 2000). Using remotely sensed data from satellites, the CASA model simulates the seasonal global climatic and edaphic controls on terrestrial ecosystem production and soil microbial respiration (Potter et al., 1993). The CASA model uses the simple ratio vegetation index from the Advanced Very High Resolution Radiometer (AVHRR) on board NOAA satellites to estimate the Fraction of Absorbed Photosynthetically Active Radiation (FA-PAR), and then estimate NPP based on the theory of light use efficiency (Monteith, 1972). These global models all suffer from a common weakness that they use a limited number of biomes to represent vast areas and ignore potentially important differences within biomes in terms of productivity and landuse history (Cohen et al., 1996). A typical cell size for the global scale models is $0.5^{\circ} \times 0.5^{\circ}$ longitude and latitude, while the spatial heterogeneity at the ecosystem level is on the order of tens to thousands of meters (Churkina et al., 1999).

Our poor understanding of the global carbon cycle leads to the difficulty in balancing the global carbon budget. A "missing sink" up to 2.8 pg of carbon is unaccounted (Detwiler and Hall, 1988). Some speculate that the missing sink is due to CO₂ fertilization and nitrogen deposition (Gifford, 1994), while others believe it may be due to regrowth of vegetation (Caspersen et al., 2000). An enhanced understanding of global carbon budget relies on an improved understanding of the roles of major factors on ecosystem carbon exchange for large areas. This study explores the impacts of forest age structure and landuse history on regional carbon budget.

2. Modeling description

A two-stage modeling strategy is taken in this investigation to study the importance of age structure and landuse history on regional ecosystem carbon budget. The first stage is to simulate the ecosystem carbon budget for a stand. An individual tree-based carbon budget model (IntCarb) at stand scale is developed in the first stage. IntCarb combines components from the ZELIG model (Urban, 1990) for forest growth and development and from the CENTURY model (Parton et al., 1987, 1993) for heterotrophic respiration. A regional carbon budget model (RegCarb) is developed in the second stage. RegCarb estimates regional carbon budget based on forest ecosystem carbon fluxes at stand scale produced by IntCarb, stand age structure and landuse history, adjusting for nonrespiratory carbon loss due to timber harvesting.

2.1. Stand scale carbon budget

2.1.1. Carbon accumulation

IntCarb simulates carbon accumulation in a forest stand by tracing increment in diameter at breast height (DBH), establishment and mortality at an annual time step for each individual tree in a small plot with the size of the canopy of a single dominant individual. Due to the small size of the plot simulated, the ecological roles of gaps created by tree mortality is emphasized, thus models which simulate growth and development in similar fashion are often called "gap models". In practice, model simulation is usually run for many plots, and their aggregated statistics are used as growth

and development for a stand. At the core of the model is the simulation of optimal growth of an individual tree in a stand as

$$\frac{dD}{dt} = \frac{GD[1 - (DH/D_{\text{max}}H_{\text{max}})]}{274 + 3b_2D - 4b_3D^2}$$
(1)

where D is DBH and H is height, G is a species-specific growth factor. The quantities of $D_{\rm max}$ and $H_{\rm max}$ are the species-specific maximum DBH and height, respectively. The parameters of b_2 and b_3 are the species-specific allometric constants between the height of a tree and its DBH as in $H=137+b_2D-b_3D^2$. The species-specific parameters in Eq. (1) for this region are from Urban et al. (1993). The actual growth in DBH is almost always less than the optimal growth as it is almost always limited by one or more of the following environmental factors: light availability, soil fertility and soil moisture and air temperature. The environmental constraints on DBH growth are simulated as

$$\Delta D = r(L) \times \min\{r(M), r(F)\} \times r(T) \times \Delta D_{\text{opt}} \quad (2)$$

where ΔD is the actual growth in DBH and $\Delta D_{\rm opt}$ is the optimal growth in DBH from Eq. (1). The functions of r(L), r(M), r(F) and r(T) are environmental constraints from light availability, soil moisture, soil fertility and temperature, respectively, each of which takes a value between 0 and 1. The function $\min\{\cdot\}$ returns the smaller value between r(M) and r(F).

Establishment of new individual trees is simulated as a stochastic process, and is based on relative potential inseeding rates for each species. The potential establishment rates are modified by ground level shading, soil moisture and fertility and temperature during the simulation. The constrained rates are used to define a probability of establishment for each species, and new trees are generated stochastically based on these probabilities.

Tree mortality arises from two sources: natural (age-related) mortality and that due to environmental stress, and is modeled as stochastic events. The age-related natural mortality is based on the assumptions that: (1) 1% of individuals survive to reach a species-specific maximum age and (2) mortality is constant with respect to age. Stressed individuals are subject to a mortality rate that only 1% of stressed trees will survive 10 years (Botkin et al., 1972a).

As IntCarb simulates growth of each individual in DBH which is directly related to the overall growth for a tree, we can derive annual NPP for a stand from DBH growth without complicated simulation for photosynthesis and autotrophic respiration. Carbon content for each individual is estimated as the sum of carbon content in five tree parts: leaves, branches, stems, fine and coarse roots. The amount of carbon contained in each part of a tree is estimated through allometry as in the following equation:

$$ln(Y_i) = (a+b) ln(d)$$
(3)

where $ln(\cdot)$ denotes natural logarithm, and Y_i is the total biomass for a tree part. DBH (D) is measured in centimeters. The empirical coefficients a and b are available from the literature for all tree parts except for fine roots (Gholz et al., 1979; Grier and Logan, 1977). Biomass for fine roots is estimated by assuming that annual fine root production is equivalent to that of new leaves. Though this assumption may cause errors, reliable estimate of fine root production remains a challenge. A similar assumption was taken in FOREST-BGC (Running and Coughlan, 1988) and HYBRID (Friend et al., 1997). The conversion coefficient from biomass to carbon used in this study is 0.5 (Raich et al., 1991; Brown and Lugo, 1982).

Annual NPP is the amount of carbon that leads to growth, which is estimated as the sum of carbon gain for all individuals in a stand. Annual carbon gain for a tree part can be estimated as

$$\Delta Y_i = Y_i(t) - Y_i(t-1) \tag{4}$$

where ΔY_i is the annual carbon gain in a tree part as referenced by the subscript. The corresponding total carbon in a tree part at years t and t-1 are $Y_i(t)$ and $Y_i(t-1)$, respectively. The carbon gain for the leaves should include leaf litter fall. Therefore, the annual NPP can be expressed as

$$NPP = \sum_{j} \sum_{i} \Delta Y_{ij}$$
 (5)

where carbon increment summation over i refers to the five tree parts: leaves, branches, stems, fine and coarse roots in a single tree, and summation over j refers to all individuals in a stand. Eq. (3) is applied to each individual before litter fall for leaves, branches and roots happens as litters are part of NPP.

The purpose to trace the carbon content for each tree part is to facilitate simulation of decomposition in the model. At the end of each year after annual NPP is estimated, the litter fall and mortality subroutines are called. The litter fall subroutine removes 20% of current total leave carbon (M.E. Harmon, 2000, personal communication). Litter fall from branches is estimated based on the allometric relationship between tree size and dead branch production. The "litter fall" from fine roots below-ground is assumed to be 80% (Running and Gower, 1991). When mortality happens, all five parts of a tree will be added to the detrital carbon pools, and the same allometries is used to estimate the carbon content for dead trees as those for the live trees.

2.1.2. Heterotrophic respiration

The decomposition of the detrital components in IntCarb follows the CENTURY model (Parton et al., 1987, 1993) as illustrated in Fig. 1, but it is implemented at a monthly time step and the maximum decomposition rate for each carbon pool has been scaled accordingly. The solid boxes in the figure indicate carbon pools. Decomposition, as indicated by the solid arrows in Fig. 1, is associated with release of carbon in the form of CO₂. The models and their parameters used to simulate the decomposition of carbon pools are listed in Table 1. The dashed boxes indicate detrital carbon sources and the dashed arrows indicate separation of carbon in quality.

The carbon quality for the evergreen needleleaf forest described by the ecophysiological characteristics used in the Biome-BGC model (Kimball et al., 1997) is adopted here. The labile:cellulose:lignin ratio for leaf litter is 0.32:0.44:0.24, and the labile:cellulose:lignin ratio for fine roots is 0.30:0.45:0.25, and the lignin:cellulose ratio for wood is 0.76:0.24. The lignin to cellulose ratio for wood is also applied to branches and coarse roots. The surface litter includes the above-ground parts of dead trees and the litter fall from leaves and branches. The root litter includes annual turnover from fine roots, the coarse and fine roots from dead trees. Each detrital component is separated into labile, cellulose and lignin compartments. The labile portion becomes the metabolic carbon pool in the model.

The effect of temperature on decomposition is treated uniformly as an exponential (Q_{10}) response using a Q_{10} of 2.0 (Raich et al., 1991; Potter et al.,

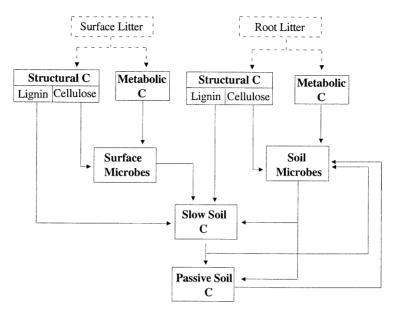


Fig. 1. Decomposition of detrital components. The solid boxes indicate carbon pools. Decomposition, as indicated by the solid arrows, is associated with release of carbon in the form of CO₂ (Table 1). The dashed boxes indicate detrital sources and the dashed arrows indicate separation of carbon in quality.

1993). Assuming the optimal decomposition temperature is 30 °C, the temperature effect on decomposition is simulated as (Potter et al., 1993)

$$f(T) = Q_{10}^{(T-30.0)/10.0} (6)$$

where T is the average monthly air temperature for surface carbon pools and soil temperature for soil carbon pools. Monthly mean air temperatures were used for decomposition of surface structural, metabolic and microbial carbon pools. Monthly mean soil temperatures at 20 cm were used for decomposition of soil carbon pools. Because the stochastic weather submodel in IntCarb only produces monthly mean air temperature and total precipitation, the monthly mean soil temperatures at 20 cm are predicted through an empirical relationship built from observations at watershed 10 from 1982 to 1991 in HJA.

$$T_{\rm s} = 2.3554 + 0.7042 \times T_{\rm a} \tag{7}$$

where T_s and T_a are monthly mean soil temperature at 20 cm and air temperature, respectively. The R^2 for Eq. (7) is 0.90.

The effect of soil moisture on decomposition is simulated as (Raich et al., 1991).

$$f(M) = 0.8(M_{\text{sat}})^B + 0.2 \tag{8}$$

where M_{sat} is an empirical parameter determined by soil texture, and

$$B = \left[\frac{M^a - (M_{\text{opt}})^a}{(M_{\text{opt}})^a - 100^a} \right]^2 \tag{9}$$

where M is the monthly soil moisture (% saturation). $M_{\rm opt}$ is the optimal soil moisture content at which no restraint is put on decomposition, i.e. f(M)=1.0. The parameter a is an empirical parameter related to soil texture. The range of f(M) in Eq. (8) is between 0.2 and 1.0.

IntCarb uses an improved water balance model to replace the one in the original ZELIG model. The new water balance model puts a limit on evapotranspiration when precipitation is less than the potential evapotranspiration.

$$W_t = W_{t-1} + P - E_{A} (10)$$

where W_t and W_{t-1} are soil water content (cm) at current and previous months, respectively. Current month precipitation is P. The actual evapotranspiration is E_A , which is estimated from

Table 1 Models simulating the decomposition of carbon pools as shown in Fig. 1^a

Carbon pool	Decomposition model	Decomposed components
Surface structure (lignin C_{1L})	$\Delta C_{1L} = k_1 f(T) f(M) L_c C_{1L}$	CO ₂ (0.30) Slow <i>C</i> (0.70)
Surface structure (cellulose C_{1C})	$\Delta C_{1C} = k_1 f(T) f(M) L_c C_{1C}$	CO ₂ (0.60) Surface microbes (0.40)
Soil structure (lignin C_{2L})	$\Delta C_{2L} = k_2 f(T) f(M) L_c C_{2L}$	CO ₂ (0.30) Slow <i>C</i> (0.70)
Soil structure (cellulose C_{2C})	$\Delta C_{2C} = k_2 f(T) f(M) L_c C_{2C}$	CO ₂ (0.55) Soil microbes (0.45)
Soil microbes (C_3)	$\Delta C_3 = k_3 f(T) f(M) T_{\rm m} C_3$	$CO_2(F_t)$ Slow $C(1 - F_t - C_{ap})$ Passive $C(C_{ap})$
Surface microbes (C_4)	$\Delta C_4 = k_4 f(T) f(M) C_4$	CO ₂ (0.60) Slow <i>C</i> (0.40)
Surface metabolic (C_5)	$\Delta C_5 = k_5 f(T) f(M) C_5$	CO ₂ (0.60) Surface microbes (0.40)
Soil metabolic (C_6)	$\Delta C_6 = k_6 f(T) f(M) C_6$	CO ₂ (0.55) Soil microbes (0.45)
Slow $C(C_7)$	$\Delta C_7 = k_7 f(T) f(M) C_7$	CO_2 (0.55) Soil microbes $(1 - 0.55 - C_{sp})$ Passive C (C_{sp})
Passive $C(C_8)$	$\Delta C_8 = k_8 f(T) f(M) C_8$	CO ₂ (0.55) Soil microbes (0.45)

 $k_i = 0.325, 0.40, 0.6083, 0.50, 1.2083, 1.5417, 0.01667$ and 0.000375 (i = 1, ..., 8). $F_t = 0.85 - 0.68S$, where S is the fraction of silt plus clay content of soil. $C_{\rm ap} = 0.003 + 0.032T_{\rm c}$, where $T_{\rm c}$ is the fraction of clay content of soil. $L_{\rm c} = {\rm e}^{-3.0L_{\rm s}}$, where $L_{\rm s}$ is the fraction of structural carbon that is lignin. $C_{\rm sp} = 0.003 - 0.009T_{\rm c}$. $T_{\rm m} = 1.0 - 0.75S$.

$$E_{A} = \begin{cases} \min\{[P + (E_{P} - P) \times f_{D}], \\ [P + (W_{t-1} - W_{m})]\} & \text{if } P < E_{P} \\ E_{P} & \text{if } P > E_{P} \end{cases}$$
(11)

where $W_{\rm m}$ is the wilting point. The potential evapotranspiration ($E_{\rm P}$) is estimated according to Thornthwhaite and Mather (1957) which was used instead of $E_{\rm A}$ in Eq. (10) in the original ZELIG model, and $f_{\rm D}$ is a limiting factor on evapotranspiration when precipitation is less than potential evapotranspiration. The limiting factor $f_{\rm D}$ is determined by soil texture and the relative soil water content (Potter et al., 1993).

$$f_{\rm D} = \left(\frac{1+a}{1+a\theta^b}\right) \tag{12}$$

where θ is the relative soil moisture content which ranges between 0 and 1, and a and b is texture-dependent empirical coefficients.

2.2. Regional carbon budget

Extensive timber harvesting over the last century has significantly modified the age structure for the forests in this region (Harmon et al., 1990; Cohen et al., 2002). To investigate the importance of age structure for carbon budget, a regional scale carbon flux model (RegCarb) is developed to aggregate the stand scale carbon storage and fluxes from IntCarb based on forest age structure and landuse history in the region, adjusting for the nonrespiratory carbon losses

^a Decomposition of carbon pools is associated with CO₂ release, and its proportion is given in parentheses. The optimal decomposition rates (k_1, \ldots, k_8) are at the monthly time scale. The temperature and moisture effects on decomposition are f(T) and f(M).

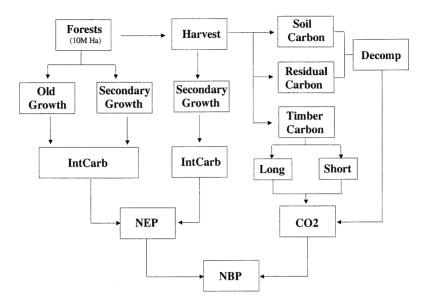


Fig. 2. Model structure for RegCarb simulating regional Net Biome Production (NBP). Four parallel simulations are incorporated simultaneously in RegCarb: succession of pre-1890 forests, succession of post-1890 secondary forest, decomposition of residual carbon left by harvest, and carbon release from timber harvested. NEP adjusted by the amount of carbon dioxide released due to harvesting (other nonrespiratory carbon loss, such as wild fire and insect damage, not considered here) leads to NBP for the region.

from timber harvesting in the meantime (Fig. 2). The total annual NEP for the entire region can be estimated as

$$NEP_{T} = \sum_{age} NEP(age) \times A(age)$$
 (13)

where NEP(age) (Mg C/ha) is NEP for stands at a given age in the region and A(age) (ha) is the total area of stand at a given age. IntCarb provides RegCarb with NEP(age). Without disturbance, the shape of the frequency distribution of stand age will not change, but the distribution curve will shift 1 year toward the higher end each year. Eq. (13) can be applied for a large area with a single IntCarb simulation by adjusting the age distribution each year. In reality, the age structure changes rapidly due to natural and human disturbances. In this study, published literatures on landuse history provide RegCarb with data on stand age structure, A(age).

To adjust nonrespiratory carbon loss, the amount of timber harvested has to be traced each year. Timber harvesting only takes the commercially valuable portion of carbon from the stand, usually the bulk part of the stem. Based on the landuse history, we obtained the areas of forests harvested with respect to stand age each year. The total timber carbon harvested can be estimated as

$$C_{\rm H} = \beta \times \sum_{\rm age} C_{\rm ST}(\rm age) \times A_{\rm H}(\rm age)$$
 (14)

where $C_{\rm H}$ (Mg C) is the total timber carbon harvested, and $C_{\rm ST}$ (age) (Mg C/ha) is the total stem carbon content for a stand at a given age. The total area harvested for a given age of stand in the region is $A_{\rm H}$ (age) (ha). The harvesting efficiency of stem carbon is β (0 < β < 1). Timber carbon taken away from the field will be gradually released into the atmosphere, which is called the nonrespiratory carbon loss. The rate of carbon release depends on timber usage: long-term use or short-term use.

$$R_{\rm n} = \lambda \frac{C_{\rm H}}{\gamma_{\rm L}} + (1 - \lambda) \frac{C_{\rm H}}{\gamma_{\rm S}} \tag{15}$$

where R_n (MgC) is the nonrespiratory carbon loss from timber carbon and λ is the fraction of timber carbon that goes to long-term use. The life time for long-term and short-term timber carbon are γ_L and γ_S in years, respectively.

The harvesting residuals, including leaves, branches, stems (stumps and tips) left on the ground, and fine and coarse roots left in the soil, will remain on site. Harvesting residual carbon for leaves, branches, and roots is estimated with Eq. (3), harvesting residual carbon for stems (stumps and tips) is estimated as

$$C_{\rm R} = (1 - \beta) \times \sum_{\rm age} C_{\rm ST}(\rm age) \times A_{\rm H}(\rm age)$$
 (16)

where C_R denotes the residual carbon from the stems after harvesting, i.e. the stumps and tips, and the symbols on the right side of Eq. (16) have the same meaning as in Eq. (14). The harvesting residual carbon will merge with the existing carbon pools to become the initial condition for secondary regeneration. Carbon release from harvesting residuals is part of heterotrophic respiration. Due to the fact that timber

harvesting may occur in stands across a wide range of ages (Cohen et al., 2002), the amount of harvesting residual carbon depends on the age of the stand harvested. Regeneration over harvested old-growth sites may have significantly higher initial carbon content in the soils and on the ground than regeneration over harvested younger stand sites. To simplify the simulation process, the harvested residual carbon is pooled and simulated in a separate module. The initial carbon content above- and below-ground is determined by two rounds of spin run of IntCarb. The first spin run of the model starts with empty carbon pools in the beginning for 600 years. The second round of spin run starts with initial carbon content above- and below-ground at the end of the first spin run. The initial carbon content for a stand at a given age harvested is taken from the second spin run of the model. The NBP for a region is estimated as

$$NBP = NEP_{T} - R_{n} \tag{17}$$

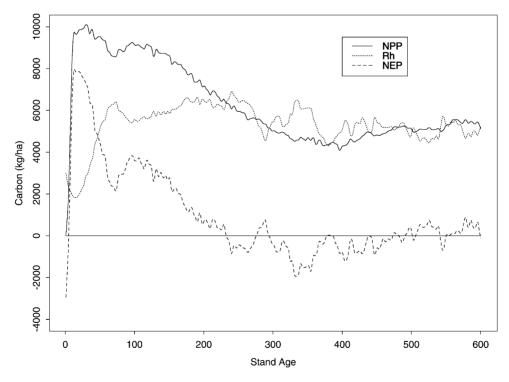


Fig. 3. Forest ecosystem carbon fluxes simulated by IntCarb for a typical stand in the H.J. Andrews Experimental Forest. The Net Primary Productivity (NPP), the heterotrophic respiration (R_h), and the Net Ecosystem Productivity (NEP) are all strongly dependent on stand ages. A stand can be a carbon sink for up to 200 years old. The long-term role of old-growth stands is carbon neutral to the atmosphere. For any particular year, an old-growth can be either a carbon sink or source.

RegCarb is applied to the 10 million ha of commercial forests in the US Pacific Northwest. First the forest of the region is divided into pre-1890 forests and post-1890 forests. Eq. (13) is used to simulate NEP for pre-1890 forests, and Eq. (14) is used to simulate the nonrespiratory carbon loss for the harvested areas. Carbon budgets for post-1890 regenerated stands is also estimated by Eq. (13) as the harvesting residual carbon left on site (including both above- and below-ground) is handled separately.

3. Results

Forest ecosystem carbon fluxes simulated by Int-Carb for a Douglas-fir/western hemlock stand in the H.J. Andrews Experimental Forest on a site with medium soil texture is shown in Fig. 3, indicating that

ecosystem carbon fluxes vary significantly with stand age. NPP initially increases with stand age rapidly and reaches its maximum in about 30-40 years. This result matches reports in the literature (Harmon et al., 1990; Cohen et al., 1996). After the peak, NPP gradually decreases with age until about 300 years old. Then NPP stays at a relatively stable level. Heterotrophic respiration in the beginning is determined by the initial carbon content. As a stand develops producing more detrital biomass, heterotrophic respiration increases with age and eventually stabilizes and roughly balances NPP. The interannual variability of heterotrophic respiration for old-growth forest is bigger than that for NPP. This is created by the death of large individuals in the old-growth stand. As NEP is the difference between NPP and heterotrophic respiration, the interannual variability in NEP is primarily due to that from heterotrophic respiration. NEP has a

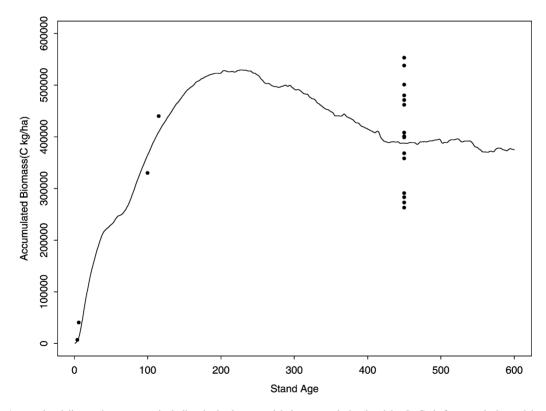


Fig. 4. Accumulated live carbon content including both above- and below-ground simulated by IntCarb for a typical stand in the H.J. Andrews Experimental Forest (solid line). The points at 450 years are observed data from the permanent plots in H.J. Andrews. Due to the exact ages are not available except old-growth age class, the observed data are all put at age 450. The two points in the middle are from Waring and Franklin (1979), and the two points in the very early age are estimated using inventory data from USDA Forest Service for two stands in the H.J. Andrews.

negative value in the beginning, almost as big as heterotrophic respiration because the newly regenerated stand do not absorb much CO₂. How long it takes for a stand to have positive NEP depends on the initial carbon content in the stand. On an annual basis, a forest stand with site conditions as in HJA can be a carbon sink to the atmosphere until about 200 years old. In the long run, the old-growth stand is relatively neutral to the atmosphere. In any particular year, an old-growth stand can either be a weak carbon sink or source depending on heterotrophic respiration. The importance of heterotrophic respiration as revealed by the model simulation is in agreement with observations by Valentini et al. (2000). Stand age has been recognized as critical to estimating regional carbon storage (Turner et al., 1995) and carbon budgets (Kimes et al., 1999; Alexandrov et al., 1999). Due to the high variation in stand age, estimating ecosystem carbon fluxes for large areas need to take forest age structure into consideration.

The various components simulated in IntCarb are difficult to measure in the field. The standing live biomass, as an exception, is relatively easy to estimate. Numerous empirical equations have been developed to estimate standing live biomass (Gholz et al., 1979; Grier and Logan, 1977). Fig. 4 shows the accumulated total biomass in a simulated forest stand with age. The total biomass increases with age and reaches its maximum at about 200 years old. After this time, loss of biomass due to mortality of large trees on an annual basis exceeds new growth. The total biomass gradually decreases from its maximum until about 400 years old, then it maintains at a fairly stable level. From Fig. 3, NPP reaches its maximum much earlier than the total accumulated live biomass. Even though NPP is decreasing, the accumulated live biomass continues to

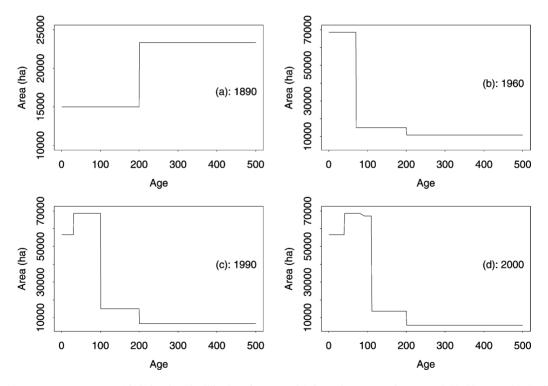


Fig. 5. (a) Age structure at year 1890 for the 10 million ha of commercial forest in western Oregon and Washington with 7 million ha in old-growth evenly distributed between 201 and 500 years and 3 million ha of secondary-growth evenly distributed between 1 and 200 years. (b) Age structure at year 1960 after removing 53,571 ha of old-growth and 15,000 ha of secondary forest at age 200 and swap the areas to the lower end of horizontal axis. (c) Age structure at year 1990 after removing 41,666 ha of old-growth forest since year 1960 and 15,000 ha of secondary forest at age 200 and swap the areas to the lower end of horizontal axis. (d) Age structure at year 2000 with harvesting continuing at year 1990 harvesting intensity.

increase, but at a slower rate. The points at age 450 in Fig. 4 are observed stand biomass from the permanent plots in old-growth forests in HJA. Since the exact ages for these old-growth permanent plots are not available, these points are plotted at age 450 to show their age class. There is a high variation for the total biomass accumulation among different old-growth forest stands. Though the simulation is not calibrated to any particular stand, IntCarb does capture the average level of the biomass accumulation for the old-growth forests in this region. The two points in the middle in Fig. 4 are from the literature (Waring and Franklin, 1979) and the two points at the very early years of succession are estimated for two young stands within HJA with the inventory data from USDA Forest Service. Though more validation of IntCarb is needed, these initial validations are encouraging.

Accurate stand age structure for large areas is rarely available. Based on landuse history published in the literature and a series of assumptions, a simplified stand age structure for the forests in the US Pacific Northwest is constructed from 1890 to 2000. In Western Oregon and Washington, there were 10 million ha of commercial forest land. Seventy percent of this area was old-growth in 1890 and there were only 2 million ha of old-growth remaining in 1990. Five million hectares of old-growth were cleared, of which 75% happened before 1960 (Harmon et al., 1990). Assuming timber harvesting before and after 1960 are at separate constant rates, a dynamic annual age structure for this region is constructed, as illustrated in Fig. 5.

Nonrespiratory carbon loss from timber carbon depends on the life time for long-term and short-term uses. In this study, 42% of timber harvested after 1960 and 20% of timber harvested before 1960 enter into long-term carbon pool with a life time of 200 years, and the remaining timber carbon became short-term carbon pool with a life time of 5 years. Fig. 6 illustrates the NBP estimated by RegCarb for the 10 million ha of commercial forests in the Pacific Northwest since

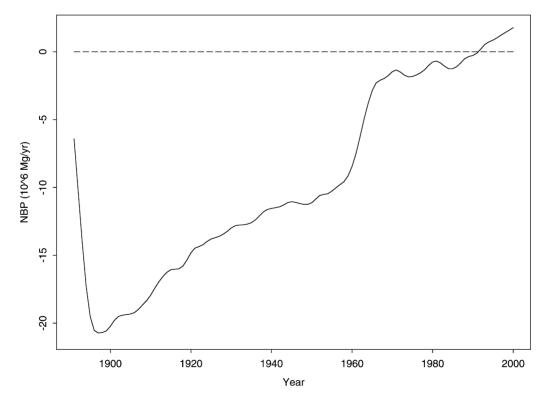


Fig. 6. The Net Biome Production (NBP) for the 10 million ha of forest in the Pacific Northwest. From 1890 to 1990, the net release of carbon is 1.0×10^9 Mg. It just became a weak carbon sink recently since the 1990s.

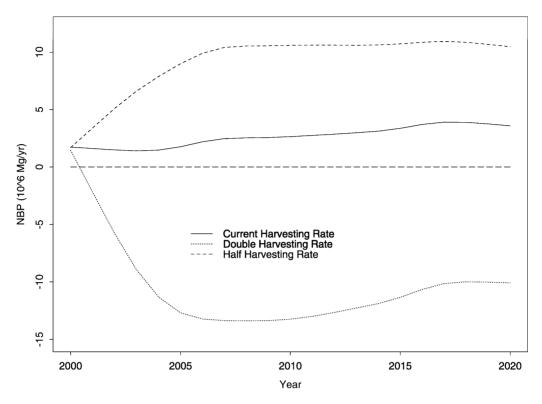


Fig. 7. Projections of the effects of harvesting on regional carbon budget. If harvesting in the future continues as in the year 2000, the 10 million ha of forest will be a carbon sink in the foreseeable future. Reducing the annual harvesting area by half more than doubles the sink size. However, if the harvesting intensity doubles, the 10 million ha of forest will immediately become a significant carbon source again.

1890. The region has been an enormous carbon source to the atmosphere due to the dramatic change in forest age structure. Only recently has the region become a weak sink as the proportion of fast growing young stands increases. The simulated total carbon released from 1890 to 1990 is 1.0×10^9 Mg which is smaller than that estimated by Harmon et al. (1990) because this estimate accounts for carbon absorption from regrowth. That the forested area in the Pacific Northwest is a carbon source to the atmosphere until 1990 agrees with the finding by Cohen et al. (1996).

To explore effects of human activities on ecosystem carbon budgets, three harvesting scenarios are projected into the future, half, the same, and doubled timber harvesting rate as that in the year 2000. The regional carbon fluxes associated with these harvesting scenarios are shown in Fig. 7. Whether the 10 million ha of forest in the Pacific Northwest is a carbon source or sink is very sensitive to the areas

of forest to be harvested each year. A similar conclusion was reached by Turner et al. (1995). If harvesting continues at the intensity of 2000, the 10 million ha of forest will remain to be a carbon sink in the future. Reducing the areas to be harvested by half more than doubles the sink. However, if the harvesting intensity doubles, the 10 million ha of forest will immediately become a significant carbon source again. The simulation results highlight the potential impacts of forest management policy on the environment.

4. Discussion

Carbon exchange between terrestrial ecosystems and the atmosphere is a complex process. There are many biotic and abiotic factors which influence the carbon exchange, including vegetation types, stand ages, topography, climate, soil, nutrients, and distur-

bances. To highlight the effect of age structure and landuse history, this investigation uses the biotic and abiotic conditions in HJA to represent the entire Pacific Northwest region. Due to such simplification, the actual magnitude of carbon fluxes may not be representative though comparable with that in the literature. However, this investigation demonstrates that stand age structure should be taken into consideration while estimating the carbon budget over large areas. The common practice of assuming uniform vegetation condition for vast areas in models simulating global carbon cycle may lead to serious bias.

Stand age structure and landuse history are critical information for RegCarb to translate from simulaitons by IntCarb at the stand scale to estimates at regional scale. However, the stand age structure and landuse history used in this study only capture the first-order variation. Accurate forest age structure information for a large area over a long-term requires tremendous accounting work by pooling information from various sources. We have attempted to construct a detailed age structure for the forests in the Pacific Northwest from published documents, but we eventually opted to use the simple age structure due to lack of continuous historical record for the entire region. An alternative to obtain forest age structure is through remote sensing. Such potential has been demonstrated in a related study by Song and Woodcock (2002) and other studies (Cohen et al., 2001; Kimes et al., 1999; Helmer et al., 2000). Obtaining forest age information from remotely sensed data to improve our carbon budget estimation will be an essential part of our future investigation.

The simulated biomass accumulation with stand age generally matches the data from the permanent plots in the H.J. Andrews Experimental Forest and some published data in the literature. However, this validation is far from enough. Rigorous validation requires the model be calibrated to various stands across an array of environmental gradients. Not only the accumulated biomass, but also the annual NPP and heterotrophic respiration need to be validated with observations. Validation is the primary challenge to all current ecosystem models. A common problem to validating models that estimate carbon fluxes for large areas is the mismatch of scales on which the data are observed and the scales on which models simulate. Models simulating global terrestrial carbon cycling are based on a

grid system that cover the entire globe. Due to computational limitations, global models have to trade off adequate grain size for the large spatial extent. A typical grid size for a global scale carbon cycle model is $0.5^{\circ} \times 0.5^{\circ}$ longitude and latitude (Churkina et al., 1999), while the spatial heterogeneity for the natural ecosystem is on the order of tens to thousands of meters. The carbon fluxes observed are usually at a stand scale. At present, there is essentially no effective approach to validate the models of global scale. The modeling scheme that has been developed in this study allows model validation at the stand level. Our future efforts will give high priority to model validation.

5. Conclusions

This investigation developed a two-stage model to study the impacts of forest age structure and landuse history on regional carbon budget. In the first stage, an individual tree-based carbon model (IntCarb) is developed to simulate forest ecosystem carbon budget at stand scale. IntCarb simulation for a typical stand in HJA indicates that forest ecosystem carbon fluxes strongly depend on its age. A forest stand can be a carbon sink for up to 200 years old. Old-growth stands are carbon neutral to the atmosphere in the long term. For any particular year, an old-growth stand can be either a carbon sink or source. The interannual variation of NEP for an old-growth stand is primarily determined by heterotrophic respiration. A regional carbon budget model (RegCarb) is developed in the second stage to estimate regional carbon budget from the simulation at stand scale by IntCarb based on regional forest age structure and landuse history, adjusting for nonrespiratory carbon loss due to timber harvesting in the meantime. Application of RegCarb to the US Pacific Northwest found that this region had been a major carbon source to the atmosphere in the past. It became a weak carbon sink only since the last decade. Projection to the future indicates whether this region is a carbon sink or source strongly depends on the intensity of timber harvesting. Initial validation based on published biomass is encouraging, but more rigorous validation is needed in the future. Current effort is continuing in deriving more detailed stand age information from remotely sensed data, and an improved version of RegCarb is under development which will incorporate other biotic and abiotic factors along with stand age structure to further reduce uncertainty in estimating forest ecosystem carbon budget over large areas.

Acknowledgements

This study was supported by NASA Grant NAG5-3439 through the Landsat Science Team. The authors thank Drs. Mark Harmon and Warren B. Cohen for valuable comments during the model development.

References

- Aber, J.D., Federer, C.A., 1992. A generalized, lumped-parameter model of photosynthesis, evapotranspiration and net primary production in temperate and boreal forest ecosystems. Oecologia 92, 463–474.
- Alexandrov, G.A., Yamagata, Y., Oikawa, T., 1999. Towards a model for projecting net ecosystem production of the world forests. Ecol. Model. 123, 183–191.
- Botkin, D.B., Janak, J.F., Wallis, J.R., 1972a. Rationale, limitations, and assumptions of a northeastern forest growth simulator. IBM J. Res. Dev. 16, 101–116.
- Botkin, D.B., Janak, J.F., Wallis, J.R., 1972b. Some ecological consequences of a computer model of forest growth. J. Ecol. 60, 849–873.
- Brown, S., Lugo, A.E., 1982. The storage and production of organic matter in tropical forests and their role in the global carbon cycle. Biotropica 14, 161–187.
- Caspersen, J.P., Pacala, S.W., Jenkins, J.C., Hurtt, G.C., Moorcroft, P.R., Birdsey, R.A., 2000. Contributions of land-use history to carbon accumulation in U.S. forests. Science 290, 1148–1151.
- Churkina, G., Running, S.W., Schloss, A.L., the participants of the Potsdam NPP model intercomparison, 1999. Comparing global models of terrestrial Net Primary Productivity (NPP): the importance of water availability. Global Change Biol. 5(Suppl. 1), 46–55.
- Cohen, W.B., Harmon, M.E., Wallin, D.O., Fiorella, M., 1996. Two decades of carbon flux from forests of the Pacific Northwest. Bioscience 46 (11), 836–844.
- Cohen, W.B., Maiersperger, T.K., Spies, T.A., Oetter, D.R., 2001. Modelling Forest cover attributes as ontinuous variables in a regional context with Thematic Mapper data. Int. J. Remote Sens. 22 (12), 2279–2310.
- Cohen, W.B., Spies, T.A., Alig, R.J., Oetter, D.R., Maiersperger, T.K., Fiorella, M., 2002. Characterizing 23 years (1972–95) of stand replacement disturbance in western Oregon forests with Landsat imagery. Ecosystems 5 (2), 122–137.
- Detwiler, R.P., Hall, C.A.S., 1988. Tropical forests and the global carbon cycle. Science 239, 42–47.
- Dixon, R.K., Brown, S., Houghton, R.A., Solomon, A.M., Trexler, M.C., Wisniewski, J., 1994. Carbon pools and flux of global forest ecosystems. Science 263, 185–190.

- Friend, A.D., Stevens, A.K., Knox, R.G., Cannell, M.G.R., 1997.
 A process-based, terrestrial biosphere model of ecosystem dynamics (HYBRID v3.0). Ecol. Model. 95, 249–287.
- Gholz, H.L., Grier, C.C., Campbell, A.G., Brown, A.T., 1979.Equations for estimating biomass and leaf area of plants in the Pacific Northwest. Forest Research Laboratory, School of Forestry, Oregon State University.
- Gifford, R.M., 1994. The global carbon cycle: a viewpoint on the missing sink. Aust. J. Plant Physiol. 21, 1–15.
- Grier, C.C., Logan, R.S., 1977. Old-growth *Psudotsuga menziesii* of A western oregon watershed: biomass distribution and production budgets. Ecol. Monographs 47, 373–400.
- Harmon, M.E., Ferrell, W.K., Franklin, J.F., 1990. Effects on carbon storage of conversion of old-growth forests on young stands. Science 247, 699–702.
- Helmer, E.H., Brown, S., Cohen, W.B., 2000. Mapping montane tropical forest successional stage and land use with multi-date Landsat imagery. Int. J. Remote Sens. 21 (11), 2163–2183.
- Jarvis, P.G., McNaughton, K.G., 1986. Stomatal control of transpiration: scaling up from leaf to region. Adv. Ecol. Res. 15, 1–49.
- Kicklighter, D.W., Bruno, M., Donges, S., Esser, G., Heimann, M., Helfrich, J., Ift, F., Joos, F., Kaduk, J., Kohlmaier, G.H., McGuire, A.D., Melillo, J.M., Meyer, R., Moore III, B., Nadler, A., Prentice, I.C., Sauf, W., Schloss, A.L., Sitch, S., Wittenberg, U., Wurth, G., 1999. A first-order analysis of the potential role of CO₂ fertilization to affect the global carbon budget: a comparison of four terrestrial biosphere models. Tellus 51B, 343–366.
- Kimball, J.S., White, M.A., Running, S.W., 1997. BIOME-BGC simulations of stand hydrologic processes for BOREAS. J. Geophys. Res.-Atmos. 102 (D24), 29043–29051.
- Kimes, D.S., Nelson, R.F., Salas, W.A., Skole, D.L., 1999. Mapping secondary tropical forest and forest age from SPOT HRV data. Int. J. Remote Sens. 20 (18), 3625–3640.
- Law, B.E., Ryan, M.G., Anthoni, P.M., 1999. Seasonal and annual respiration of a ponderosa pine ecosystem. Global Change Biol. 5, 169–182.
- Law, B.E., Thornton, P.E., Irvine, J., Anthoni, P.M., Vantuyl, S., 2001. Carbon storage and fluxes in ponderosa pine forests at different developmental stages. Global Change Biol. 7, 755– 777.
- Magill, A.H., Aber, J.D., Hendricks, J.J., Bowden, R.D., Melillo, J.M., Steudler, P.A., 1997. Biogeochemical response of forest ecosystems to simulated chronic nitrogen deposition. Ecol. Appl. 7 (2), 402–415.
- McGuire, A.D., Melillo, J.M., Kicklighter, D.W., Pan, Y., Xiao, X., Helfrich, J., Moore III, B., Vorosmarty, C.J., Schloss, A.L., 1997. Equilibrium responses of global net primary production and carbon storage to doubled atmospheric carbon dioxide: sensitivity to changes in vegetation nitrogen concentration. Global Biogeochem. Cycles 11, 173–189.
- Monteith, J.L., 1972. Solar radiation and productivity in tropical ecosystems. J. Appl. Ecol. 9, 747–766.
- Parton, W.J., Schimel, D.S., Cole, C.V., Ojima, D.S., 1987.
 Analysis of factors controlling soil organic matter levels in great Plains grasslands. Am. J. Soil Sci. Soc. 51, 1173–1179.

- Parton, W.J., Scurlock, J.M.O., Ojima, D.S., Gilmanov, T.G., Scholes, R.J., Schimel, D.S., Kirchner, T., Menaut, J.-C., Seastedt, T., Garcia, E.G., Kamnalrut, A., Kinyanario, J.I., 1993. Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide. Global Biogeochem. Cycles 7 (4), 785–809.
- Potter, C.S., Randerson, J.T., Field, C.B., Matson, P.A., Vitousek, P.M., Mooney, H.A., Klooster, S.A., 1993. Terrestrial ecosystem production: a process model based on global satellite and surface data. Global Biogeochem. Cycles 7 (4), 811–841.
- Raich, J.W., Rastetter, E.B., Melillo, J.M., Kicklighter, D.W., Steudler, P.A., Peterson, B.J., 1991. Potential Net Primary Productivity in South America: application of a global model. Ecol. Appl. 1 (4), 399–429.
- Running, S.W., Coughlan, J.C., 1988. A general model of forest ecosystem processes for regional applications. I. Hydrologic balance, canopy gas exchange and primary production processes. Ecol. Model. 42, 125–154.
- Running, S.W., Gower, S.T., 1991. FOREST-BGC, a general model of forest ecosystem processes for regional applications. II. Dynamic carbon allocation and nitrogen budgets. Tree Physiol. 9, 147–160.
- Running, S.W., Hunt, E.R., 1993. Generalization of a forest ecosystem process model for other biomes, BIOME-BGC, and an application for global scale models. In: Ehleringer, J.R., Field, C.B. (Eds.), Scaling Physiological Processes: Leaf to Globe. Academic Press, San Diego, CA, pp. 141–158.
- Schimel, D., Melillo, J., Tian, H., McGuire, A.D., Kichlighter, D., Kittel, T., Rosenbloom, N., Running, S., Thornton, P., Ojima, D., Parton, W., Kelly, R., Sykes, M., Neilson, R., Rizzo, B., 2000. Contribution of increasing CO₂ and climate to carbon storage by ecosystems in the United States. Science 287, 2004– 2006.
- Schulze, E., Wirth, C., Heimann, M., 2000. Managing forests after Kyoto. Science 289, 2058–2059.

- Shugart, H.H., West, D.C., 1977. Development of an Appalachian deciduous forest succession model and its application to assessment of the impact of the chestnut blight. J. Environ. Manage. 5, 161–179.
- Song, C., Woodcock, E.C., 2002. The spectral/temporal manifestation of forest succession in optical imagery: the potential of multitemporal imagery. Remote Sens. Environ. 82, 286–303.
- Thornthwhaite, C.W., Mather, J.R., 1957. Instructions and tables for computing potential evapotranspiration and the water balance. Publ. Climatol. 10, 183–311.
- Turner, D.P., Koerper, G.J., Harmon, M.E., Lee, J.J., 1995. A carbon budget for forests of the conterminous United States. Ecol. Appl. 5 (2), 421–436.
- Urban, D.L., 1990. A versatile model to simulate forest pattern: a user's guide to ZELIG, version 1.0. University of Virginia, Charlottesville, VA.
- Urban, D.L., Harmon, M.E., Halpern, C.B., 1993. Potential response of Pacific north-western forests to climatic change, effects of stand age and initial composition. Climat. Change 23, 247–266.
- Valentini, R., Matteucci, G., Lolman, A.J., Schulze, E., 2000. respiration as the main determinant of carbon balance in European forests. Nature 404, 861–864.
- Wang, Y.P., Rey, A., Jarvis, P.G., 1998. Carbon balance of young birch trees grown in ambient and elevated atmospheric CO₂ concentrations. Global Change Biol. 4 (8), 797– 807.
- Waring, R.H., Franklin, J.F., 1979. Evergreen coniferous forests of the Pacific Northwest. Science 204, 1380–1386.
- Weinstein, D.A., Beloin, R.M., Yanai, R.D., 1991. Modeling changes in red spruce carbon balance and allocation in response to interacting ozone and nutrient stresses. Tree Physiol. 9, 127– 146.