Carbon consequences of forest disturbance and recovery across the conterminous United States

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[1] Forests of North America are thought to constitute a significant long-term sink for atmospheric carbon. The United States Forest Service Forest Inventory and Analysis (FIA) program has developed a large database of stock changes derived from consecutive estimates of growing stock volume in the U.S. These data reveal a large and relatively stable increase in forest carbon stocks over the last two decades or more. The mechanisms underlying this national increase in forest stocks may include recovery of forests from past disturbances, net increases in forest area, and growth enhancement driven by climate or fertilization by CO_2 and Nitrogen. Here we estimate the forest recovery component of the observed stock changes using FIA data on the age structure of U.S. forests and carbon stocks as a function of age. The latter are used to parameterize forest disturbance and recovery processes in a carbon cycle model. We then apply resulting disturbance/recovery dynamics to landscapes and regions based on the forest age distributions. The analysis centers on 28 representative climate settings spread about forested regions of the conterminous U.S. We estimate carbon fluxes for each region and propagate uncertainties in calibration data through to the predicted fluxes. The largest recovery-driven carbon sinks are found in the South Central, Pacific Northwest, and Pacific Southwest regions, with spatially averaged net ecosystem productivity (*NEP*) of about 100 g C m⁻² a^{-1} driven by forest age structure. Carbon sinks from recovery in the Northeast and Northern Lakes States remain moderate to large owing to the legacy of historical clearing and relatively low modern disturbance rates from harvest and fire. At the continental scale, we find a conterminous U.S. forest NEP of only 0.16 Pg C a⁻¹ from age structure in 2005, or only 0.047 Pg C a^{-1} of forest stock change after accounting for fire emissions and harvest transfers. Recent estimates of NEP derived from inventory stock change, harvest, and fire data show twice the NEP sink we derive from forest age distributions. We discuss possible reasons for the discrepancies including modeling errors and the possibility of climate and/or fertilization (CO₂ or N) growth enhancements.

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1. Introduction

[2] The global imbalance among ocean, industrial, and land use sources/sinks of CO_2 and the amount accumulating in the atmosphere implies significant net CO_2 uptake by the terrestrial biosphere [e.g., *Schimel et al.*, 2001; *Tans et al.*, 1990]. Despite large uncertainty about magnitude and process, analyses tend to point to northern temperate and boreal lands as dominant terrestrial sinks of CO_2 but with considerable controversy regarding attribution to specific regions

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or continents [e.g., *Bousquet et al.*, 2000; *Fan et al.*, 1998; *Gurney et al.*, 2002; *Kaminski and Heimann*, 2001; *Myneni et al.*, 2001; *Tans et al.*, 1990]. However, some recent work suggests far smaller sinks in northern temperate and boreal lands [*Ito et al.*, 2008; *Stephens et al.*, 2007; *Yang et al.*, 2007].

[3] Estimates of the conterminous U.S. forest net carbon uptake from the atmosphere range from only 10 to over 200 Tg C a⁻¹ [U.S. Environmental Protection Agency (EPA), 2010; Houghton et al., 1999; King et al., 2007; Pacala et al., 2001; Turner et al., 1995] in the last 2 decades. Note that here we consider the forest stock change alone rather than the forest sector stock change, where the latter also includes carbon accumulated in wood products (see State of the Carbon Cycle Report [King et al., 2007]).

[4] Techniques for estimating forest carbon fluxes at regional to national scales include three approaches. The stock change method is exemplified in the U.S. report to the United Nations Framework Convention for Climate Change [e.g., U.S. Environmental Protection Agency (EPA), 2008]

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Figure 1. Schematic diagram illustrating stock and flux (italicized) relationships between the forest sector and atmosphere. The entire forest sector net flux (sink) as defined by the stockchange approach is: Net Flux = $\Delta C_{stocks} + \Delta C_{wood products}$. Alternatively, using our model driven estimates of *NEP* it is: Net Flux = *NEP* – *Wood Products Emissions* – *Fire*.

which uses U.S. Forest Service Forest Inventory and Analysis (FIA) data on sequential measurement of tree diameters and/or wood volumes for about 100,000 forest plots at 5– 20 year intervals. Allometric and biomass expansion factors are used to convert volume into forest carbon stocks. The rate of carbon uptake is then estimated as the difference between sequential measurements divided by the number of years in the interval.

[5] Another technique for estimating forest carbon sinks combines estimates of the stand age structure of forests with age-specific carbon accumulation rates, termed the "ageaccumulation" approach in this work. These carbon accumulation rates are inferred from carbon stocks as a function of age [e.g., Houghton, 1999], known as yield tables in forestry literature, and may be derived empirically from inventory estimates of stand volume and age or from a process oriented dynamic growth model. Finally, forest carbon sinks have been estimated from process models that account for the effects of climate variability and CO₂ and nitrogen fertilization but not necessarily for land use and disturbance processes [e.g., Schimel et al., 2000]. These effects are fully contained in the stock change method because it relies on contemporary changes in stocks, but the age-accumulation approach relies on a historical characterization of carbon stock accumulation and thus misses some of the contemporary influences (see Part 4 of Text S1 in the auxiliary material).

[6] Forest stock changes result from the sum of net ecosystem productivity (*NEP*), fire losses, and harvest (see Figure 1). Significant decreases in harvest and fire have not been observed over the past few decades so speculation as to the mechanisms underlying the stock increases have focused more on growth enhancement from either climate change or fertilization with elevated carbon dioxide or nitrogen [*Houghton*, 1999; *McGuire et al.*, 2001; *Nemani et al.*, 2002; *Pan et al.*, 2009; *Schimel et al.*, 2000; *Zhou et al.*, 2003] and on forest growth from post-disturbance recovery or fire suppression [*Caspersen et al.*, 2000; *Hurtt et al.*, 2002; *Pacala et al.*, 2001]. Though the growth enhancement hypothesis has been challenged by *Caspersen et al.* [2000] using forest inventory data, others have argued that plausible rates of growth enhancement cannot be detected using existing inventories [*Joos et al.*, 2002] and recent work presents observational evidence supporting a large climate change or fertilization induced sink [*Cole et al.*, 2010; *McMahon et al.*, 2010; *Thomas et al.*, 2009].

[7] Disturbed forests, if not converted to another land cover type, have the potential to regrow, recover, or even surpass pre-disturbance carbon stocks over decades to several hundred years. The long-standing dogma of the carbon source/sink dynamics for stand-replacing disturbance involves a rapid pulse emission followed by sizable net uptake that gradually declines [*Körner*, 2003; *Odum*, 1969]. This pattern is broadly supported by chronosequence observations of carbon stocks [*Bond-Lamberty et al.*, 2004; *Gough et al.*, 2007; *Pregitzer and Euskirchen*, 2004; *Richter et al.*, 1999; *Thornton et al.*, 2002] and forest-atmosphere net CO₂ exchange [*Amiro et al.*, 2010; *Barford et al.*, 2007], but the precise post-disturbance carbon dynamics vary by forest type and climate and this detail remains poorly characterized.

[8] The analysis reported here attempts comprehensive assessment of the carbon consequences of past and present forest disturbance and recovery across the conterminous United States. We ask if the forest age structure of the conterminous U.S. forests accounts for the stock changes reported by the FIA. Our approach utilizes the national forest inventory data (and uncertainties) to constrain the forest disturbance and recovery processes represented in an ecosystem carbon cycle model to obtain regional and national estimates of carbon consequences. The basic method can be described as having two main steps. First, we derive forest type and climate specific post-disturbance NEP trajectories by fitting a first-order terrestrial carbon cycle model (CASA, [Potter et al., 1993; Randerson et al., 1996]) to grow wood stocks consistent with FIA data. Second, these characteristic trajectories are applied to landscapes with forest age maps obtained from FIA age distributions to derive maps of NEP and biomass. As such, our approach corresponds to the ageaccumulation method for estimating forest carbon sinks as described above. Results represent carbon dynamics of forested ecoregions across the conterminous U.S. to provide a continental-scale view of forest recovery from past disturbances. In addition, we formally propagate the uncertainty in FIA age-biomass trends using a Monte Carlo approach, as well as examine to what degree results are sensitive to uncertainty in the model's parameterization of carbon turnover time, and dependence on light, moisture, and temperature. Discrepancies between FIA estimates of stock changes and those from our age-accumulation modeling are assessed in terms of modeling errors and potential growth enhancements above and beyond recovery, similar to Houghton [2003].

2. Methods

2.1. Overview

[9] The core of our approach is to estimate the frequency (F) of land area in a region (A_{reg}) , as well as the flux or stock of carbon (Q) each within strata of stand age, forest type (e.g., Aspen-Birch), and site productivity (high or low) (denoted with a, f, p subscripts). Regions are defined according to the

¹Auxiliary materials are available in the HTML. doi:10.1029/2010GB003947.



Figure 2. Conterminous U.S. distribution of forest type groups shown with thick state boundaries that trace regions from the Resource Planning Act Assessment by the U.S. Forest Service. Colors differentiate FIA forest type groups. The rectangles represent areas where gridded climate and phenology were used in the simulation of fluxes and stocks for each forest type within each rectangle.

Resource Planning Act Assessment by the U.S. Forest Service. From this we calculate the regional mass flux or stock $(Q_{reg,s})$ for a particular climate setting (subscript *s*) within each region, as well as its uncertainty (δ , described further below), according to

$$Q_{reg,s} = \sum_{a} \sum_{f} \sum_{p} Q_{afp} F_{afp} A_{reg}, \qquad (1)$$

where F is the frequency of forest area adjusted to sum to unity over the three strata and obtained from the regional FIA samples of the area of forest land as described in section 2.2, A_{reg} is the total forested area in the region, and subscripts are: a for stand age, f for forest type group, and p for productivity class. The work reported here is part of a larger project to incorporate stand age derived from Landsat time series data. In this parallel effort, specific scenes for Landsat time series were obtained from a statistically rigorous sampling procedure of forest type spatially dispersed within Eastern and Western regions [Goward et al., 2008]. Here we use the climate (temperature, precipitation, incident solar radiation) and phenology for each scene (Figure 2) to simulate fluxes and stocks for each forest type and productivity class within the scene. The scenes within a region are generally good representations of the region except for the Pacific Southwest where coastal forests are not well represented. The scene level fluxes are then aggregated to regional forest fluxes and stocks by averaging across the number of climate settings (scenes, N_s) in a region as

$$Q_{reg,s} = \frac{1}{N_s} \sum_{s} Q_{reg,s}$$

$$\delta Q_{reg,s} = \frac{1}{N_s} \sum_{s} \delta Q_{reg,s},$$
(2)

and conterminous U.S. estimates (subscript *nat*) are obtained from the sum over regions

$$Q_{nat} = \sum_{\substack{reg \\ reg}} Q_{reg}$$

$$\delta Q_{nat} = \sum_{\substack{reg \\ reg}} \delta Q$$
(3)

We note that our estimates do not account for possible changes in forest carbon due to changes in forest area, though in section 4 we explain why this is unlikely to contribute a large carbon source or sink given the rates of current-day net land conversion.

[10] The relationship between fluxes and stocks can be diagramed as shown in Figure 1. The so-called forest sector sources/sinks refer to the net flux between the atmosphere and forest stocks plus wood products stocks. The inventory approach to calculating the net forest-atmosphere flux involves a measured change in carbon stocks over a specified period. A change in forest carbon stocks can occur because of changes in the physiological fluxes of photosynthesis and ecosystem respiration (balanced as NEP), as well as changes in disturbance for example by fire or harvest. NEP can then be inferred as the difference between ΔC_{stocks} and removals from fire and harvest. The net forest sector flux to the atmosphere is the sum of ΔC_{stocks} and $\Delta C_{wood products}$. This approach, used in national reports to United Nations Framework Convention on Climate Change, derives $\Delta C_{wood products}$ from independent harvest records and empirical decay constants for wood products and landfills.

[11] Our approach is to calibrate our modeled biomass as a function of age using forest inventory data. We then apply the biomass and associated *NEP* from forest disturbance and

recovery to the landscape based on the forest area reported by the FIA within strata of age, forest types and productivity classes within each region. In our modeling framework an important driver of ΔC_{stocks} is net primary production (NPP), and the turnover times of wood and detrital pools. NPP allocated to leaves and fine roots is quickly decomposed and cannot represent a persistent (>decadal) sink. The turnover rates of wood and its immediate detrital pool, coarse woody debris, are much slower, on the order of decades, and thus able to account for long-term net carbon fluxes (on the order of a century). Fluxes from large stocks of slowly overturning soil pools are also slow to respond to disturbance. By the time these large soil pools are affected by disturbance, recovery may have already occurred. This phenomenon is expressed as a low sensitivity of NEP to the slow turnover pools in recovering forests (see Text S1, Part 1). Of course the slow soil pools are a significant source or sink in conditions where changes in fluxes into the slow pools are large and longer term such as in permanent conversion from or to forest. This approach allows us to map NEP from recovery, one of the key atmospheric flux components needed to understand source/sink processes. NEP is a purely biological flux dependent on photosynthesis and respiration alone. Fluxes out of the forest arising from harvest or fire combine with NEP to produce net biome productivity (*NBP*) which is equivalent to ΔC_{stocks} . Note that we have neglected the generally smaller fluxes that contribute to NBP such as lateral fluxes of carbonate and organic matter in liquid form as well as volatile organic carbon emissions [see Chapin et al., 2006].

2.2. Data Sources and Modeling

[12] Flux trajectories are derived by fitting forest growth, mortality and shedding, and allocation parameters within the Carnegie-Ames-Stanford Approach (CASA) carbon-cycle process model [Potter et al., 1993; Randerson et al., 1996] to accumulate carbon in aboveground wood biomass consistent with forest inventory data. Productivity in CASA is represented with a light use efficiency approach in which *NPP* is proportional to the fractional absorption of photosynthetically active radiation (f_{PAR}) times an efficiency term modulated by environmental conditions. NPP is allocated to leaves, roots, and wood which have specific turnover rates that reflect the delivery of carbon to nine detrital pools on the surface and in the soil. These pools decompose at specific turnover rates that are also modulated by environmental conditions. Disturbance causes NPP to initially decrease, and removes or transfers carbon between live and detrital pools, the atmosphere, and forest harvest. In this implementation, we adjust the default rate of productivity to match carbon accumulation observed in age-accumulation trajectories from forest inventory data.

[13] Inventory data were obtained from the FIA field plots (FIA Database Version 4), providing means and sampling errors for two attributes: 1) all live, oven-dry aboveground wood biomass, and 2) area of forest land. The quotient of these attributes provides biomass per unit area. Each attribute was sampled within strata of forest type group (28 classes), age (20 year age classes to 200+ years), and lumped into high and low productivity classes, defined as 120 to >225 cubic feet acre⁻¹ annum⁻¹ and 20 to <120 cubic feet acre⁻¹ annum⁻¹ respectively. Inventory samples were drawn

for regions defined by the Resource Planning Act Assessment by the U.S. Forest Service that divides the conterminous U.S. into the Northeast (NE), Southeast (SE), Northern Lakes States (NLS), South Central (SC), Northern Prairie States (NPS), Rocky Mountain North (RMN), Rocky Mountain South (RMS), Pacific Southwest (PSW), and Pacific Northwest (PNW) region (Figure 2). FIA data on forest carbon and area that are available via World Wide Web download include variances for each. However, these variances cannot be exactly combined to estimate uncertainty because of unknown covariance between carbon stock and area [Bechtold and Patterson, 2005]. Statisticians from the FIA (Charles Scott and colleagues, USFS National Inventory and Monitoring Applications Center) processed the national plot data to provide our study with custom products that we employed in this analysis, namely the aboveground live wood biomass per unit area and its variance for each major forest type, age cohort, productivity class, for each region shown in Figure 2. We confirmed that the data in this custom delivery were nearly identical to those obtained from other web-based data servers maintained and made available by the FIA.

[14] For this implementation we drive the CASA model with the f_{PAR} from a smoothed version of the MODIS MOD15A2 product [Nightingale et al., 2009] for each forest type group as well as climatological seasonality of monthly weather using NASA Goddard Institute of Space Sciences (GISS) air temperature anomalies [Hansen et al., 1999] added to a temperature climatology [Leemans and Cramer, 1991], GISS solar radiation [Zhang et al., 2004], and Global Precipitation Climatology Project (GPCP) precipitation [Adler et al., 2003]. These meteorological driver data were sampled at the 1-degree scale while f_{PAR} was provided at 1 km resolution then averaged for each forest type within each of the 28 simulation climate domains. As such, we obtain carbon flux trajectories for each combination of simulation domains (n = 28), forest-type group (n = 3 to 10), and productivity class (n = 2). Forest type group is specified at a 0.01 degree resolution obtained from Zhu and Evans [1994] (http://www.fia.fs.fed.us/library/maps/). Grid cell-level fractions of forest land in high and low productivity classes for each forest type and stand age within each region are specified from county level FIA data.

[15] We modified CASA to capture disturbance impacts on the carbon cycle as follows. The post-disturbance decline and ensuing recovery of *NPP* and fractional allocation to wood (τ) are modeled as:

$$NPP(t) = NPP_{\max}(1 - ce^{-kt}), \qquad (4)$$

$$\tau = \min[1, (t-1)/8 \text{ years})]/3,$$
 (5)

where t is years since disturbance, NPP_{max} is the climatologically averaged net primary productivity independent of a disturbance legacy, c (= 1.5) determines the magnitude of disturbance-induced reduction in NPP, k (= 0.8) determines the rate of NPP recovery, and min is the minimum operator. We introduced this dynamic recovery of NPP after disturbance based on the well documented recovery of NPP [e.g., Amiro et al., 2000; Hicke et al., 2003]. The dynamics of allocation were intended to capture initial investment of NPP



Figure 3. Characteristic trajectories of aboveground live wood biomass regrowth and associated carbon sources/sinks (expressed as net ecosystem productivity, *NEP*) following a stand-replacing disturbance in high productivity Douglas-fir stands of the Pacific Northwest. Results are from the CASA model fit to regrow stocks consistent with 25 independent samples from the forest inventory data (red circles). Net releases in the year following disturbance are as low as $-3000 \text{ g C m}^{-2} \text{ a}^{-1}$ (see Text S1, Part 2, Figure A2.2) rising to above $-500 \text{ g C m}^{-2} \text{ a}^{-1}$ in the second year of regrowth.

into herbaceous biomass with increasing allocation to woody vegetation with age [e.g., *Jokela et al.*, 2004; *Law et al.*, 2002].

[16] In order to parameterize the amount of biomass killed by a disturbance we adopt the following treatment. Regardless of the pre-disturbance biomass, we set the postdisturbance biomass to 50% of the aboveground live wood biomass reported in the 0-20 year age class. This constrains early regrowth to pass through the youngest age-class in the FIA sample. We then estimate the corresponding fraction of live wood, leaves, and roots killed based on the ratio of their abundance prior to disturbance relative to those immediately after disturbance. Eighty percent of the disturbancekilled aboveground wood and all of the disturbance-killed leaves are assumed to be taken off site and entrained into wood products or promptly combusted and are collectively accounted for as "removals" (fire and harvest), akin to the treatment by Turner et al. [1995]. The remaining 20% of disturbance-killed aboveground wood is subject to on-site post-disturbance decomposition as it enters the coarse woody debris pool, also consistent with Turner et al. [1995]. Disturbance-killed roots decompose on-site, for which 30% of dead coarse roots are assumed to enter a belowground coarse woody debris pool, and 70% of dead coarse roots and all dead fine roots enter the soil metabolic and structural pools, broadly consistent with results presented by Gough et al. [2007] and Meigs et al. [2009]. We note that these and other prescriptions are uncertain, likely vary among disturbance and forest types, and are the subject of ongoing research. In summary, biomass killed in a disturbance event is the difference between pre-disturbance biomass and 50% of the 0-20 year biomass reported by the FIA data. Of the killed biomass, 80% of aboveground wood and all leaves are removed (via harvest or fire) and 20% of the killed aboveground wood enters the coarse woody debris pool. The belowground wood and roots killed by disturbance remain on site to decompose. Figure 3 offers an example, in which aboveground biomass is reduced to $2.5/30 \text{ kg C m}^{-2}$, or <10%, and 80% of this 90% reduction in biomass is assumed to be removed (harvest or fire) while the other 20% is left to decompose on site.

[17] With this approach it is then possible to estimate biomass removals as:

$$R = A_1 B_{pre} \left(1 - f_{left} \right), \tag{6}$$

where A_1 is the area of forested land assigned a stand age of one year based on the FIA age histogram, B_{pre} is the predisturbance aboveground biomass, and f_{left} (= 0.8) is the fraction of biomass left to decompose on-site. Each of these varies by forest type, region, and productivity class. This estimate is subject to errors in the area of forest assigned to this young age class, the age of forests prior to disturbance and correspondingly the biomass pre-disturbance, and uncertainty in the fraction of biomass in disturbed forests that is taken off-site as wood products. Removals from non-stand replacing harvests are not considered in this approach but later in section 4 we attempt to quantify the impacts of this assumption.

[18] The next step in our model parameterization involves calculating the wood production - wood age pair that allows the best match to the inventory data of aboveground stock recovery, with the following multistep procedure. First, we calculate a target aboveground live wood biomass $(B^*, \text{ in g C m}^{-2})$ from the mean in the 100 to 200 year old age classes, including successively younger age classes in 20 year increments to ensure a minimum of two samples. The target age $(A^*, \text{ in years})$ is obtained from the average of old classes sampled to derive B^* . Second, we approximate the rate of annual aboveground live wood biomass produc-tion (P_w , in g C m⁻² a⁻¹), which is a function of *NPP* and wood allocation, that would be required to obtain B^* by A^* for a range of possible wood turnover times (A_w) spanning 30 to 300 years in increments of 10 years by solving a simplified integral form of the differential equation for biomass with time $(dB/dt = P_w - B/A_w)$ to yield:

$$P_w = \frac{B^*}{A_w \left(1 - e^{\frac{-A^*}{A_w}}\right)}.$$
(7)

Thus, we obtain an array of possible P_w - A_w pairs that would grow the target biomass by the target age. In a few particular

cases this approach yielded implausible wood ages, but with negligible consequence for the scales of analyses presented in this study. The third step is to select the pair that provides a biomass recovery curve most like the inventory sample assessed as that which minimizes the sum of squared error between modeled and sampled aboveground live wood biomass. Modeled biomass is calculated at the sample ages (t, in years) according to:

$$B(t, A_w) = B_o e^{\frac{-t}{4_w}} + P_w A_w \left(1 - e^{\frac{-A^*}{4_w}}\right),$$
(8)

where B_0 is an assumed initial biomass of 200 g C m⁻². Last, we linearly rescale the model's default monthly *NPP* values to provide an annual total *NPP*_{max} inferred from the fitted rate of P_{w} , as:

$$NPP_{\max} = \frac{P_w}{\tau \alpha},\tag{9}$$

where $\tau (= 1/3)$ is the allocation of *NPP* to wood and $\alpha (= 0.75)$ is the fraction of this that is allocated to the aboveground wood pool (stems and branches) instead of belowground (coarse roots).

[19] Following determination of P_w and A_w parameters, characteristic carbon flux trajectories (Q_{afp}) are developed from, first, a 1000 year spin-up to steady state carbon pools. This is followed by a disturbance prior to the disturbance of interest with 75 years of regrowth for all forest types except loblolly pine and longleaf/slash pine (30 years) and Douglas-fir (200 years). The age of trees at harvest is set to be just older than the typical peak in age histograms reported by the FIA (see Part 2 and Figure A2.3 in Text S1), except where harvest rotations are known to be short (SE and SC pines), or where harvest over previous decades tended to target old growth forests with high economic value (Douglas-fir [Cohen et al., 2002]). This "pre-disturbance" is important in that it establishes the amount of live carbon subject to disturbance-induced disposition, meaning taken off-site as removals or decomposing on-site. Finally, we simulate the most recent disturbance after which we allow 200 years of regrowth to characterize carbon dynamics with stand development. These procedures result in a group of carbon stock age trajectories analogous to yield tables.

[20] We have not modified CASA's default treatment of heterotrophic respiration emerging from microbial decomposition of soil and litter carbon and associated transfers among carbon pools. The general equation for the rate of heterotropic respiration from a specific carbon pool is

$$Rh_{pool} = C_{pool}k_{pool}W_{resp}T_{resp}M,$$
(10)

where C_{pool} is the amount of carbon in a pool, k_{pool} is the pool-specific decay rate constant, W_{resp} and T_{resp} control how respiration depends on soil moisture and temperature states, and M is the carbon assimilation efficiency of the microbes. Total heterotrophic respiration is the sum of that from each of the nine detrital pools.

2.3. Uncertainty Analysis

[21] A formal propagation of uncertainty from sampling errors (coefficient of variation, CV) for forested area (± 10 to 100%) and total aboveground live biomass (± 10 to 100%),

and volume to carbon conversion $(\pm 7\%)$ are all included. The uncertainty in inventory aboveground live biomass per unit area is propagated to the predicted fluxes and aboveground live biomass with a Monte Carlo procedure analogous to Tier 2 uncertainty estimation in the IPCC Good Practice Guide [Intergovernmental Panel on Climate Change (IPCC), 2000]. The model was fit to 25 different biomass regrowth trajectories, where each trajectory was generated from random samples of the normally distributed aboveground live wood biomass for each age class (25 draws of biomass per unit area from each of 10, 20-year age classes). Forcing the fitted trajectory to conform to the assumption that biomass increases monotonically and saturates with age strongly constrains the resultant age-accumulation curves and their variances (Figure 3). An additional 7% uncertainty is used to account for tree volume to carbon conversion [Smith and Heath, 2001]. Put together this method involved over 130,000 simulations of age-dependent dynamics of forest carbon fluxes and stocks. The uncertainty of forest area and aboveground live biomass per unit area is obtained from the FIA data.

[22] As shown in equations (1)–(3) above, independent uncertainties in the product of flux or stock with area are combined as $\delta Q_{total} = (\frac{\delta Q_{afp}^2}{Q_{afp}^2} + \frac{\delta A_{afp}^2}{A_{afp}^2})^{1/2}$ [*Taylor*, 1997]. We adopt a conservative assumption of non-random error propagation for which uncertainty is additive over forest types, productivity classes, and ages, and also additive spatially for a simulation domain, a region, or the nation. This uncertainty aggregation is analogous to a Tier 1 uncertainty described in the IPCC Good Practice Guide [*IPCC*, 2000].

[23] Uncertainty in *NEP* also derives from model structure (not analyzed) as well as model parameterization of light, moisture, and temperature sensitivity of heterotrophic respiration and/or *NPP* expressed in the CASA model. As described in Text S1, Part 1, Section 1, we analyzed *NEP* responses to a 2% increase of six representative parameters including the maximum light use efficiency, moisture dependence of *NPP*, optimal temperature for *NPP*, turnover time of the slow soil carbon pool, and both the Q10 and moisture dependence of heterotrophic decomposition of soil carbon. We use a 2% change in parameter value in order to obtain a detectable response in *NEP* but for ease of discussion the sensitivities are divided by two and expressed as % change in *NEP* for a 1% change in parameter value (see Text S1, Part 1).

3. Results

3.1. Carbon Trajectories

[24] Using CASA as a controlled growth model accurately reproduces the accumulation of aboveground forest carbon stocks with time since a stand replacing disturbance as informed by FIA data (Figure 3), imposing a powerful, albeit partial, observational constraint on net ecosystem carbon flux trajectories with stand age. Additional data on litter, woody debris and soil carbon dynamics would provide much needed additional constraints on estimated ecosystem C dynamics. More rapid regrowth of aboveground stocks in the high productivity class causes higher amplitude trajectories for carbon stocks and fluxes (Figures A2.1 and A2.2 and Part 2 in Text S1) with larger post-disturbance sources

Table 1. Regional Distribution of Forest Area, Live Biomass (Live *B*), Ratio of *EPA* [2008] to This Study's Forest Area, Ratio of *EPA* [2008] to This Study's Live Biomass, Net Ecosystem Productivity (*NEP*), and Fraction of Forest That Is Less Than 25 Years Old and Less Than 5 Years Old

Region ^a	Area (10^9 m^2)	Live B (Tg C)	f _{EPA08} Area ^b	$f_{\rm EPA08}$ Live $B^{\rm c}$	$NEP (Tg C a^{-1})$	Percent < 25 Years	Percent < 5 Years
NE	339	3,253	1.11	1.01	32 ± 5.5	10	2
NLS	212	1,236	0.99	1.11	12 ± 1.3	16	3
SE	355	2,621	1.00	0.94	30 ± 3.5	39	8
SC	384	3,220	1.27	1.00	40 ± 4.2	37	8
RMN	192	1,189	0.98	1.10	7 ± 1.8	21	5
RMS	493	1,815	0.81	0.97	11 ± 5.5	1	0
PSW	127	1,522	1.06	0.95	13 ± 2.8	11	2
PNW	202	2,162	1.05	1.13	18 ± 3.0	19	4
Total/Mean	2,303	17,017	1.03	1.08	164 ± 27.7	17	4

^aNE, Northeast; NLS, Northern Lakes States; SE, Southeast; SC, South Central; RMN, Rocky Mountain North; RMS, Rocky Mountain South; PSW, Pacific Southwest; PNW, Pacific Northwest.

^bRatio of EPA [2008] to this study's forest area.

"Ratio of EPA [2008] to this study's live biomass.

that give way to stronger sinks with ensuing forest regrowth. The Monte Carlo simulation approach provides an envelope of trajectories (Figure 3) that enables formal uncertainty propagation through all scales of the analysis (regional forest types to conterminous U.S. forestlands). Absolute uncertainty surrounding NEP tends to peak where forest uptake is maximum (peak *NEP*) and then diminishes with forest age (Figure 3). An important exception, not shown in Figure 3, is the often large uncertainty in carbon emission in the years immediately following disturbance; large because of variation in the pre-disturbance carbon stocks and the amount of dead wood that decomposes on-site. The timing of NEP crossover from source to sink is surprisingly insensitive to variability in biomass accumulation (not shown), and generally occurs at ages <20 years (e.g., Figure 3; Figures A2.1 and A2.2 and Part 2 in Text S1) consistent with many reported chronosequence fluxes [e.g., Bond-Lamberty et al., 2004; Gough et al., 2007; Goulden et al., 2011; Law et al., 2004; Litvak et al., 2003; Noormets et al., 2007; Pregitzer and Euskirchen, 2004]. Patterns of post-disturbance uptake of carbon in regrowing forests vary widely across regions of the conterminous U.S. as well as by forest type group and productivity class (Figures A2.1 and A2.2 and Part 2 in Text S1). Forest inventory data describing the recovery of aboveground live wood biomass carbon with stand development act as a strong constraint on the modeled carbon cycle including the rates of litter and soil carbon turnover and decay.

[25] Our analysis of the sensitivity of the model to parameters revealed that nearly all of the sensitivities are less than 1% indicating general dampening of parameter perturbations and suggesting that uncertainties in these parameterizations do not expand as they propagate through to modeled *NEP* (see Text S1, Part 1, Table A1.1). Model structure and parameter uncertainties are not included in our analysis but are expected to add about $\pm 10\%$ based partly on a sensitivity analysis presented in Text S1.

3.2. Continental Patterns

[26] Regional variations in disturbance rates and *NEP* across the conterminous U.S. reflect harvesting practices and regional climates (Table 1; also Table A2.1 and Figures A2.1–A2.3 in Text S1). Forests growing in relatively dry settings (e.g., Rocky Mountain South (RMS)) have low

NEP, contrasted by high carbon sequestration rates in the Pacific Southwest and Northwest, as well as Southeastern and South Central regions (Table A2.1 in Text S1). The largest rates of disturbance, and the largest sinks of carbon stimulated by forest recovery from recent disturbance ("regrowth sinks"), are in Southeastern (SE), South Central (SC), and Pacific Northwest (PNW) regions. These regional biologically driven sinks do not reflect net biome productivity because recovery trajectories do not include the fate of disturbance-induced carbon removals such as carbon taken offsite to lumber, pulp and paper mills or released promptly on-site by natural and anthropogenic fires (see schematic in Figure 1). This is addressed further in the discussion where we present the forest-to-atmosphere carbon exchange.

[27] At the continental scale, the biological recovery sink (*NEP*) is estimated to be 164 \pm 28 Tg C a⁻¹ (Table 1), or about 71 g C m⁻² a⁻¹ averaged for the 230 million hectares of forestland represented here. Nearly all (84%) of this NEP sink results from net growth of live carbon stocks with only a small fraction shared among soil carbon (6%), litter carbon (2%), and coarse woody debris (8%) stocks (Table 2). Our sample includes 93% of the conterminous U.S. forestland, reported to be 250 million hectares [EPA, 2008]. Our analysis did not include the Northern Prairie States region ($\sim 6\%$ of total area and \sim 5% of total carbon) because the effort was originally connected to a Landsat remote sensing analysis whose random sample did not draw Landsat scenes for this region. As verification, our stand-age histograms by region generally correspond well with a similar presentation of the same basic data as recently published by Pan et al. [2011]. Comparing to regional statistics of forest area and live biomass reported by the EPA [2008] we find good correspondence overall (Table 1).

[28] The estimated uncertainty arising from forest area, aboveground wood biomass, and conversion of diameter measurements to volume and carbon produced relatively small uncertainty estimates in our biomass and fluxes. This is partly due to the continuous, monotonically increasing, and saturating growth form imposed by the process-model approach. This functional form is more plausible than one that would allow abrupt increases and decreases in above-ground live wood biomass with stand development (i.e., stand age) as are commonly found in the inventory data when arrayed as a chronosequence (e.g., Figure 3, 110–150 year

Table 2. Changes in Carbon Stocks (Tg C a^{-1}) in the Year 2005 Reported in Different Studies

	This Study	EPA [2008]
Δ Total Soil C	3	9
ΔLitter C	1	15
Δ Coarse Woody Debris (CWD)	4	16
ΔCWD Below	0	_
Δ Live C	39	133
Total Stock Change	47	173
Removals ^a	117	162
Harvest ^b	107 ^c	132
Wildfire Emissions ^d	10	30
NEP ^e	164	335
Wood Products Emissions ^f	102	102
Wood Products Storage ^g	5	30
Forest Sector-Atmosphere Exchangeh	52	203

^aFor *EPA* [2008] calculated as: Removals = Wildfire Emissions + Harvest.

Harvest. ^bThis study inferred as: Harvest = Removals – Wildfire Emissions.

^cItalicized values are inferred from mass balance.

^dThis study estimated wildfire emissions from the Global Fire Emissions Database v3 (GFED3) [*van der Werf et al.*, 2010].

^cFor the purposes of this table calculated as $NEP = \Delta$ Total Soil C + Δ Litter C + Δ CWD + Δ CWD Below + Δ Live C + Removals; values differ from those in Table 1 due to differences in the method of aggregation and associated averaging of terms.

^fThis study adopted values reported by the EPA [2008].

^gThis study calculated as Wood Products Storage = Removals – Wood Products Emissions – Wildfire Emissions.

^hThis study calculated as Forest Sector-Atmosphere Exchange = NEP – Wood Products Emissions – Wildfire Emissions.

biomass). Imposing the model's growth form has the effect of filtering out some of the variance inherent in chronosequence trajectories of biomass with stand age. Other uncertainties arising from model structure and assumptions about disturbance severity/type, age, partial cutting, natural wood turnover, and a possible age-related decline in productivity are evaluated by judging the impacts of these factors on model output through sensitivity analyses (see Text S1, Part 1, Section 2).

[29] We used the 1km forest type map to produce a gridded map of *NEP* and its uncertainty (from variances in FIA data) for the conterminous U.S. (Figure 4). Within each region each forest type considered was assigned the regional estimate of *NEP* for that forest type and region. Regional forest *NEP* sinks range from >25 to 200 g C m⁻² a⁻¹ with eastern and western forests generally ranging from 75 to 100 g C m⁻² a⁻¹. The RMS region is predicted to be uniformly <50 g C m⁻² a⁻¹. The discontinuities conforming to state borders between West Virginia and Virginia and between Washington and Idaho occur because the same forest types in each neighboring region have regionally specific and different growth and disturbance rates.

[30] As an independent evaluation of our predicted stocks and fluxes we compared our results with five available studies on chronosequences for forest types in the conterminous U.S.. These studies sometimes do not include estimates of both fluxes and stocks for different aged forests and estimates used various biometric and flux measurement approaches. The small number of sites with available data, variability in the data, and issues of extrapolating fine scale measurements to regional responses do not justify quantitative comparisons and demonstrate the need for more of these types of measurements and for finer scale modeling. The results of these comparisons are shown in Text S1, Part 3, Figure A3.1. Agreement varies widely between the comparisons at the different sites/regions.

4. Discussion

[31] Comparing estimates of the conterminous U.S. forest NEP sink from multiple studies (Table 3) reveals a general separation between age-accumulation and stock-change methods. This comparison spans estimates for the 1980s to more recent years (e.g., 2005-2006), but this may be justified because atmospheric inversions seem to indicate a longterm mean sink in North America during the '80s and '90s but with large interannual variability [Baker et al., 2006]. Four of the six age dependent analyses that seek to represent carbon emissions and sequestration with post-disturbance recovery provide lower estimates of the forest NEP sink when compared to the four stock-change analyses, with 82 g C m⁻² a⁻¹ versus 154 g C m⁻² a⁻¹ averaged across their respective studies, or 189 Tg C a⁻¹ versus 354 Tg C a⁻¹ when integrated across U.S. forest area. This is even true when process-oriented studies rely on forest inventory data to prescribe the rate of aboveground carbon stock recovery with time, as well as the area of forest of different ages. For example, regarding NEP alone we find general agreement with Turner et al. [1995] who reported 203 Tg C a⁻¹ compared to our estimate of 164 Tg C a^{-1} . In contrast, the EPA [2008] stock-change estimate of forest NEP is twice as large as this study's age-accumulation result (335 compared to 164 Tg C a^{-1} , Table 2). The disparity between the stockchange method and these other, age-accumulation results is likely due to large annual to decadal increases in stocks measured in the inventory that then implies greater NEP (regrowth). What causes this general disagreement remains unclear, though growth enhancement is a plausible explanation of the difference, consistent with recent publications [Cole et al., 2010; Luyssaert et al., 2010; McMahon et al., 2010; Thomas et al., 2009]. Effects of growth enhancement are implicit in the stock-change method but not well incorporated in the age-accumulation methods that emphasize effects of regrowth dynamics, even when these methods rely on inventory-derived chronosequences to constrain biomass accumulation as in the present study (see Part 4 in Text S1 for an illustration of this). There is also one study reported in Table 3 including only the effects of climate and CO₂ fertilization based on an ensemble of models for the conterminous U.S. [Schimel et al., 2000]. If this sink were added to the forest recovery (age-yield table) estimates the results would be more in line with the stock change approach.

[32] We note that the *EPA* [2008] estimate of total removals is 38% higher than that estimated with our modeling approach (= 162/117, Table 3). About half of the difference is due to elevated fire emissions reported by the *EPA* [2008], however this estimate is much higher than the rate of forest fire emissions being reported elsewhere [e.g., *van der Werf et al.*, 2010]. This difference translates directly into the *NEP* estimated from the stock change method, and elevates the *EPA* [2008] estimate by 20 TgC a⁻¹ relative to the estimate from our approach. The *EPA* [2008] report also estimates 25 TgC a⁻¹ greater removals by harvest. There are two ways we could adjust our methodology to try to match this rate of removal. We could either, a) increase the amount



Figure 4. Map of average (a) net ecosystem productivity and (b) uncertainty expressed as one standard deviation (*NEP* in g C $m^{-2} a^{-1}$) for forests of the conterminous U.S.

of biomass removed by disturbances on average by increasing the age and hence biomass of disturbed forests, b) increase the amount of biomass removed on average by removing a larger fraction of pre-disturbance biomass and leaving less to decompose on site, or c) increase the area of forests disturbed by increasing the young-aged fraction of forests if we believe the stand age attribute offers a biased representation. All of these would increase removals but they would have different effects on NEP. The first option would decrease NEP because more disturbance-killed material would be left on-site to decompose and be emitted from forests. The second approach would increase NEP because of reduced on-site decomposition. The third approach would decrease NEP because a larger fraction of forested area would be concentrated at young stand ages (<15 year old) where NEP is either a large negative value or near zero (Figures A2.1 and A2.2 in Text S1). And in the extreme case that we simply adjusted our NEP estimate upwards to cover the difference in removals, the *EPA* [2008] estimate would still be 126 TgC a^{-1} higher than the estimate emerging from our age-accumulation method.

[33] A term-by-term comparison between stock changes reported from inventory methods and those derived in the current study's age-accumulation approach indicates that a change in live carbon stocks makes up a large portion of the difference in *NEP* estimated with the two methods (Table 2). Annual increases in soil carbon, coarse woody debris, and litter pools are also noticeably lower in the present analysis compared to those reported by the *EPA* [2008; 2010] (Table 3). Because our method, necessarily, produces aboveground live wood biomass and forest area estimates that are consistent with, or wholly derived from, the inventory itself (Table 1), our relatively low estimate of annual changes in live stocks (Table 2) does not appear to be caused by underestimation of a) stocks, or b) forest area. These differences translate to the full forest sector-

Source	Approach	Mean NEP	Low	High	ΔC_{stocks}	Harvest	Fire
Schimel et al. [2000] ^b	Р	80					
This Study ^c	AA	164	136	192	47	107	10
Houghton et al. [1999] ^d	AA	182			10	92	80
Turner et al. [1995] ^e	AA	203			79	124	0
Houghton [2003] ^f	AA	207			35	92	80
Woodbury et al. [2007] ^g	ΔC_{stocks}	270	256	293	108	132	30
<i>EPA</i> [2008] ^g	ΔC_{stocks}	335			173	132	30
Birdsey and Heath [1995] ^h	ΔC_{stocks}	368			211	127	30
Hurtt et al. [2002] ^d	AA	372	282	442	230	92	50
Pacala et al. [2001] ^d	synthesis	392	312	472	220	92	80
King et al. [2007] ^d	$\dot{\Delta} C_{stocks}$	411	383	439	236	145	30

Table 3. Forest Carbon *NEP* and Stock Change for the Conterminous U.S. (Tg C a^{-1}) From This and a Sample of Previously Published Estimates^a

^aEstimates are classified according to approach: age structure–C accumulation (*AA*), stock change ($\Delta C_{stocks} = NBP$), or process model (*P*), where *P* is a process model ensemble result that accounts for CO₂ and climate effects [*Schimel et al.*, 2000; *Pacala et al.*, 2001] and combines approaches for an overall estimate and range. Low and High refers to 1 standard deviation about the mean estimate.

^bFor 1980–1993.

^cFor 2005, C stock change = NEP - Harvest - Fire (see Table 2), our total removals are 117 Tg C a⁻¹ that includes fire and harvest, assume fire at 10 Tg C a⁻¹ (see GFED3 of *van der Werf et al.* [2010] and *Zheng et al.* [2011]).

^dFor the 1980s.

^eFor ~1990.

^fFor 1990s, harvest and fire from Houghton et al. [1999].

^gFor 2005.

^hFor 1992.

atmosphere net exchange, whereby the stock-change method estimates a much larger forest sector C sink than obtained with this study's age-accumulation approach (Table 2).

[34] Our maps of conterminous U.S. forest *NEP* and its uncertainty (Figure 4) are one of the first of which we are aware (though see *Woodbury et al.* [2007]) and will be used in further study of the impact of the forest disturbance fluxes on atmospheric CO_2 as a boundary flux for atmospheric transport models much as gridded fire, fossil fuel burning, and ocean CO_2 fluxes are prescribed in forward and inverse atmospheric modeling [e.g., *Peters et al.*, 2007]. Complete accounting of forest sector fluxes would additionally require maps of fire [e.g., *van der Werf et al.*, 2010] and wood products emissions. These studies will allow assessment of the detection limits for the magnitude and spatial variability of sinks in top-down studies.

[35] This study's approach imposed a number of simplifying assumptions that were necessary given the initial scope of our work. Below we address some of these and their potential implications regarding interpretation of our results.

[36] (1) We assume characteristic regrowth trajectories regardless of disturbance type even though the nature of post-disturbance carbon dynamics is sure to vary between fire, harvest, hurricane, and the severity of disturbance. For instance, around twice as much coarse woody debris (CWD) may remain on site after a severe fire compared to clear-cut harvest [*Tinker and Knight*, 2000]. This remaining detritus provides a source of CO₂ for a prolonged period after disturbance. Using data reported by Smith et al. [2009] and the National Interagency Fire Center (to account for Alaskan fires) we estimate that for the year 2004 the ratio of burned area to harvested area in the eastern U.S. was about 0.30 compared to 0.46 in the west. In terms of carbon removals though, our forest fire estimates from the Global Fire Emissions Database v3 (10 Tg C a^{-1}) are much smaller than our estimated harvest removals (107 Tg C a^{-1}). Because the total removals are dominated by harvest, as is the total area disturbed, accounting for differences caused by fire versus

harvest would not significantly change our results or conclusions. Furthermore, some but not all of this variation is captured by the Monte Carlo approach, as well as with stratification by site productivity and across regions. Partial disturbances such as defoliation events are not represented with the current methodology, and discussed further below.

[37] (2) Our assumption of equivalence between forest age and time since disturbance does not account for the effects of partial disturbance that allows older aged trees to remain among regenerating cohorts or the dynamic state of old forests that have reached the age of natural mortality and reestablishment. This particular issue has been examined by *Bradford et al.* [2008] for a subalpine forest system. In that study a large part of the age versus years since disturbance discrepancy arose in stands undisturbed for long periods of time (>200 years), longer than what we analyze in this work. From FIA data we estimate that about 3% of forested land is >200 years old for conterminous U.S.

[38] (3) Our analysis is sensitive to biases in the ages associated with the aboveground live wood biomass trajectories, as explored in an extensive sensitivity analysis described in Text S1, Part 1, Section 2. For instance, if the FIA ages are older (younger) than actual stand ages, our predicted recovery sink is underestimated (overestimated). This, of course, is an issue with any approach proposing to use FIA age structure information to estimate fluxes and stocks [e.g., *Pan et al.*, 2011]. Despite this sensitivity, we note that bias in stand age is not likely to be large enough to explain the major differences between the stock-change and age-accumulation methods (Table A1.2 in Text S1).

[39] (4) The FIA data we used to construct aboveground live wood biomass trajectories include the effects of partial cuts, which are a significant component of disturbance in U.S. forests contributing >50% of the total harvested area [*Smith et al.*, 2009]. Reported stand ages reflect the trees not cut while the plot level biomass will be lower in these cases producing lower regional aboveground live wood biomass for mid and older aged stands. These partial cutting practices

(e.g., salvage logging, selective logging, thinning), which remove biomass from forested plots without resetting the FIA-recorded stand age, could have a substantial influence on the forest NEP estimate. The implicit inclusion of plots that experienced partial cutting (not fully stocked) likely results in correct biomass estimates but lowers the slope of regrowth trajectories resulting in some underestimation of NEP. In an extensive sensitivity analysis (Text S1, Part 1, Section 2) we find strong sensitivity to such biases, with a 10% elevation of biomass leading to a 14% elevation of conterminous U.S. forest NEP. This is equivalent to a 2.3 Tg C a^{-1} increase in NEP for each 1% increase in biomass. Despite this large sensitivity to biomass trajectories, to account for the approximately 160 Tg C a⁻¹ difference, the reported biomass would need to have been underestimated by 70% (= 160 Tg C $a^{-1}/2.3$ Tg C a^{-1} per 1% increase in biomass). Additional sensitivity analyses examining effects of natural, partial disturbances that lead to wood turnover and on site decomposition (e.g., ice storms, blowdowns, insect damage) indicate that they are also unlikely to present a large error/bias in our estimate.

[40] (5) We do not take into account annual changes in forest area which could contribute to the discrepancy between recovery and stock change approaches. The *EPA* [2008] reports indicate that forest area has been increasing at a rate of 0.24% a^{-1} since 1990. If we assume that new forests would range between 1 to 5 kg C m⁻² over an age range of 0 to 20 years (e.g., see Figure 3) then the average accumulation rate for these forest would be about 250 g C m⁻² a^{-1} . Correcting this for the increase in forest area produces an added 1.7 Tg C a^{-1} sink, indistinguishable within the uncertainties of our method.

[41] (6) It has been proposed that forest carbon sinks may be driven by long-term trends in temperature, precipitation, nitrogen deposition, and atmospheric CO₂. Responses to these trends are embedded in the biomass-age trajectories from the inventories in complex ways and more recent increases in growth may not be accounted for in our approach (see Text S1. Part 4 for a thorough examination of this). Others have addressed this and concluded that forests are not responding in a systematic way to these trends [Caspersen et al., 2000], that forest inventory data are not precise enough to resolve expected responses to trends [Joos et al., 2002], and that a smaller number of inventory measurements on forests of known disturbance history do indeed show strong trends in growth enhancement correlated with trends in temperature and atmospheric CO₂ [McMahon et al., 2010; Thomas et al., 2009]. In a study of global terrestrial carbon sinks using CASA, Thompson et al. [1996] showed that in order to obtain a terrestrial carbon sink of $\sim 2 \text{ Pg C/yr}$ broadly consistent with top-down sink estimates, NPP has to undergo a sustained increase of 0.18% per annum. Similar estimates have been reported by others [e.g., Joos et al., 2002]. Our own sensitivity analysis (not shown) showed that a sustained increase in NPP of 0.2% per annum would increase live biomass in a typical 60 year old forest by approximately 5% and is thus a weak or undetectable signal in a biomass chronosequence. A 0.2% annual increase in NPP is implausibly large sensitivity of photosynthesis to CO₂ ($dNPP/NPP \ge CO_2/dCO_2$ of ~0.96, or near proportional response) and would require other positive feedback

mechanisms such as nitrogen fertilization and/or climate trends to operate in parallel. We conclude that plausible responses of forest sinks to climate and CO_2 or N cannot be resolved with FIA biomass-age trajectories alone such as those we utilize here and that have been proposed by others [e.g., *Pan et al.*, 2011].

[42] The approach described here is also sensitive to uncertain parameters including rates of wood mortality and coarse woody debris decomposition, as well as the amount of dead aboveground and belowground biomass left to decompose onsite following disturbance. It lacks a standing dead wood pool that may be important because it decomposes much more slowly than dead wood in contact with the forest floor [e.g., Harmon and Hua, 1991; Harmon et al., 2004; Janisch et al., 2005]. In our ongoing efforts, literature is being exhaustively explored to better constrain these and other parameters and processes. Additional effort is being invested in attributing disturbances to particular drivers based on spatial and geospatial records of fire and insect outbreaks. While valuable, it is unlikely that such refinements and constraints will reconcile the large differences between the age-accumulation and stock-change approaches, something that may benefit from a close collaboration with inventory experts to clarify differences of approach and accounting, as well as more comprehensive assessment of possible growth enhancement effects. Future efforts at improving this study's approach will include more detailed prescriptions of type and severity of disturbances, further comparisons with site observations as they become available, and analyses of top-down atmospheric constraints on source/sink magnitude and distributions. Estimates would also be better constrained if additional data on litter, dead wood and soil organic carbon dynamics were available from field studies.

5. Conclusions

[43] Forest Inventory and Analysis data provide unique and valuable information about disturbance history and associated carbon stocks and fluxes with forest recovery. By using these data to constrain forest growth rates in a carbon cycle model, this study provides a more detailed estimate of carbon sources and sinks from recent forest disturbance and recovery across regions and forest types of the U.S.. One of our key findings is a much smaller net sink of carbon in conterminous U.S. forests than previously estimated with the stock-change approach as used in UNFCCC reporting [EPA, 2008]. The source of across study inconsistencies among national estimates of stocks and fluxes remains largely unexplained. The paucity of observed net ecosystem productivity and biomass chronosequences limits our ability to evaluate modeled responses. These types of observations are critically needed in order to adequately test models representing disturbance and subsequent recovery.

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Carbon consequences of forest disturbance and recovery across the conterminous United States

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Introduction

This online material, made available in a single .pdf document, offers additional and deeper details on (1) analyses of how sensitive our results are to possible errors and biases (Part 1); (2) results of net ecosystem productivity and forest area within strata of forest-type and productivity class for each region (Part 2); (3) comparison of this study's results to a few *in situ* measurements of forest chronosequences (Part 3); and (4) the limited representation of growth enhancements in chronosequences and with the age-accumulation method (Part 4).

Part 1. Model Sensitivity Analysis

Section 1. Sensitivity of NEP to Light, Moisture, and Temperature Parameterizations Table A1.1. Results of sensitivity experiments expressed as the response coefficient, S, and equivalent to the percent change in an NEP characteristic caused by a 1% change in parameter, Section 2. Sensitivity of NEP to Errors in Biomass Accumulation with Stand Age Table A1.2 Conterminous US forest carbon fluxes and stocks as presented in the core manuscript for comparison to four sensitivity experiments.

Part 2. Forest Type Group- and Region-Specific NEP Trajectories and Area Distributions with Age and Associated Model Statistics.

Table A2.1. Region-average statistics for forest types contributing at least 5% of the region's total forest area.

Figure A2.1. Forest Type Group and Productivity Class – specific trajectories of net ecosystem productivity (NEP) following stand replacing disturbances by regions of the conterminous U.S.

Figure A2.2. Forest Type Group and Productivity Class – specific trajectories of net ecosystem productivity (NEP) in the first 20 years following stand replacing disturbances by regions of the conterminous U.S.

Figure A2.3. Forest type group- and region-specific area distributions from FIA data expressed as a fraction of total forested area by forest type in each region. Only those forest types contributing greater than 5% to region-total forested area are shown.

Part 3. NEP and biomasss accumulation age trajectory comparison between *in situ* observations of forest chronosequences and constrained-modeling

Figure A3.1. Modeled and inventory-derived live biomass as well as modeled and flux-tower derived NEP for available chronosequences including results from five sites.

Part 4. Limited representation of growth enhancements in chronosequences and the ageaccumulation method

Figure A4.1. Simulated trajectories of biomass accumulation with stand age (b,d), and the temporal derivative of biomass with stand age (a,c) for three different cases. The "No Enhancement" case adopts a constant growth rate. The "Enhanced Trajectory" case has a linear increase in growth rate at 0.2% per year for 100 years. The "Chronosequence Enhancement" illustrates the inferred rate of biomass accumulation assuming the same 100-year, linear increase in growth rate.

Figure A4.2. Simulated trajectories of the temporal derivative of biomass with stand age (top) for two cases. The "Chronosequence Enhancement" case illustrates the inferred rate of biomass accumulation assuming the same 100-year, linear increase in growth rate. The "Contemporary Enhancement" case demonstrates the rate of increase that would be observed in forests of different stand ages after their unique histories of growth enhancement. Also shown is the ratio of these growth rates (bottom) illustrating the degree to which a chronosequence inherently underestimates contemporary growth enhancements, particularly in older stands.

Part 1. Model Sensitivity Analysis

Section 1. Sensitivity of NEP to Light, Moisture, and Temperature Parameterizations

Owing to uncertainty in the parameterization of light, moisture, and temperature sensitivity of heterotrophic respiration and/or net primary productivity represented in the CASA model, here we present results of experiments exploring *NEP* response to a 2% elevation in one of six representative parameters including the maximum light use efficiency, moisture dependence of *NPP*, optimal temperature for *NPP*, turnover time of the slow soil carbon pool, and both the *Q10* and moisture dependence of heterotrophic decomposition of soil carbon. These sensitivity experiments were performed for the full forest type and productivity class strata of each climate setting but are presented in Table A1 as average responses within US forest regions for tractability and clarity. Parameter adjustment was imposed uniformly to the equilibrium spin-up and post-disturbance phases of simulation.

Characteristics of the post-disturbance *NEP* trajectory are used to represent the temporal dynamics of sensitivity to parameter perturbations, highlighting the minimum *NEP* (negative), maximum *NEP*, and *NEP* at 100 years. We also studied shifts in the time of cross over from source to sink but found almost no sensitivity and have therefore not presented these results in tabular form. Sensitivity was calculated as the Response Coefficient (Kacser and Burns, 1973), *S*, that is, the relative change in the flux caused by a relative change in a parameter (*P*):

$$S = \frac{\Delta NEP}{NEP} \frac{P}{\Delta P}.$$
 A1.1

When S = 1 the relative change in flux is proportional to the relative change in parameter. Though we imposed a 2% increase in parameter magnitude to calculate *S*, for clarity we discuss results in terms of the % change in NEP for a 1% change in parameter value.

Parameterizations and corresponding perturbations are briefly described here while more complete descriptions can be found elsewhere [*Potter et al.*, 1993; *Randerson et al.*, 1996]. E_{max} is the maximum light utilization efficiency for net primary productivity, and is treated as a global parameter with adjustment depending on the dataset used to characterize the absorbed fraction of photosynthetically active radiation (f_{PAR}). The actual light utilization efficiency can be reduced by multiplicative moisture and temperature scalars represented by *NPPmoist* and *Topt*. Both are nonlinear functions of either moisture or temperature. A general form for the calculation of *NPP* in the CASA model is:

$$NPP = f_{par} E_{max} W_{NPP} T_{NPP}, \qquad A1.2$$

where W_{NPP} and T_{NPP} depend on soil moisture and temperature states with functional forms involving *NPPmoist* and *Topt* parameters. Thus E_{max} , *NPPmoist*, and *Topt* are the key parameters influencing the rate of monthly *NPP* with attendant downstream consequences for carbon pools and respiration rates.

Heterotrophic respiration emerging from microbial decomposition of soil and litter carbon is calculated as:

$$Rh_{pool} = C_{pool} k_{pool} W_{resp} T_{resp} M , \qquad A1.3$$

where C_{pool} is the amount of carbon in a pool, k_{pool} is the pool-specific decay rate constant, W_{resp} and T_{resp} depend on soil moisture and temperature states, and M is the carbon assimilation efficiency of the microbes. The temperature dependence of Rh (i.e. T_{resp}) involves an exponential, Q10-type relationship of the form:

$$T_{resp} = Q_{10}^{(T-30)/10},$$
 A1.4

where *T* is soil temperature in degrees Celsius, and thus Q10 represents the increase in soil biotic activity per 10 degree Celsius rise in soil temperature. In addition to Q10 perturbations, we explored sensitivity to the decay rate of the "slow" carbon pool, as well as a key parameter, called *bgmoist* in the model, controlling how decomposition rate depends on soil moisture and folded into the W_{resp} scalar.

Results

Nearly all of the response coefficients are less than 1 indicating general dampening of parameter perturbations and suggesting that uncertainties in these parameterizations do not expand as they propagate through to modeled *NEP* (Table A1). Note that in cases where the sign of both the min and max were the same (all tested parameters except slow pool turnover) it means that the amplitude of the flux variations around the cross over date were dampened (negative *S*) or amplified (positive *S*) relative to the control. Changes in the amplitude are generally caused by changes in the carbon pool sizes as a result of the parameter perturbation. For instance increasing *Emax* causes *NPP* to increase thus increasing carbon pools in the pre-disturbance condition resulting in a greater amplitude in response after disturbance. Similarly increasing the *Q10* and respiration moisture stress causes smaller, predisturbance detrital pool sizes, less carbon to respire after disturbance and less carbon to accumulate as the system becomes a sink. Note that *S*<|0.2| should not be considered significant.

Beginning with maximum light use efficiency, a 1% increase in maximum light use efficiency lowers the minimum *NEP* by 1% corresponding to elevated equilibrium carbon pools and the associated 'background' emission from heterotrophic respiration. The near proportionality of maximum *NEP* and *NEP* at 100 years to *Emax* results from elevation of *NPP* and the greater capacity for carbon storage by the system. Sensitivity of *NPP* to the soil moisture parameter depends on climatic setting, with no effect in wet climates (e.g. NE, SE) and elevation of *NPP* in drier climates (e.g. RMS, PSW) where the dynamic has the same temporal characteristics to that described for elevation of maximum light use efficiency. However, sensitivity of *NEP* to *NPP* moisture limitation was always less than 1 with a maximum of about 0.5.

Elevating the optimal temperature generally reduces *NPP* caused by increased low temperature inhibition of photosynthesis and this produces a consistent reduction in the amplitude of the post-disturbance *NEP* dynamics. Because the model's optimal temperature is defined as the monthly temperature in the month of maximum *fPAR* and because maximum *fPAR* tends to occur in the hottest part of the year, any increase in optimal temperature imposed in this sensitivity experiment tends to diminish *NPP*. The magnitude of this reduction scales with the degree to which cool temperatures inhibit annual *NPP*. Results indicate relatively high sensitivity of the model's *NEP*, generally less than -1 and as low as -1.5. In other words, a 1% error in the optimal temperature parameterization translates into a 1.5% error in the amplitude of the post-disturbance *NEP* trajectory. Sensitivity to optimal temperature parameterization is highest where the optimal

temperature is highest (e.g. SE and SC), indicating that winter *NPP* may be underestimated in these seasonal environments.

As for the annual turnover time of the slow soil carbon pool (default is 0.2 yr^{-1}), a 1% increase has the modest effect of lagging decomposition of soil carbon. Pre-disturbance, the increase in turnover time results in an increase in the size of the slow pool, however, because the turnover time of this pool is slow relative to the initial response to disturbance the sensitivity of the flux soon after disturbance (when *NEP* reaches its minimum) is insignificant. The maximum *NEP* typically occurs around 20 to 50 years after disturbance (Figure A2) within the time scale of the slow pool turnover and shows a small stimulation. Had we chosen to perturb the litter pools, which have faster turnover times, we expect the sensitivity of *NEP* to be larger in the initial years with the minimum perhaps changing sign since disturbance causes a large portion of the previously live root pool to be transferred to the soil litter pool. The mild suppression of *NEP* at 100 years is because the lag makes slightly more carbon available for release by heterotrophs at this later stage.

Perturbations of Q10 and the moisture sensitivity of decomposition present the most complicated patterns arising from a balance between substrate and rate effects. Temporal trend indicates initial suppression then elevation and again suppression of Rh over the 100 year post-disturbance period shown here. Elevation of the Q10 parameter reduces the pre-disturbance soil C pools thereby reducing the carbon feeding heterotrophic respiration. However, dominance of this substrate limitation effect gives way to the competing effect of an enhanced rate of decomposition as seen by slightly diminished maximum *NEP* associated with elevated *Rh*. Ultimately, the relatively high rate of decomposition slightly diminishes *Rh* at 100 years and thus elevates *NEP* as it trends toward zero. Sensitivity to Q10 can be high with values exceeding +/-1 in one particular case (1.6 for the NE region *NEP* at 100 years).

Sensitivity to moisture dependence of decomposition tends to exhibit temporal dynamics opposite to those of Q10 as it tends to slightly diminish rather than enhance the rate of respiration and correspondingly enhance the pre-disturbance soil carbon pools and correspondingly enhance the rate of respiration. However, the sensitivity to this parameter is very low with values typically less than +/-0.1.

Conclusions

The crossover point from source to sink is insensitive to the values of the major influential parameters in the model. The magnitude of the initial source and maximum sink strength is sensitive to those parameters that affect the equilibrium detrital pool sizes (*Emax*, *NPP* moisture scalar, *NPP* optimum temperature, Q10 of respiration). Not surprisingly, the fluxes are sensitive to the *NPP* moisture scalar only for those cubes that experience water stress, for example, western states. *NEP* is only weakly sensitive to the parameterization of moisture stress on *Rh*.

Table A1.1. Results of sensitivity experiments expressed as the response coefficient, *S*, and equivalent to the percent change in an *NEP* characteristic caused by a 1% change in parameter, where the *NEP* characteristics are the minimum and maximum values in a 200 year trajectory of recovery from disturbance as well as the value at 100 years. Note that a negative value indicates a response that pushes *NEP* towards zero. For example a -0.5% change in negative minimum *NEP* indicates a 0.5% less negative value relative to the reference case. Results are averaged across all forest types present in forest service regions.

Region	<i>NEP</i> Characteristic	Maximum Light Use Efficiency	NPP moisture scalar	Optimum Temperature	Slow Pool Turnover	Q10	Respiration Moisture Scalar
	min	1	0	-1.1	0.00	-0.4	-0.03
NE	max	1	0	-1.1	0.12	-0.1	-0.01
	100y	1	0	-1.1	-0.43	1.6	0.11
	min	1	0	-0.9	0.00	-0.6	-0.04
NLS	max	1	0	-0.9	0.14	-0.2	-0.01
	100y	1	0	-0.9	-0.19	0.9	0.07
	min	1	0	-1.4	0.00	-0.3	-0.03
SE	max	1	0	-1.4	0.12	-0.1	-0.01
	100y	1	0	-1.4	-0.12	0.3	0.04
	min	1	0.02	-1.3	0.01	-0.2	-0.01
SC	max	1	0.02	-1.3	0.13	-0.1	-0.01
	100y	1	0.02	-1.3	-0.21	0.5	0.04
	min	1	0.30	-0.7	0.00	-0.8	0.04
RMN	max	1	0.30	-0.7	0.11	-0.2	0.01
	100y	1	0.30	-0.7	0.00	0.5	-0.02
	min	1	0.54	-1.3	0.00	-0.6	0.13
RMS	max	1	0.54	-1.3	0.10	0.0	0.01
	100y	1	0.54	-1.3	-0.10	0.7	-0.15
PSW	min	1	0.30	-0.9	0.00	-0.7	0.07
	max	1	0.30	-0.9	0.14	-0.1	0.01
	100y	1	0.30	-0.9	-0.06	0.5	-0.05
PNW	min	1	0.18	-0.5	0.00	-0.7	0.05
	max	1	0.18	-0.5	0.10	-0.1	0.01
	100y	1	0.18	-0.5	-0.11	0.9	-0.06

Section 2. Sensitivity of NEP to Errors in Biomass Accumulation with Stand Age

In this section we explore the sensitivity of our *NEP* results to four possible errors in our use of the FIA-reported biomass accumulation with stand age to constrain the carbon cycle model. The first experiment examines effects of possible errors in the stand age of forests and the corresponding temporal structure of carbon accumulation curves. To assess such effects we adjusted the ages in the biomass-age curves to be 5 years younger or 5 years older and studied their effects on regional and national *NEP* in forests. This shifted the 20-year forest age class bins with centers of $\{10, 30, 50, ... 190\}$ to become $\{5, 25, 45, ... 185\}$ or $\{15, 35, 55, ... 205\}$, effectively shifting the biomass versus age curve to the left or right, respectively.

The second experiment examines effects of natural, partial disturbances (e.g. insect outbreaks, blowdowns, ice storms) on aboveground live biomass (*AGB*) recorded in FIA plots. Such disturbances would reduce aboveground live biomass and hence cause an underestimate of growth, underestimate of wood decomposition, and underestimate of ecosystem respiration in our modeling, with unclear effects on *NEP* dynamics and continental-scale forest carbon sinks. To assess sensitivity to such an error we increased the wood turnover parameter by 10% and forced *NPP* to respond such that the modeled biomass still provides an optimal match to the biomass-age observations but yielding a new set of *NEP* trajectories.

The third experiment examines effects of biomass partial cutting practices (e.g. salvage logging, selective logging, thinning treatments) that remove biomass from forested plots without resetting the FIA-recorded stand age. To assess sensitivity to this error we elevated biomass to simulate what would be the effect of missed partial removals. We imposed a 10% increase in biomass across all age classes except the first 0-20 year class.

The fourth experiment tests how our results might change if we allow wood productivity (P_w) to be elevated in younger forests. To do this while still matching the rate of biomass accumulation observed in the forest inventory we needed to also allow wood turnover to adjust. We created a slightly modified model fitting routine that allowed us to implement the original inverse negative exponential increase (Equation 4) but up to a new maximum *NPP* (*NPP_{max}*) at 10 years since disturbance. This maximum rate was sustained until 20 years after disturbance followed by a linear decline to a fixed *NPP* (*NPP_{fix}*) value at 50 years since disturbance. Correspondingly, we fit one additional parameter to accommodate this more complex post-disturbance dynamic of *NPP*, the ratio of *NPP_{max}* to NPPfix, sampled over a range of 1.1 to 1.5. With a simple factorial exploration we then selected the set of (*NPP_{fix}*, *NPP_{max} / NPP_{fix}*, *A_w*) that minimized the difference between modeled and observed biomass with time since disturbance.

Each of the modeling experiments were applied to the full suite of regions, forest type groups, and productivity classes to obtain four new sets of results. Presentation of results focuses on how conterminous US forest carbon fluxes and stocks respond to these possible sources of error.

Results

Increasing wood turnover by 10% did not increase *AGB*, which was still constrained to match FIA observations, but did increase *NPP* by 18% (Table A1.2). Despite this increase in primary productivity, the faster rate of live wood turnover (shedding plus mortality) led to larger heterotrophic respiration, and hence the net effect on *NEP* was relatively subtle (3%). This suggests that even if natural, partial disturbances are missed, the net effect on our estimate of the conterminous US forest *NEP* is modest to negligible.

Elevating biomass by 10% led to the expected increase in *AGB* and necessitated a 21% increase in *NPP* to supply the additional carbon storage (Table A1.2). This translated into a 14% increase in *NEP*, as some of the additional carbon inputs return to the atmosphere via elevated heterotrophic respiration stimulated by increased woody debris inputs as *AGB* turns over. This experiment indicates strong sensitivity of our conterminous US forest *NEP* estimate to partial cuttings that remove wood from forested plots.

Decreasing stand age by 5 years (Stand Age -5 years) forces the model to grow more biomass earlier in the age trajectory and thus elevates AGB (+5%) at the continental scale (Table A1.2). This increases NPP (+28%) but also heterotrophic respiration and thus has a relatively muted effect on NEP (+5%). Increasing stand age by 5 years (Stand Age +5years) has opposite but asymmetric effects, with a 5% reduction in AGB, but only a 3% reduction in NPP and 1% reduction in NEP. This asymmetry indicates greater sensitivity to an old bias than a young bias in the reported stand age classes. While this nonlinearity in response to stand age biases makes generalization somewhat complicated, overall, the modest sensitivity to stand age errors suggests that our estimate is not likely to be largely adjusted by such biases.

Elevating productivity in younger forests also elevated *NEP* temporarily. However, heterotrophic respiration is similarly elevated though with a temporal lag associated with the residence time for carbon in the ecosystem. Together this leads to initially elevated *NEP*, but this effect is not sustained, particularly as *NPP* declines and R_h is releasing carbon from pools that are elevated relative to that which would be achieved in steady-state with the current rate of *NPP*. Most importantly, allowing for this elevated rate of *NPP* in young forests (<50 years old) only slightly elevated the *NEP* for the conterminous U.S. and its aboveground biomass, at about +1% and +3% respectively.

Conclusions

Our estimate of *NEP* integrated across forests of the conterminous US is sensitive to possible biases in the rate of biomass accumulation with stand age that may be implicit to our use of the FIA data as a constraint on the growth model. It is not sensitive to a temporally dynamic *NPP*, with elevation in younger forests. Furthermore, effects of partial disturbances that lead to wood decomposition on site are not expected to present a strong source of error in our estimate. However, partial cutting practices (e.g. salvage logging, selective logging, thinning) that remove biomass from forested plots without resetting the FIA-recorded stand age could have a substantial influence on the net forest sink estimate, with a 10% elevation of biomass leading to a 14% elevation of conterminous US forest *NEP*. The estimate is also sensitive to the temporal structure of carbon accumulation in live wood, with greater sensitivity to an old bias than a young bias in stand age classes.

Table A1.2 Conterminous US forest carbon fluxes and stocks as presented in the core manuscript for comparison to four sensitivity experiments. Parenthetical values in the *NEP* column report 1 standard deviation around the mean.

	NEP	NPP	AGB
	$[Tg C a^{-1}]$	$[Tg C a^{-1}]$	[Pg C]
Original Results	164 (28)	1451	13.0
Wood Turnover Increased 10%	169 (30)	1714	13.2
Biomass Increased 10%	187 (32)	1761	14.2
Stand Age –5 years	173 (30)	1860	13.7
Stand Age +5 years	162 (33)	1401	12.3
Dynamic Productivity	166 (35)	1503	13.3

Part 2. Forest Type Group- and Region-Specific *NEP* Trajectories and Area Distributions with Age and Associated Model Statistics.

Figure A2.1. Forest Type Group and Productivity Class – specific trajectories of net ecosystem productivity (*NEP*) following stand replacing disturbances by regions of the conterminous U.S.



Figure A2.2. Forest Type Group and Productivity Class – specific trajectories of net ecosystem productivity (*NEP*) in the first 20 years following stand replacing disturbances by regions of the conterminous U.S.



Figure A2.3. Forest type group- and region-specific area distributions from FIA data expressed as a fraction of total forested area by forest type in each region. Only those forest types contributing greater than 5% to region-total forested area are shown.



Stand Age Class [years]

					Aboveground
USFS	USDA FIA	Annual	Annual	Aboveground	Biomass @
Region	Forest Type Group	NEP	NPP	Biomass $(1 - C - \frac{2}{2})$	200-years
NE	WhiteRedJackP	71	1105	9	11
NE	SprFir	46	717	5	10
NE	OakHic	108	863	9	15
NE	MapBeeBir	90	824	8	12
NLS	WhiteRedJackP	65	311	4	12
NLS	SprFir	34	255	3	4
NLS	OakHic	70	602	5	8
NLS	ElmAshCot	59	433	4	7
NLS	MapBeeBir	77	347	5	11
NLS	AspBir	48	447	3	6
SE	LongleafSlashP	43	813	4	8
SE	LobShort	134	1093	5	12
SE	OakPine	66	838	5	13
SE	OakHic	70	917	6	11
SE	OakGumCyp	103	638	7	17
SC	LobShort	110	906	4	16
SC	OakPine	63	649	4	12
SC	OakHic	79	700	6	12
SC	OakGumCyp	107	877	7	13
SC	ElmAshCot	83	566	5	14
RMN	DougFir	32	336	5	16
RMN	PonderosaP	40	207	4	11
RMN	FirSprMtnHem	39	375	5	12
RMN	LodgepoleP	38	402	5	10
RMS	PinJun	10	75	1	2
RMS	DougFir	37	246	5	7
RMS	PonderosaP	32	258	4	5
RMS	FirSprMtnHem	47	260	6	9
RMS	LodgepoleP	40	332	5	7
RMS	AspBir	52	265	4	10
RMS	WestOak	7	182	1	6
PSW	PonderosaP	58	428	5	15
PSW	FirSprMtnHem	132	628	13	23
PSW	CaMixCon	89	617	9	14
PSW	AspBir	137	836	14	14
PSW	WestOak	76	475	7	11
PSW	TanoakLaurel	160	1477	11	15
PNW	DougFir	90	1079	11	25
PNW	PonderosaP	46	321	4	11
PNW	FirSprMtnHem	89	510	9	18
PNW	ElmAshCot	52	919	7	16
PNW	HemSitkaSpr	88	1343	13	25
PNW	AlderMaple	110	1374	8	15
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Table A2.1. Region-average statistics for forest types contributing at least 5% of the region's total forest area.

Part 3. *NEP* comparison between flux tower chronosequences and constrained-modeling

As an independent evaluation of our predicted stocks and fluxes we compared our results for a number of available studies on chronosequences for forest types in the conterminous US. These studies sometimes do not include estimates of both fluxes and stocks for different aged forests and estimates used various biometric and flux measurement approaches. The few sites with available data, variability in the data, and issues of extrapolating fine scale measurements to regional responses do not justify quantitative comparisons and demonstrate the need for more of these types of measurements and for finer scale modeling. The results of these comparisons are shown in Part 3, Figure A3.1. Agreement varies widely between the comparisons at the different sites/regions.

Our PNW Douglas-fir NEP trajectory agrees reasonably well with results reported by Schwalm et al. [2007]. The ponderosa pine chronosequences of live biomass accumulation and NEP reported by Law et al. [2003] are highly variable but our predictions of live biomass and NEP are lower and higher respectively at young ages in comparison. Our modeled NLS jack pine biomass trajectory follow that reported by [Rothstein et al., 2004] except perhaps that their biomasses at older ages indicate greater saturation of growth rate. The FIA data on biomass density with age differed little between high and low productivity classes explaining the lack of separation in our modeled biomass and NEP trajectories. The only non-conifer chronosequence available for evaluation was for aspen/birch in Michigan (NLS) reported by Gough et al. [2007]. We found little difference between biomass trajectories for productivity classes in this case owing to a lack of data for the high productivity class in this region leading us to use the low productivity class to describe biomass recovery for both strata. Correspondingly, the Gough et al. [2007] biomass and NEP measurements are higher than our simulations. For slash pine in the SE we tend to have higher biomass at young ages relative to both observations by Clark et al. [2004]. The steeper biomass recovery reported in the observations is reflected in the higher values of NEP compared to our model system. Our comparisons to the few readily available chronosequence data show that such measurements are of insufficient quantity to adequately evaluate our results. One exception may be our large under-prediction of NEP for slash pine in the SE. The SE and SC regions represent two of the top three NEP sink regions and the top two in percent of area disturbed (Table 1). Significant underestimation of NEP for pine in these regions could contribute to the lower national values that we derive. Note that we are comparing our regional trajectories to specific sites which are likely biased towards high biomass and productivity. In general this is a problem with any comparisons of this type involving extrapolation of plot to kilometer scale measurements to larger spatial scales.

Figure A3.1. Modeled and inventory-derived live biomass as well as modeled and flux-tower derived *NEP* for available chronosequences including results from five sites, where HP and LP refer to high and low productivity classes with error bars representing one standard error about the mean, and blue circles represent data drawn from specific studies as noted. In every case except (b) which represents recovery after fire, the recoveries represent those following harvest.



Part 4. Limited representation of growth enhancements with chronosequences and the age-accumulation method

Growth enhancement effects such as fertilization by CO₂ or N-deposition are not fully captured in chronosequence trajectories. This can be well illustrated with a set of simple simulations. We perform three simulations where in each case we simulate changes in biomass with time (*t* in years) using the differential equation, $dBdt = P_w - kB$. We assume a mean residence time for carbon in live wood of 50 years (k = 1 / 50 years = 0.02 years⁻¹) and a base rate of wood productivity (P_w) of 0.2 kgC m⁻² year⁻¹ implying an NPP of 0.88 kgC m⁻² year⁻¹ given our model's assumption of 1/3 allocation to wood and 75% allocated aboveground. Net tree growth (i.e. sequestration in live biomass) can be calculated for each of the three cases based on the annual differences in biomass in each time series (i.e. $B(t_2) - B(t_1)$).

The first simulation represents a "No Enhancement" case, in which the annual wood productivity parameter, P_w , is static. We implement the growth equation from an initial starting biomass of 1 kgC m⁻² year⁻¹ and simulate a trajectory for 100 years. The second simulation illustrates an "Enhanced Trajectory", where P_w has moved from low to high linearly over the past 100 years. Given an annual CO_2 growth rate of 1 to 2 ppm / 380 ppm we would expect maximum growth enhancement at a linear rate of 0.25% to 0.53% per year. However not all of this is expected to translate into increased NPP, and observations suggest an NPP response ratio of about 50% or less (dNPP/NPP x CO₂/dCO₂). This led Joos et al. [2002] to adopt a maximum rate of 0.1%/year increase in NPP. For the purpose of this illustrative exercise we adopted a higher rate of potential enhancement in our numerical experiment, at a fixed rate of 0.2% per year of the original, non-enhanced rate. We adopted this rate here in part because it is possible that at least in the US, forests could well be responding to multiple positive factors including enhanced N inputs, wetter conditions, and warmer conditions. It is worth noting that if enhancement was sustained for 100 years at this rate, and if we assume an average residence time of 20 years for ecosystem C (as in *Thompson et al.* [1996]), we estimate contemporary sinks comparable to 60 gC m⁻² a^{-1} . This translates to 150 TgC a⁻¹ if extrapolated uniformly to 250 million hectares of forest in the conterminous US and could explain the difference between our A&A result and the sink estimate obtained from the stock change method.

In the 100-year "Enhanced Trajectory" simulation, the last year illustrates the contemporary growth rate that would be observed in a 100 year old forest today. To estimate the contemporary growth rate that would be observed in a 50 year old forest today, we need to simulate a similar trajectory only starting with the enhanced growth rate trajectory representative of the past 50 years (not the first 50 years of the 100-year "Enhanced Trajectory"). Correspondingly, we develop a family of enhanced-growth trajectories for forests of different ages today, and sample the biomass and growth rate (dBdt) in the last year of each simulation. This set of samples illustrates the "Contemporary Enhancement" effect for all stand ages and is representative of the actual rate of growth that would be expected to be observed today.

The third set of simulations represents what we would see from a "Chronosequence Enhancement" composed of forests that have experienced enhancement over the past 100 years at the same rate of 0.2% per year. To represent this we need to simulate a specific trajectory for every forest age so that it experiences its unique growth-rate history (e.g. 20 year old forest has seen a 20-year ramp in P_w unlike the first 20 years of growth for a 120 year old forest). This case emulates what would be measured in an inventory survey of forests of different ages such as that used in the present work to describe the expected rate of carbon accumulation with time with a chronosequence. To obtain the chronosequence series we sample the biomass for forests of different ages at the final year of simulation and construct an inferred rate of net tree growth from the annual differences in biomass in this chronosequence time series of biomass.

Results and Discussion

Our analysis compares the "No Enhancement", "Enhanced Trajectory, "Contemporary Enhancement", and "Chronosequence Enhancement" cases in Figures A4.1 and A4.2. The first illustration demonstrates how the 100-year old "Enhanced Trajectory" captures the full effect of contemporary enhancement in the 100th year but naturally has initially no enhancement in its first year of growth when P_w is equal to the value used in the unenhanced case (Figure A4.1a). In contrast, the chronosequence series would capture the full effect of contemporary enhancement for young-aged forests, but none of the enhancement effect influencing forest growth in older aged stands (Figure A4.1c). This is because for the chronosequence case, the derivative in biomass representative of growth rates in a 100 year old forest is approximated from the difference in biomass between 99 and 100 year old stands. The conditions that gave rise to this difference in biomass are representative of the growth rates that existed 100 years prior when the enhancement effect was negligible. Thus for the chronosequence case time can be thought of as running backwards with respect to the representation of the enhancement effect (Figure A4.1c). This illustrates how a chronosequence is certain to underestimate the effect of contemporary enhancements, with increasing underestimation as stand age increases. To demonstrate this point we need to compare the effect of contemporary enhancement to that inferred from a chronosequence. Such a comparison is presented in Figure A4.2 where the degree of underestimation is seen to increase exponentially with stand age.

Most importantly, the large standard error (i.e. 100% of the mean) inherent to a chronosequence use of inventory data precludes detection of enhancement. The very large variability of the inventory data themselves was also noted as problematic in the work by *Joos et al.* [2002]. Even with the relatively large stimulation rate adopted in the current simulations (0.2% per year), the accumulated effect on forest biomass is small (i.e. 10%) relative to the mean biomass in an unenhanced case (Figure A4.1d). The signal to noise ratio is particularly small for young aged forests, where the amount of biomass for a given stand age is nearly identical between forests with and without enhancement (Figure A4.1d). This is the principle that led *Joos et al.* [2002] to correctly conclude that an enhancement effect cannot be resolved from a chronosequence given their typical variability. We reiterate that point here using an even higher rate of *NPP* stimulation. We also offer additional insight into how a chronosequence necessarily underestimates contemporary enhancement effects, and that even if such an effect could be detected above the noise in a chronosequence, the degree of underestimation increases progressively with stand age.

In summary, this simple set of numerical experiments offers an instructive orientation to the challenges and limitations associated with using a chronosequence to detect contemporary enhancement effects. The first problem is that a signal of enhancement is very small relative to the noise typical of inventory-derived chronosequences. Furthermore, effects of contemporary enhancements are chronically underestimated by a chronosequence estimate of biomass change with time, becoming progressively worse with increasing stand age. Enhancement effects would be best evidenced by carbon accumulation rates estimated for young stands. Unfortunately, this is also where the signal to noise ratio in an inventory-derived chronosequence is often most troublesome.

Conclusions

The age-specific accumulation of biomass in a forest as inferred from a chronosequence chronically underestimates the contemporary enhancement effect that might be taking place in forests today (Figure A4.2). The degree of underrepresentation increases with increasing stand age. This is because the chronosequence series includes contemporary effects of enhancements in very young stands, but by their nature chronosequences detect a progressively smaller fraction of contemporary enhancements as stand age increases. Even more important, though, is that even if contemporary enhancements might be captured by a chronosequence approach of deriving biomass accumulation in younger stands, the signal to noise ratio in an inventory-derived chronosequence is very small. Therefore, it is very likely that growth enhancement effects are under-represented with the age-accumulation approach which represents contemporary carbon accumulation based on fits to inventory-derived chronosequences. Though not detectable in chronosequences, a small growth enhancement spread over all forests can be expected to have a large impact on national carbon stock estimates.



Figure A4.1. Simulated trajectories of biomass accumulation with stand age (b,d), and the temporal derivative of biomass with stand age (a,c) for three different cases. The "No Enhancement" case adopts a constant growth rate. The "Enhanced Trajectory" case has a linear increase in growth rate at 0.2% per year for 100 years. The "Chronosequence Enhancement" illustrates the inferred rate of biomass accumulation assuming the same 100-year, linear increase in growth rate.



Figure A4.2. Simulated trajectories of the temporal derivative of biomass with stand age (top) for two cases. The "Chronosequence Enhancement" case illustrates the inferred rate of biomass accumulation assuming the same 100-year, linear increase in growth rate. The "Contemporary Enhancement" case demonstrates the rate of increase that would be observed in forests of different stand ages after their unique histories of growth enhancement. Also shown is the ratio of these growth rates (bottom) illustrating the degree to which a chronosequence inherently underestimates contemporary growth enhancements, particularly in older stands.

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