

## Effects of agriculture and timber harvest on carbon sequestration in the eastern US forests

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Received 5 June 2013; revised 3 December 2013; accepted 7 December 2013; published 13 January 2014.

[1] Forest carbon (C) sequestration in the eastern US will largely be driven by the interactive effects of disturbance due to land use change or management, climate, elevated CO<sub>2</sub>, and air pollution during the 21<sup>st</sup> century. In this study, we parameterized a process-based model (TEM-Hydro2) to quantify the effects of agriculture and timber harvest, climate, elevated CO<sub>2</sub>, and ozone on C sequestration during the 20<sup>th</sup> and the 21<sup>st</sup> century. We have not included the effects of natural disturbance such as fire, insect outbreaks, hurricanes, and tropical storms during the course of this study. Our site-specific comparisons suggest that C recovery of forests after anthropogenic disturbance depends on the time since disturbance and amount of C in different pools, including wood product pools with residence times ranging from 1 to 100 years. Our 20<sup>th</sup> century regional simulations show that recovery following anthropogenic disturbance and elevated CO<sub>2</sub> increased net carbon exchange (NCE), or net gain in the sink strength, by 64 and 32%, respectively, while ozone decreased NCE by 18%. However, there was a net loss of C due to disturbance if accounting from 1700. The 21<sup>st</sup> century simulation using the SRES A2 emissions resulted in an increase in NCE by 79% following partial annual timber harvest and 31% due to CO<sub>2</sub> fertilization, whereas climate and ozone decreased NCE by 12 and 8%, respectively. Our modeling results indicate that anthropogenic disturbance is an important factor to include for improving model accuracy in simulating C stocks and fluxes of eastern temperate forests.

**Citation:** Dangal, S. R. S., B. S. Felzer, and M. D. Hurteau (2014), Effects of agriculture and timber harvest on carbon sequestration in the eastern US forests, *J. Geophys. Res. Biogeosci.*, 119, 35–54, doi:10.1002/2013JG002409.

### 1. Introduction

[2] Natural and anthropogenic disturbances such as hurricanes, fires, logging, land use change, and insect damage have a significant effect on vegetation and the carbon (C) and nitrogen (N) dynamics of terrestrial ecosystems [Clark *et al.*, 2010; Davis *et al.*, 2009; Foster *et al.*, 1997; Grant *et al.*, 2007; Li *et al.*, 2003; Nunery and Keeton, 2010; Thornton *et al.*, 2002; Williams *et al.*, 2012]. Historically, timber harvests, forest transition to agriculture, and agricultural abandonment have been the

major drivers of C sources and sinks in eastern US forests [Albani *et al.*, 2006; Houghton and Hackler, 2000a; Houghton *et al.*, 2000c; Houghton *et al.*, 2012]. In addition to disturbance, C sources and sinks are determined by the interactive effects of climate, elevated CO<sub>2</sub>, N deposition, and ozone [Aber *et al.*, 2001; Ollinger *et al.*, 2002; Pan *et al.*, 2009; Thornton *et al.*, 2002; Zhang *et al.*, 2012]. While some disturbances (e.g., hurricanes, fires) cause large-scale tree mortality, others (e.g., surface fires, selective logging) affect community structure and organization without causing substantial mortality [Dale *et al.*, 2000]. Following disturbance, C recovery due to forest regrowth begins when Net Primary Productivity (NPP) exceeds heterotrophic respiration (R<sub>h</sub>) [Caspersen *et al.*, 2000] and regrowth can lead to an increase in the C sequestration rate compared to mature forest [Caspersen *et al.*, 2000; Hooker and Compton, 2003; Schulze *et al.*, 2000] depending on the severity and time since disturbance. While the sequestration rate of a recovering forest may be elevated above that of a mature forest, the loss of C during disturbance can cause a long-term net reduction of ecosystem C [Kashian *et al.*, 2006]. Currently, temperate forests of the conterminous US are accumulating

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2169-8953/14/10.1002/2013JG002409

substantial amounts of C, and the size of the sink is likely due to the interactive effects of historical disturbance, climate change, elevated CO<sub>2</sub>, and N deposition [Caspersen *et al.*, 2000; Goodale *et al.*, 2002; Ollinger *et al.*, 2002; Pan *et al.*, 2011; Pinder *et al.*, 2012; Zhang *et al.*, 2012].

[3] Partitioning the effect of different environmental drivers on NPP requires an understanding of the controlling physiological and ecological processes. In the case of forest disturbance, proper attribution of C to different pools (e.g., vegetation, soil, detritus) is paramount for identifying the temporal change from C source to sink [Myneni *et al.*, 2001; Thornton *et al.*, 2002]. Postdisturbance ecological succession can be crucial in determining the trajectories of C storage [Davis *et al.*, 2009; Humphreys *et al.*, 2005; Law *et al.*, 2001], where successional change in NPP affects C sources or sinks through time [Gough *et al.*, 2007; Thornton *et al.*, 2002]. Furthermore, ecological processes that influence C storage in the forest floor depend both on the production of litter and fine roots, and the rates of decomposition [Currie, 2003]. Thus, accurately quantifying the effects of various drivers on C fluxes requires information on how plants regulate photosynthesis, respiration, growth, and decay as a function of several environmental stressors (climate, elevated CO<sub>2</sub>, and atmospheric pollution), including the severity and time since disturbance.

[4] Knowledge of previous land use is crucial to understanding the effects of land use change on C dynamics [Chen *et al.*, 2004; Foster *et al.*, 2003; Magnani *et al.*, 2007; Pan *et al.*, 2011; Pregitzer and Euskirchen, 2004; Shevliakova *et al.*, 2009]; however, until recently there has been little focus on understanding the effects of regional land use history on C dynamics of forested ecosystems. Previous studies report regrowth following agricultural abandonment and timber harvest as a dominant factor affecting C uptake [Albani *et al.*, 2006; Arora and Boer, 2010; Birdsey *et al.*, 2006; Houghton and Hackler, 2000a; Hurtt *et al.*, 2002; McKinley *et al.*, 2011; Rhemtulla *et al.*, 2009; Xiao *et al.*, 1998], while others suggest that such enhancement is temporary and may be overestimated [Goodale *et al.*, 2002; House *et al.*, 2002]. While there is a widespread pattern of immediate postdisturbance C loss, followed by C recovery, factors such as the frequency and severity of disturbance can substantially alter postdisturbance C dynamics [Amiro *et al.*, 2010; Davis *et al.*, 2009]. Additionally, postdisturbance C dynamics can be influenced by the fate of the disturbed C. If the disturbance is of a nature that the tree biomass is converted to wood products, the C balance of the disturbance will be sensitive to the type of product and its half-life [Finkral and Evans, 2008; Skog, 2008; Skog and Nicholson, 1998]. For example, converting tree biomass to long-lived wood products (e.g., dimensional lumber) reduces the size of the C loss relative to short-lived wood products (e.g., paper products).

[5] In the eastern US, hurricanes, logging, conversion to agriculture, and insect outbreaks are the primary agents of disturbance in temperate forests [Amiro *et al.*, 2010; Canham and Loucks, 1984; Chen *et al.*, 2013; Clark *et al.*, 2010; Vanderwel *et al.*, 2013; Williams *et al.*, 2012], with fire being a primary disturbance agent historically [Houghton *et al.*, 2000c; Nowacki and Abrams, 2008; Van Lear and Harlow, 2000]. While the frequency and severity of these disturbance agents can alter the C trajectory of forested ecosystems [Houghton,

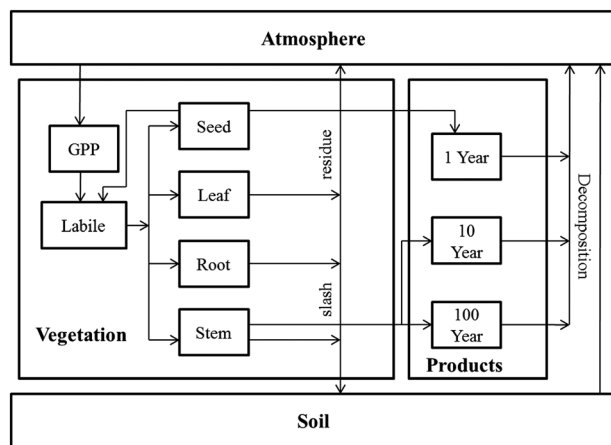
2003], regrowth following disturbance will eventually transition the disturbed area from C source to sink [Amiro *et al.*, 2010; Hurtt *et al.*, 2002]. The factors affecting this transition are numerous and investigation into the importance of different factors has yielded a range of results. Where some studies suggest that time since disturbance is the most important factor, with limited effect of interannual variation in climate or environmental change [Birdsey *et al.*, 2006; Zhang *et al.*, 2012], others suggest that climate, elevated CO<sub>2</sub>, and air pollution (including N deposition and ozone) are the primary drivers affecting C uptake [Joos *et al.*, 2001; McGuire *et al.*, 2001; Pan *et al.*, 2009; Schimel, 1995]. However, uncertainty surrounding the effects of these factors at regional scales requires further investigation.

[6] The purpose of this study was to partition the effects of anthropogenic disturbance (timber harvest, land use transition to crops and pasture, and permanent abandonment of agriculture), climate, CO<sub>2</sub> fertilization, and ozone on seasonal and annual dynamics of C cycling in the eastern US. We hypothesized that (i) conversion to agriculture and timber harvest would result in immediate C losses to the atmosphere by increasing respiration and reducing leaf biomass, while regrowth following agricultural abandonment and timber harvest would transition the ecosystem from the C source to a sink as a function of time since disturbance, and amount of C in different product pools; (ii) warming would decrease net C uptake due to increased autotrophic and heterotrophic respiration; (iii) moisture limitation due to warming would decrease net C uptake due to both reduced photosynthesis and increased autotrophic and heterotrophic respiration; (iv) CO<sub>2</sub> fertilization would result in an enhancement of C uptake, while such effect would be offset by increased autotrophic and heterotrophic respiration due to warming; and (v) tropospheric ozone would cause a decline in C uptake due to damage to stomatal cells. We parameterized the Terrestrial Ecosystem Model (TEM-Hydro2) using long-term measurements at Harvard forest, MA and validated it against four eddy covariance (EC) sites that have experienced a history of agriculture or timber harvest. We then used the validated model to quantify the effects of agriculture and timber harvest, elevated CO<sub>2</sub>, and increasing ozone on net carbon exchange (NCE) for forests in the eastern US and to project future C dynamics as a function of timber harvest, elevated CO<sub>2</sub>, climate, and ozone across eastern US forests.

## 2. Methods

### 2.1. Model Description

[7] The Terrestrial Ecosystem Model (TEM) is a biogeochemical model that uses information on climate, elevation, soils, and vegetation to estimate ecosystem level C and N fluxes [Raich *et al.*, 1991]. TEM has been used to examine the patterns of terrestrial C dynamics and quantify the effects of CO<sub>2</sub> fertilization, climate change, disturbance, and air pollution on the global C cycle [Felzer *et al.*, 2009; Tian *et al.*, 1999]. The relationship between C, N, and water is captured by simulating multiple pools of vegetation C and N in leaves, active and inactive stem, fine roots, and a labile pool [Felzer *et al.*, 2011]. In this study, we used the modified version of TEM (TEM-Hydro2) that has three important modifications including changes in optimal temperature for photosynthesis and microbial respiration, and an open N cycle. While TEM



**Figure 1.** Following disturbance in TEM-Hydro2, nonliving biomass is partitioned into four different pools as a function of the plant component. These different product pools represent the time until decomposition in years.

was originally developed to simulate carbon-nitrogen-water cycling in mature ecosystems [Raich *et al.*, 1991], the altered model formulation in TEM-Hydro2 has improved model dynamics for simulation of land use change [Felzer, 2012]. TEM inputs include climate (surface temperature, diurnal temperature range, precipitation, vapor pressure, and clouds — which are used to produce Photosynthetically Active Radiation (PAR)), atmospheric constituents ( $\text{CO}_2$ , N deposition, ozone), and land data (land cover and land use, soil texture, and elevation). The model is run with monthly climate forcing data using a daily time step.

[8] Photosynthesis is modeled as the maximum rate of C assimilation, which is a function of several environmental variables including light, moisture, temperature,  $\text{CO}_2$ , ozone, and nutrient availability [Raich *et al.*, 1991]. The light response is calculated as a hyperbolic function, where leaf-level light response is integrated to the canopy level as a function of leaf area index (LAI) and distribution of light (PAR) within the canopy. LAI is explicitly modeled as a product of leaf C and biome-dependent specific leaf area (SLA). In TEM-Hydro2, the optimum temperature for photosynthesis is based on the average daytime temperature of the growing season compared to the warmest daytime temperature of the year to account for a more realistic measure of leaf level photosynthesis. Maintenance respiration is a function of temperature and tissue N, while growth respiration is assumed to equal 25% of the C allocated to new tissues.

[9] The hydrology is based on a one-layer bucket model of soil moisture [Vorosmarty *et al.*, 1998], which has been modified employing [Shuttleworth and Wallace, 1985] formulation that explicitly considers both evaporation and plant transpiration. Water fluxes from the canopy and soil are determined based on meteorological forcing and aerodynamic resistance (soil, canopy, canopy air-space, and atmosphere), and further depend on the ratio of plant extractable water to the maximum amount of extractable water in a given soil column. The water balance includes precipitation in the form of rain and snow, snowmelt, evapotranspiration, and runoff. Comparisons to specific watersheds in the eastern US are presented in Felzer *et al.* [2009].

[10] Soil C and N dynamics are modeled as a function of litter production, decomposition rates, soil moisture, and temperature [Felzer *et al.*, 2011; Raich *et al.*, 1991]. Inputs of C and N into the soil pool result from leaf, stem, and root detritus, while outputs result from efflux of C and N from the soil surface and hydrologic leaching from dissolved organic and inorganic compounds. The production of C and N in soil depends on fine root turnover and microbial decomposition, which are temperature and moisture dependent. The root respiration is modeled as an exponential function of Q10 (rate of change in respiration with  $10^\circ\text{C}$  temperature increase), roughly doubling for a short-term temperature increase of  $10^\circ\text{C}$ . However, the model accounts for the fact that respiration down-regulates with continuous warming and uses LaRS [Hanson *et al.*, 2004] formulation to model root respiration. Microbial respiration is based on the approach of Lloyd and Taylor [1994] and does not assume acclimation. TEM-Hydro2 uses a one-layer soil model to simulate decomposition rates and temperature effects on soil. Because decomposition rates, soil moisture content, and temperature vary throughout the soil column, we altered the temperature- and moisture-dependent heterotrophic respiration function allowing it to equilibrate over longer time scales. While this modification was intended to capture the C losses associated with different decomposition pools throughout the soil column, such as more recalcitrant carbon, this modification had little effect on net carbon uptake.

[11] We currently account for two types of single event disturbances that occurred at the eddy covariance sites: timber harvest, and agricultural abandonment at the site level, and realistic, repeated disturbances such as timber harvest, land use transitions to cropland and pasture, and permanent abandonment of croplands and pasture at the regional level, based on Hurtt *et al.* [2006] (Figure 1). Changes in photosynthetic capacity following these disturbances are simulated by change in leaf C, which is a function of the transfer of C from the seed pool to the labile pool. Plant respiration following timber harvest is represented by introducing the effect of changing mortality rates with stand development on C stored in vegetation and soils. Mortality rates change with stand age as competition for environmental resources causes individual plants in the community to die during stand development. In TEM-Hydro2, these changes in mortality are implicitly simulated as changes in litterfall C and N, which are estimated as a proportion of vegetation C and N. Other changes include development of a reduced-form open N cycle to allow for N inputs and outputs including N fixation, N deposition, and leaching from DIN and DON pools [Felzer, 2012; Hayes *et al.*, 2011]. N uptake during stand development is dependent on fine root biomass, including available soil N, soil moisture, and temperature. A complete description of the model N cycle is available in Felzer [2012].

[12] Surface-level ozone production is primarily the result of photochemical reactions of carbon monoxide (CO), methane ( $\text{CH}_4$ ), and other hydrocarbons in the presence of  $\text{NO}_x$  [Felzer *et al.*, 2007] which affects vegetation and crops by direct cellular damage once it enters through the stomata [Mauzerall and Wang, 2001]. In TEM-Hydro2, we model the detrimental effects of ozone on stomatal conductance based on Reich [1987] and Ollinger *et al.* [1997]. Because ozone damage to trees and crops is largely cumulative, the

net damage is modeled as a function of healing rate minus new damage [Felzer *et al.*, 2009]. The healing rate is a function of LAI and healing time which is modeled as a sum of two expressions: one that allows for cellular repair through addition of new leaves when LAI is constant or decreasing, and the other that allows for rapid recovery of leaves when LAI is increasing. The damage rate is based on stomatal conductance, a PFT-dependent damage coefficient, and an ozone exposure index (AOT40) which varies spatially across the eastern US.

## 2.2. Phenology

[13] Improved modeling of carbon-nitrogen-water cycling requires successfully capturing both vegetation dynamics (allocation, phenology, photosynthesis, and respiration), and the physics governing water and energy fluxes between the surface and atmosphere. To accomplish this, we have modeled biomass pools by separating them into five different parts: leaves, fine roots, active and inactive stem tissue, and labile pool. C uptake from the atmosphere is dependent on specific leaf area and leaf biomass, while N acquisition from the soil is dependent on fine root biomass. C and N are transferred to the labile pool awaiting allocation to the structural compartments (leaf, stem, and roots). The allocation of C and N to structural compartments is based on a cost-benefit analysis that determines the timing, magnitude, and tissue of new growth allowing us to capture the successional change in vegetation C and N dynamics. The cost-benefit analysis is performed at daily time step, where leaves are added if the expected marginal benefit exceeds the expected marginal cost. Evergreen plants accrue C during all seasons, while cold-deciduous plants only accrue C in warm season ( $T_{day} > T_{crit}$ , where  $T_{crit} = 8^{\circ}\text{C}$  and  $T_{night} > T_{min}$ , where  $T_{min} = 0.0^{\circ}\text{C}$  for temperate deciduous forests). When the temperature is greater than the critical temperature, construction costs are lower and leaf construction occurs at a faster rate earlier in the season.

[14] Photosynthesis typically is modeled as a parabolic function of temperature, with an optimum temperature dependent upon the vegetation type [Berry and Bjorkman, 1980; Sall and Petterson, 1994]. The optimum temperature is allowed to acclimate under changing climatic conditions. However, warming-induced moisture stress limits photosynthesis in both evergreen and deciduous forests capturing the interactive effects of temperature and moisture on productivity. The optimum temperature for evergreen and deciduous stands was obtained from the literature (ST 1). The net C assimilation depends on stomatal conductance such that water use efficiency is a function of C gain per unit of water transpired by plants. Moisture stress is calculated as a function of plant water demand and available soil moisture.

## 2.3. Land Use Change and Stand Development

[15] TEM-Hydro2 uses a dynamic cohort approach to account for land use change and management. The model assumes that the grid is initially covered by undisturbed vegetation. Following conversion to agriculture, agricultural abandonment, or timber harvest, a new cohort of vegetation develops and the land area subjected to these anthropogenic disturbances is subtracted from the original cohort and added to the new disturbed cohort. Land use change related C and N fluxes from the system are calculated, and the terrestrial C

and N stocks are adjusted within the new disturbed cohort to account for the initial effect of agriculture or timber harvest. Vegetation regrowth and the associated C and N dynamics following land use change occur within the context of local environmental conditions for the new cohort.

[16] Following forest conversion to agriculture, agricultural abandonment or timber harvest, C and N in dead biomass are transferred to slash-, residue-, and product-pools (1, 10, and 100 years). Harvested crops are consumed during the same year and are thus entirely allocated to the 1 year product pool because of the absence of woody biomass. Wood and wood products are allocated to three pools (1, 10, and 100 years) that are differentiated by their turnover rates. The amount of C transferred to wood products at any given time is based on the temporal pattern of wood harvesting and vegetation type. We, however, did not attempt to include the complex pattern of spatial transfer in wood and wood products across the eastern US and assumed that transfer of C to wood and wood products is relatively constant based on Harmon *et al.* [1990] and McGuire *et al.* [2001]. We also did not include the export of wood products to different locations and assumed that wood products are deposited in the same location as a function of the decay constant. The loss of C from the three product pools occurs on an annual basis. For example, the release of C from the 100 year product pool represents 1% of the initial C released into the atmosphere annually over a period of 100 years [McGuire *et al.*, 2001]. While we have accounted for the initial extraction and final disposal of forest products, complete life cycle analysis including C losses during the processing, production, use and re-use of forest products [Ayres *et al.*, 1998; Azapagic, 1999; Heath *et al.*, 1996; Row and Phelps, 1996] is not considered in this study.

## 2.4. Model Parameterization and Validation

[17] The model uses three parameter classes to initialize and control the magnitude of C and N fluxes: biome-independent (constants), biome-dependent (vegetation and soil specific values), and calibration parameters (ST 1–4). Biome-independent parameters include constants such as Q10 for respiratory losses [Hanson *et al.*, 2004; Lloyd and Taylor, 1994], half saturation constant (kc), which may vary depending on literature values [Curtis and Wang, 1998; Norby *et al.*, 1999; Norby *et al.*, 2005], and soil surface resistance. The biome-dependent parameters include half saturation constants for CO<sub>2</sub> and N uptake, optimum temperature for photosynthesis, specific leaf area, minimum stomatal conductance, and ozone damage coefficient. We first used data from long-term intensively studied field sites to estimate the vegetation and soil specific parameters for temperate coniferous, temperate deciduous, grasslands, and croplands using target values of C and N stocks and fluxes from those sites. During the process, the calibration parameters are tuned until the model estimated stocks and fluxes approximate the observed target values such as vegetation C and soil C (ST 2–4). A key point is that TEM is calibrated to both C and N stocks and fluxes, requiring data from long-term ecological sites. The larger network of eddy covariance flux sites is not sufficient to calibrate TEM, since it is only flux based.

[18] The calibration parameters include the C assimilation rate ( $C_{max}$ ), which is a multiplier to GPP and NPP, the maintenance respiration rate ( $K_{ra}$ ), which is an inversely related

multiplier to VEGC, the heterotrophic respiration rate ( $K_d$ ), which is an inversely related multiplier to SOILC, the average life of heartwood ( $\tau_{\text{heartwood}}$ ), which is a multiplier to VEGC, N mineralization ( $M_{\text{nut}}$ ), which is a multiplier to available nitrogen in soil ( $N_{\text{av}}$ ), and N loss (NLOSS), which is an inversely related multiplier to  $N_{\text{av}}$ . This implies that larger  $M_{\text{nut}}$  increases the net N mineralization rate, while larger NLOSS decreases the pool of available nitrogen for plant uptake. Warming will result in more net N mineralization, which increases the size of the available N pool, allowing for more plant N uptake but also more N loss through leaching or denitrification (which is not explicitly modeled). Model validation compared to observed DIN leaching rates is explored in *Felzer* [2012]. These calibration parameters are then used to drive C and N stocks and fluxes across similar biomes during model extrapolation to other grids with different climate and soil types. The details on biome-dependent, biome-independent, and calibration parameters are available in *Felzer et al.* [2009].

[19] Calibration for all biomes is done without disturbance assuming that the undisturbed forest is in a state of equilibrium. Harvard Forest, MA served as both our temperate deciduous (mixed deciduous) and temperate coniferous (pine plantation) calibration sites. Konza Prairie, KS is our grassland calibration site (ST 2) and croplands are calibrated based on Kellogg Biological Station, MI similar to *Felzer* [2012]. Harvard Forest has an overstory composition that consists of 70% deciduous and 30% coniferous trees and dominant genera include *Quercus*, *Acer*, *Betula*, *Pinus*, and *Tsuga*. A hurricane in 1938 blew down 70% of the vegetation [*Foster*, 1988; *Foster and Boose*, 1992]. Currently, the forest is approximately 81 years old and has not yet reached maturity [*Barford et al.*, 2001]. During calibration, we assumed that the current state of Harvard Forest stocks is 80% of maximum biomass [*Barford et al.*, 2001] and adjusted our target values to be larger than the measured values to account for the fact that we are calibrating to a mature, equilibrated forest. The Konza Prairie is dominated by tall grasslands, while our cropland calibration is based on Maize.

[20] We used EC data, with site-specific disturbance histories, from Duke Forest, NC, University of Michigan Biological Station (UMBS), MI, Willow Creek, WI, and Walker Branch, TN to validate the model (ST 5). Duke Forest is a temperate coniferous forest which was clear-cut in 1983 and replanted with loblolly pine (*Pinus taeda*). UMBS and Willow Creek are temperate deciduous forests that were logged in 1923 and 1933, respectively. UMBS consists primarily of *Acer*, *Quercus*, and *Populus*; Willow Creek consists primarily of *Acer*, *Tilia*, and *Fraxinus*. Walker Branch was cleared for agriculture in 1901, abandoned in 1942, and is comprised of *Acer*, *Quercus*, and *Pinus*. The sites were selected based on at least four years of available level 4 gap-filled data from the EC (Ameriflux network; <http://public.ornl.gov/ameriflux/>) database, with known disturbance history [*Cook et al.*, 2004; *Gough et al.*, 2008; *Stoy et al.*, 2005; *Urbanski et al.*, 2007; *Wilson and Baldocchi*, 2001]. While anthropogenic disturbance has been the major driver of C stocks and fluxes at the EC sites, frequent droughts and low-intensity fires have been observed at Duke Forest and UMBS, respectively. Willow Creek and Walker Branch have no documented evidence of natural disturbance. Our climate input (i.e., temperature, precipitation, vapor pressure, and net

irradiance), air pollution (ozone and N deposition), and hydrological model (i.e., soil moisture) should enable us to capture effects of drought.

[21] To validate the calibrated model against EC measurements, we introduced site-specific land use history and simulated postdisturbance C dynamics. These simulations were conducted over a 100 year period, where we substituted the Climate Research Unit (CRU) data with EC data (temperature, precipitation, vapor pressure, temperature range, and cloudiness) for the specific years of EC data availability. We then compared model estimates of evapotranspiration (ET) and Net Ecosystem Productivity (NEP) to gap-filled EC latent energy and Net Ecosystem Exchange (NEE) values, as well as biometric NEP, defined as the difference between gross primary productivity and total ecosystem respiration, estimates. However, for our regional simulation, we computed Net Carbon Exchange (NCE) which accounts for C emissions resulting from conversion during disturbance and the decomposition of the product pools [*McGuire et al.*, 2001] and is calculated as:

$$NCE = GPP - R_a - R_h - E_c - E_p$$

where GPP is gross primary productivity,  $R_a$  is autotrophic respiration,  $R_h$  is heterotrophic respiration,  $E_c$  is the C emissions during the conversion of undisturbed natural ecosystems to areas of human use, and  $E_p$  is the sum of C emissions from the decomposition of products. Positive NCE indicates a C sink, while negative NCE indicates a C source to the atmosphere. Where the forest is undisturbed,  $E_c$  and  $E_p$  are equal to 0 and NCE equals NEP, but any disturbance substantially alters the  $E_c$  and  $E_p$ , resulting in differences between NCE and NEP.

[22] To evaluate model uncertainty and bias in the simulated ET and NEP at respective sites, we used two different approaches. We calculated the root mean square error (RMSE) between the monthly observed and simulated C and water fluxes and used the Nash-Sutcliffe coefficient of efficiency [*Nash and Sutcliffe*, 1970] to quantify the difference between observed and simulated monthly ET and NEP. The Nash-Sutcliffe coefficient of efficiency (E) is the ratio of absolute squared differences between the predicted and observed values to the variance of the observed values. The value of E ranges from  $-\infty$  to 1, where 1 represents a perfect fit between the observed and simulated values.

## 2.5. Historical and Future Simulations

[23] Our site level simulations accounted for recovery following agricultural abandonment and timber harvest (clear-cut and selective logging), while our regional historical simulations accounted for recovery following repeated clear-cut, land use transitions to cropland and pasture following clear-cut, and permanent abandonment of cropland and pasture in the eastern US during the period 1701–2000. To examine the role of anthropogenic disturbance on changes in vegetation C stocks in the eastern US, we extracted grids that have been subjected to timber harvest, forest transition to agriculture, and cropland abandonment and compared our modeled results with Forest Inventory and Analysis (FIA) vegetation C at a county level. Because of the limitations of comparing the entire grid-based vegetation C with FIA vegetation C at a county level, we only considered grids

**Table 1.** The Biomes of Eastern US and Their Areas in 1701, 1990, and 2000, and Comparison of Change in Area in 1700 and 1990 Between *Houghton and Hackler* [2000a] and *Hurt et al.* [2006] Used for Simulation in This Study<sup>a</sup>

Biome	This Study (10 <sup>6</sup> ha)			[ <i>Houghton and Hackler</i> , 2000a] (10 <sup>6</sup> ha)	
	1701	1990	2000	1700	1990
Mixed Forest	132.68	78.75	80.99	145.1	51.6
Deciduous Forest	102.13	49.93	52.21	75.7	50.8
Coniferous Forest	8.17	2.63	2.85	NA	NA
Croplands	2.46	80.1	76.41	0.3	139.2
Pasture	2.85	36.88	35.83	45.8	25.3
Total	248.29	248.29	248.29	266.9	266.9

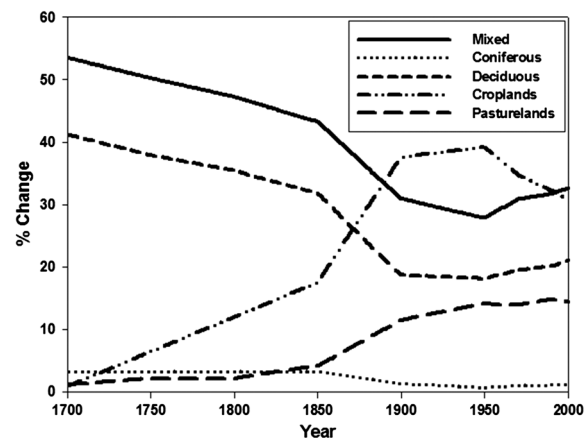
<sup>a</sup>The area for different biomes in the eastern US based on *Houghton and Hackler* [2000a] was calculated considering East North Central, Northeast, and Southeast from the conterminous US because separate data for the eastern US were unavailable.

with repeated human disturbance where total harvest area during the period 1901–2000 exceeds the total area of a grid (> 100% area harvested). Our regional future simulations were based on two approaches: partial annual harvest where the proportion of total area within a grid is harvested annually over the simulation period and stochastic harvest where total area harvested within a grid is removed in a single event. The stochastic harvest occurs randomly once in 100 years within a given grid. We have only simulated timber harvest in the forested region of the eastern US during our future simulation because the first-order changes in forest area in the conterminous US will be small (3% reduction) in the next few decades [*Alig et al.*, 2003]. Our historical regional coverage was based on the *Hurt et al.* [2006] land use transitions from 1700 (developed into cohorts), while our future regional coverage was based only on grids containing over 50% forest in the year 2000. During our regional simulation, we simulated the transfer of biomass to different product pools based on *Harmon et al.* [1990] where 58% of the biomass was converted to short-term (1 and 10 year) and 42% to long-term (100 year) pools. Conversion of croplands to natural vegetation following abandonment was accomplished by initializing soil C and N, updating rooting depth, and transitioning cropland to plant functional type (PFT) specific parameter values. Harvest of agricultural biomass is simulated prior to abandonment and occurs when the growing degree days passes a certain threshold [*Neild and Newman*, 1990]. The complex mosaic of agricultural changes and timber harvest is simulated as a function of area affected, allocation of C to slash, residue, and product pools, and biome-specific parameter values.

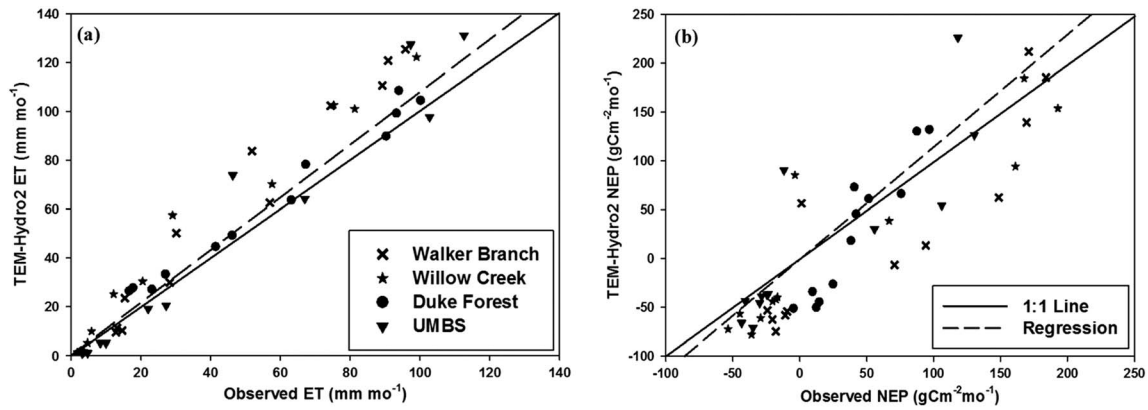
[24] To quantify the site-specific effects of N deposition, we ran simulations with and without N deposition at each of the eddy covariance sites, using historical (CRU) and eddy covariance climate data with specific land use history. We used wet N deposition data based on National Atmospheric Deposition Program (NADP, 2010) to estimate the current amount of wet N deposition at Duke Forest (7.64 kg ha<sup>-1</sup> yr<sup>-1</sup>), Willow Creek (6.2 kg ha<sup>-1</sup> yr<sup>-1</sup>), Walker Branch (7.6 kg ha<sup>-1</sup> yr<sup>-1</sup>), and UMBS (6.2 kg ha<sup>-1</sup> yr<sup>-1</sup>). We fit the N-deposition rate from preindustrial to current following the change in atmospheric CO<sub>2</sub> concentration. N deposition was added directly into the dissolved inorganic nitrogen

(DIN) pool from where it was either lost through leaching or taken up by plants.

[25] We ran regional historical simulations to isolate the effects of land use history, elevated CO<sub>2</sub>, and ozone on C sequestration during the 20<sup>th</sup> century over the eastern US. The model was run in transient mode for 120 years using historical climate data, where the first 40 years are used to initialize terrestrial C and N pools. Climate data, including cloudiness, air temperature, precipitation, temperature range, and vapor pressure, were obtained from the Climate Research Unit [*Mitchell et al.*, 2004] at a spatial resolution of 0.5° longitude × 0.5° latitude. Annual atmospheric carbon dioxide concentrations are from *Keeling et al.* [1995]. Historical ozone levels (AOT40 index) are derived from the Environmental Protection Agency's (EPA) Clean Air Status and Trends Network (CASTNET; <http://www.epa.gov/castnet>). The model also uses spatially explicit data sets of soil texture [*GSDTG*, 2000], elevation [*Hastings et al.*, 1999], predisturbance natural vegetation [*McGuire et al.*, 2001], and a historical land-cover data set [*Hurt et al.*, 2006]. The historical land-cover data set developed by *Hurt et al.* [2006] includes repeated disturbances such as land use conversion to cropland and pasture, timber harvest, and secondary land use from 1701 to 2000. We simulated NCE across the region using the spatially explicit, gridded input data layers (0.5° longitude × 0.5° latitude spatial resolution), including vegetation type. Plant response for each PFT is a function of local climatic conditions, atmospheric gases, soil properties, and biome-dependent parameters. Our historical regional simulation was carried out based on transient land-cover data sets [*Hurt et al.*, 2006] assuming that C and N stocks and fluxes change across broad temporal and spatial scales as observed in our site level simulations. Within a particular grid, we used area weighted averaging to account for the effects of disturbance on the vegetation cohort distribution with the assumption that landscape elements do not interact horizontally [*Houghton et al.*, 2000c].



**Figure 2.** Temporal change (%) in the area covered by mixed, coniferous and deciduous forest, croplands, and pasturelands during the historical period. The total area at the beginning and end of historical period is unchanged; however, there is annual change in the area covered by forest, croplands, and pasture due to change in land use practices during the historical period.



**Figure 3.** Comparison of TEM-Hydro2 and eddy covariance for (a) average monthly ET and (b) average monthly NEP for all sites (Duke, UMBS, Walker Branch, and Willow Creek) that have been subjected to cropland abandonment and timber harvest across the eastern US.

[26] Temporal dynamics of the *Hurt et al.* [2006] land use change data set used in this study suggest that cropland in the eastern US increased by  $73.95 \times 10^6$  ha from 1701 to 2000 (Table 1 and Figure 2). The rapid expansion of agriculture occurred during the period 1851–1900 with an accompanying decrease in area covered by mixed and deciduous forests. Pastures increased by  $32.98 \times 10^6$  ha from 1701 to 2000, with most of the increase taking place after 1980. The total forested area declined to a low of  $116 \times 10^6$  ha (44%) by the 1940s, then increased to  $136 \times 10^6$  ha (14%) during the period 1950–2000. All three forest types (mixed, deciduous, and coniferous) show decline in area between 1701 and 2000, with the most rapid decline occurring in mixed and deciduous forest (Table 1 and Figure 2).

[27] Future simulations were conducted to project the effect of timber harvest, climate, elevated  $\text{CO}_2$ , and ozone on C sequestration during the 21<sup>st</sup> century. The simulations were carried out with climate projections from the National Center for Atmospheric Research (NCAR) CCSM3 model based on the SRES A2 emission scenario. The A2 scenario is a relatively warm scenario representing a world with increasing population and greenhouse gas emissions that have not peaked by the end of 21<sup>st</sup> century. All climate data including precipitation, air temperature, vapor pressure, cloudiness, and daily temperature range for the future simulations were obtained from NCAR CCSM3 model. The future ozone data were based on year 2000 values allowed to vary as in the Multiscale Atmospheric Transport and Chemistry (MATCH) scenario from *Felzer et al.* [2005].

[28] Future simulations (2001–2099) included a partial annual harvest and a single event timber harvest assuming that forest change in the eastern US will remain fairly constant during the 21<sup>st</sup> century. Because future land use changes in the eastern US are highly uncertain and depend on several factors that operate at local, national, and regional scales including sustainable land use practices, land use policy, population pressure, and economic demands of forest products [Drummond and Loveland, 2010] and require development of different scenarios to make future projection, we have assumed that land use change will remain constant during the 21<sup>st</sup> century in this study. During the future simulation,

we first determined the total harvest area within a grid based on 20<sup>th</sup> century harvest rates. Partial harvest was simulated by removing the proportion of area compounded annually over the course of 21<sup>st</sup> century, while single event timber harvest was simulated by removing the total harvest area within a grid only once during the period of simulation. In the event that over 100% of the grid were harvested (Figure S1a), we removed half the harvested material over two periods separated by 50 years. We only considered grids that were greater than 50% forested in year 2000 based on *Hurt et al.* [2006] and excluded croplands and pasture during our future simulations (Figure S1b). While TEM accurately accounts for the lack of forest coverage in the upper Midwest based on *Hurt et al.* [2006], the observed forest cover from the USDA Northern Research Station confirms that forest cover should be larger in this region. We carried out five different simulations to isolate the effects of anthropogenic disturbance, climate,  $\text{CO}_2$  fertilization, and ozone on past and future C storage in the forests of the eastern US. We did not include N deposition in these experiments because gridded, long-term transient estimates of N deposition are still under development. To isolate the contribution of each stressor (anthropogenic disturbance, climate,  $\text{CO}_2$ , ozone) to NCE, simulations were run with the particular stressor held constant for both the historical (1701–2000) and future (2001–2099) periods. The effect of each stressor was then quantified as the difference between

**Table 2.** Comparison of Mean Annual Evapotranspiration (ET) Modeled Using TEM-Hydro2 and Measured Using Eddy Covariance (EC) at Four Different EC Sites<sup>a</sup>

Site ID	Eddy ET (mm yr <sup>-1</sup> )	TEM-Hydro2 (mm yr <sup>-1</sup> )	% Difference	RMSE	NC
DUK	680	750	9	20	0.66
WLK	570	740	22	23	0.82
WIL	390	525	11	21	0.66
UMBS	510	550	7	16	0.85

<sup>a</sup>The sites are Duke (DUK), Walker Branch (WLK), Willow Creek (WIL), and University of Michigan Biological Station (UMBS). Percent difference is the difference between the modeled and the measured values, while root mean square error (RMSE) and Nash-Sutcliffe error of efficiency (NC) are calculated as the difference between the monthly EC and TEM-Hydro2 ET.

**Table 3.** Comparison of Mean Annual Carbon Fluxes ( $\text{g C m}^{-2} \text{ yr}^{-1}$ ) Modeled With (DIST) and Without (UND) Anthropogenic Disturbance Using TEM-Hydro2 and Measured Using Eddy Covariance (EC) and Biometry at Four Different EC Sites<sup>a</sup>

Site ID	EC NEE	Biometric	DIST NEP	UND NEP	% Diff.	RMSE	NC
DUK	489	NA	321	140	-34	54	-0.67
WLK	750	252	360	180	-52	62	0.50
WIL	360	106	150	50	-58	59	0.60
UMBS	170	73	189	80	11	61	0.51

<sup>a</sup>The sites are Duke (DUK), Walker Branch (WLK), Willow Creek (WIL), and University of Michigan Biological Station (UMBS). Percent difference is the difference between the modeled and the measured values, while root mean square error (RMSE) and Nash-Sutcliffe error of efficiency (NC) are calculated as the difference between the monthly EC and disturbed TEM-Hydro2 carbon fluxes.

the control (including historical anthropogenic disturbance) and the single-stress simulation. To quantify the effects of historical anthropogenic disturbance, we included a model run with only mature forests. The effects of  $\text{CO}_2$  fertilization were quantified by holding  $\text{CO}_2$  constant at 280 ppm, while the effects of ozone were captured by excluding ozone for the historical period and holding it constant at the year 2000 level for the future projection. In this study, we have only isolated the effect of future climate considering that the effect of historical climate on NCE has been small relative to disturbance and elevated  $\text{CO}_2$  [McGuire *et al.*, 2001].

### 3. Results

#### 3.1. Evapotranspiration

[29] The modeled evapotranspiration (ET) showed a tendency for overprediction as compared to observed values when compared in aggregate (Figure 3). The absolute bias was largest at Walker Branch by  $120 \text{ mm yr}^{-1}$  (Table 2). The root mean square errors (RMSE) at all sites were within  $\pm 20 \text{ mm yr}^{-1}$ , indicating that the model captured monthly variability well when compared with EC ET (Table 2). Similarly, the Nash-Sutcliffe error of efficiency (E) for all sites was greater than 0.6 indicating that the model agreed well with the observed values (Table 2). The Nash-Sutcliffe errors are based on monthly, rather than annual values, and so they do generally show that the model is getting the correct seasonality at most of the sites. Differences between the EC and simulated ET were partly due to energy imbalance at EC sites, which is discussed below.

#### 3.2. Net Ecosystem Productivity (NEP) and Leaf Area Index (LAI)

[30] Modeled NEP agreed well with EC measurements when compared in aggregate (Figure 3b). Site-specific comparisons indicate an annual under-prediction of NEP as compared to observed NEE by  $390 \text{ g C m}^{-2} \text{ yr}^{-1}$  (Table 3 and Figures S2–S6). However, at these sites, our modeled NEP values were closer to biometric measurements of NEP. The RMSE values were within the range of  $\pm 60 \text{ g C m}^{-2} \text{ yr}^{-1}$  for all site EC measurements. Comparisons of modeled NEP with observed NEE over the growing season (May–August) showed that TEM-Hydro2 captured summer variability well when compared to observed NEE (S2b).

Similarly, comparisons of C fluxes among EC between the human-disturbed and undisturbed simulations showed that undisturbed simulations substantially underestimated the size of the C sink. The Nash-Sutcliffe errors of efficiency (E) for all sites were over 0.5 except Duke Forest (Table 3). Comparison of simulated and observed maximum LAI between the sites showed strong agreement ( $R^2 = 0.90$ ; Figure S2d).

#### 3.3. Land Use History, $\text{CO}_2$ Fertilization, Nitrogen Deposition, and Ozone

[31] As the previous validation results were run without N deposition, we examined the role of N deposition in accounting for the difference in NEP following N deposition (Table 4). Incorporating N deposition in simulations at the EC sites resulted in a slight to moderate increase in C sequestration for all sites except Walker Branch (see discussion). However, N deposition did not substantially alter the C fluxes at most of the sites.

[32] Simulations to isolate the effects of agricultural abandonment and timber harvest at our specific sites showed that immediately following anthropogenic disturbance, all sites were a net source of C, taking years to decades to transition back to a net sink (Figure 4). The net C released immediately following timber harvest (clear-cut) was similar at Duke, Willow Creek, and UMBS (Figure 4) because biomass allocation to product pools was the same across sites. Similarly, forest transition to croplands in 1901 and abandonment in 1942 resulted in a source of C for longer time period at Walker Branch. Cumulative NCE with and without anthropogenic disturbance (Figure 4 and Table 3) showed that the C sink is highly dependent on the time since disturbance and the allocation of C to product pools. Recently disturbed Duke Forest is still a substantial C source compared to other sites that were disturbed in the early 20th century.

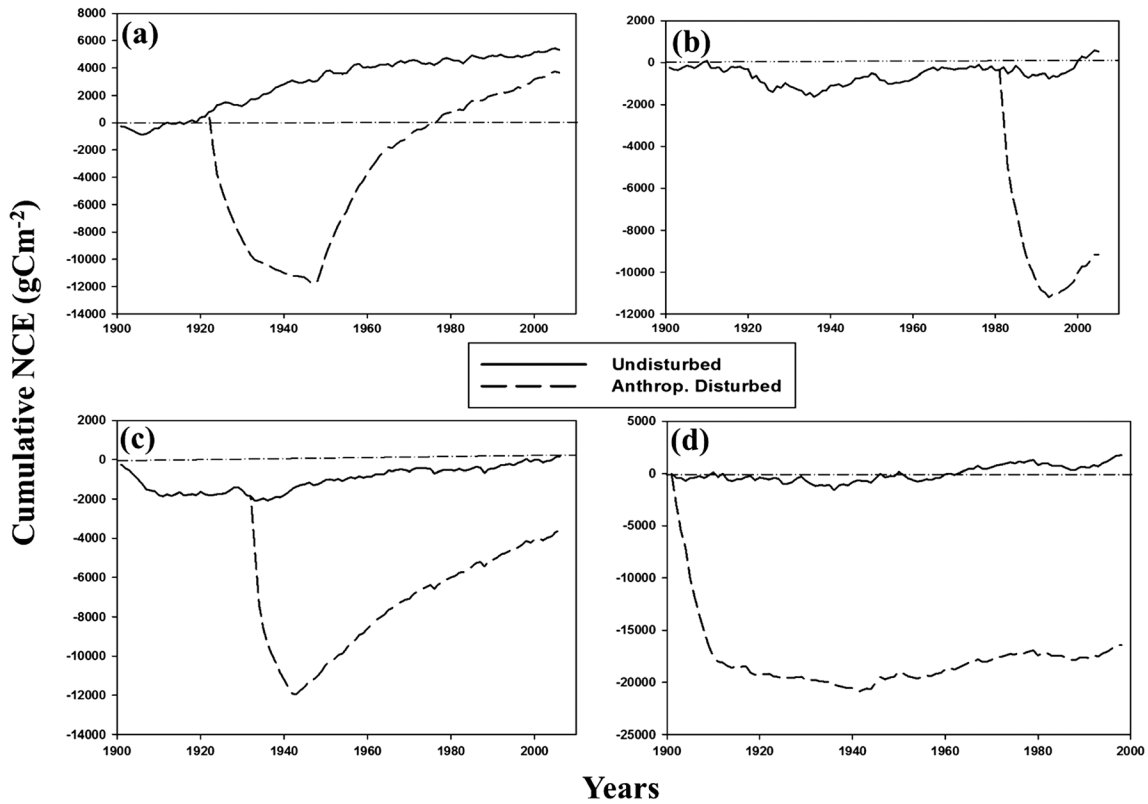
[33] Over the historical period, comparison of grid-based modeled vegetation C with FIA vegetation C indicates that TEM-Hydro2 overestimated vegetation C by 21% (Figure 5). Our model results for the eastern US forest region indicate that agricultural conversion and timber harvest released  $64.3 \text{ Tg C yr}^{-1}$ , a net reduction in total NCE of 105% compared to the undisturbed simulation. Across different time periods, there was a substantial change in C stocks and fluxes (Table 5, 6), where peak C losses occurred prior to 20<sup>th</sup> century followed by recovery during the 20<sup>th</sup> century. During the historical period, forest recovery following anthropogenic disturbance increased the C sequestration rate and the regional C sink was further enhanced by  $\text{CO}_2$  fertilization (Figure 6). Across the region, elevated  $\text{CO}_2$  accounted for 12% of the increase

**Table 4.** Comparison of Carbon Fluxes With and Without Nitrogen Deposition, Using TEM-Hydro2, at Four Different EC Sites<sup>a</sup>

Site ID	N Deposition ( $\text{kgN ha}^{-1} \text{ yr}^{-1}$ )	NEP (Without N-dep) ( $\text{gC m}^{-2} \text{ yr}^{-1}$ )	NEP (N-dep) ( $\text{gC m}^{-2} \text{ yr}^{-1}$ )	% Difference
DUK	7.6	314	321	2
WIL	6.2	138	150	8
WLK	7.6	360	360	0
UMBS	6.2	182	189	5

<sup>a</sup>Percent difference is the difference between the simulated NEP with and without N deposition.

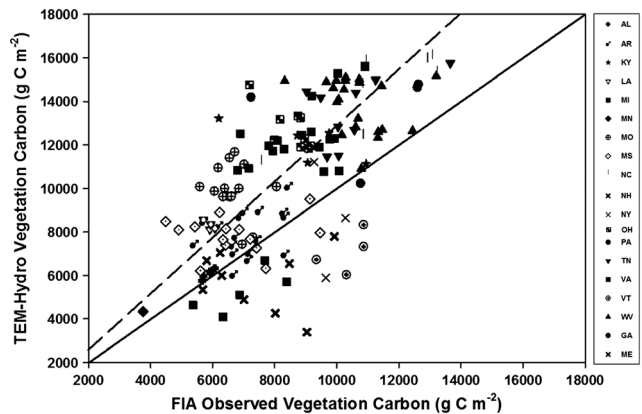




**Figure 4.** Cumulative modeled NCE for undisturbed (solid line) and anthropogenic disturbance (dotted line) at the (a) University of Michigan Biological Station, (b) Duke, (c) Willow Creek, and (d) Walker Branch.

in NCE with no effect of ozone because we simulated no change in ozone level prior to 1900. Over the course of the 20<sup>th</sup> century, recovery following anthropogenic disturbance accounted for 73.9 Tg C yr<sup>-1</sup> sequestered in the region equivalent to a 64% increase in NCE when compared to undisturbed simulation (Figure 7 and Table 7). Similarly, elevated CO<sub>2</sub> increased net C uptake by 32%, while ozone decreased uptake by 18% during the course of 20<sup>th</sup> century. Over the future simulation period (2001–2099), forest recovery following repeated and stochastic timber harvest as a mechanism of anthropogenic disturbance accounted for 269.4 and 276.2 Tg C yr<sup>-1</sup> sequestered in the region, respectively. Individual grids display substantial differences in C dynamics between partial annual and stochastic disturbance (Figure 8), but when averaged over the entire region, the two simulations are nearly similar in NCE by the end of the 21<sup>st</sup> century, even though the C gain in the vegetation is greater in the partial, annual disturbance. Across the region, partial harvest accumulated more C in vegetation (19,741 gC m<sup>-2</sup>) compared to stochastic harvest (17,760 gC m<sup>-2</sup>) equivalent to a net increase in vegetation C by 11%. When compared to the simulation without anthropogenic disturbance, partial and stochastic timber harvest accounted for 79–80% and CO<sub>2</sub> fertilization accounted for a 31% of the C sequestered in the eastern US. Across the region, climate and ozone resulted in a decrease in NCE by 12% and 8%, respectively (Figures 8, 9 and Table 7). We also explored the additive effects of various factors considered in this study, which are presented

in Table 7, where all factors combined resulted in a net C uptake of 73.9 and 269.4 Tg C during the historical and future (partial harvest) period, respectively; while climate, elevated CO<sub>2</sub>, and ozone together resulted in net C uptake by 26.6 and 55.5 Tg C during the historical and future period, respectively.



**Figure 5.** Comparison of TEM-Hydro2 and FIA observed vegetation C across the eastern US. TEM-Hydro2 vegetation C were obtained at a grid level and compared with county level FIA observed vegetation C using Carbon Online Calculator (COLE) tool.

**Table 5.** Average Stocks and Fluxes During the Course of Pre-20<sup>th</sup> Century (1701–1900), 20<sup>th</sup> Century (1901–2000), and Recent Decade (1991–2000)<sup>a</sup>

Stocks/Fluxes	1701–1900	1901–2000	1991–2000
NCE	−45.7	29.8	65.2
NEP	5.63	132.9	174.84
NPP	667	593	673
VegC	14,893	6564	6080
SoilC	3810	4112	4573
E <sub>R</sub>	1343	1001	1112

<sup>a</sup>Units: NCE = g C m<sup>−2</sup> yr<sup>−1</sup>, NPP = g C m<sup>−2</sup> yr<sup>−1</sup>, Veg C = g C m<sup>−2</sup>, Soil C = g C m<sup>−2</sup>, and E<sub>R</sub> = g C m<sup>−2</sup> yr<sup>−1</sup>.

## 4. Discussion

### 4.1. Comparison of EC NEE, Biometric NEP, and Modeled NEP

[34] The overestimation of modeled ET compared to measured ET at Duke, Willow Creek, and Walker Branch may be due to energy imbalance issues associated with EC measurements [Kucharik et al., 2006; Luo et al., 2003]. Wilson et al. [2002] found that the sum of latent and sensible heat flux is less than the sum of net radiation, resulting in an average change in heat storage by 20%. Simulated NEP underestimated the measured NEP at all of our sites. Examination of diurnal and seasonal differences between simulations and measured NEP indicated that the difference is due to the underestimation of night and winter respiration (S2–S6). Research at Walker Branch has shown that EC measurements underestimated the C fluxes at night and during the winter [Baldocchi and Meyers, 1998; Baldocchi et al., 2000; Curtis et al., 2002; Hanson et al., 2004; Schaefer et al., 2008]. Thornton et al. [2002] found similar results at Duke Forest, where BIOME-BGC underestimated EC NEE by 30%. Results from these previous studies suggest that the disparity between our model results and measured values may in part be due to measurement error which was in the range of −58 to +11%. Although disparity between EC NEE and modeled NEP is evident at individual sites (S2(a–b); S3–S6), model NEP agreed well with EC NEP when compared in aggregate with a slight underprediction during the winter and a slight overprediction during the summer depending on the site (Figure 3).

[35] Our modeled NEP lies between the EC NEP and biometric measurements, where TEM-Hydro2 overestimated the biometric measurements and underestimated the EC measurements at most of the study sites. The difference between the modeled and biometric measurements may be due to temporal dynamics of ecosystem processes where soil respiratory losses lag behind C gains [Barford et al., 2001]. In a study of North American deciduous forests, Curtis et al. [2002] found weak correlation between biometric and EC NEP at Walker Branch, UMBS, and Willow Creek and attributed that to different periods of data collection and uncertainty associated with the two methods. In a similar study at UMBS, Gough et al. [2008] found that individual year comparison of EC and biometric C fluxes differed by 13–148%, while C fluxes converged to within 1% when averaged over the 5 year period. The multiyear convergence of EC and biometric C fluxes was due to the lag between late-season canopy photosynthesis and its allocation to tree

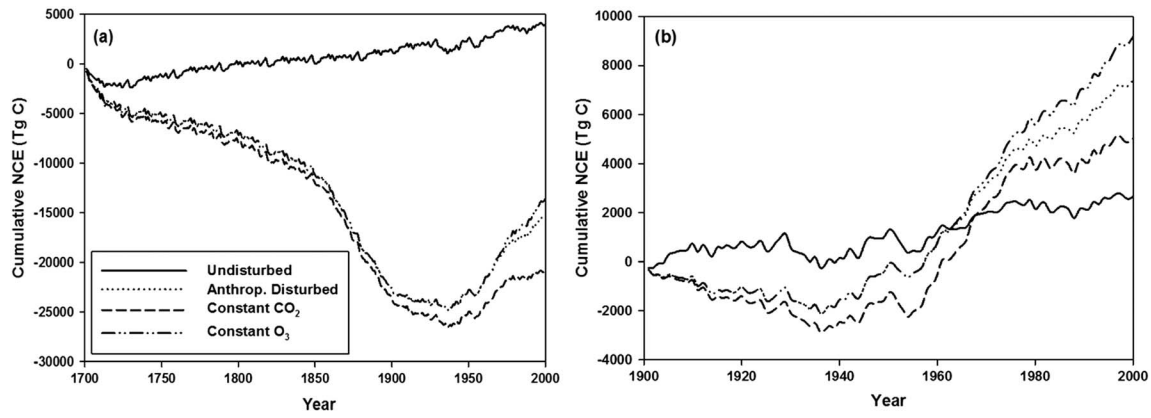
growth the following spring. Other sources of uncertainty among the modeled, EC, and biometric C fluxes may be associated with the modeling of soil organic matter. TEM-Hydro2 uses a simple one-layer model for soil organic matter decomposition that may have overestimated the soil respiration at our study sites, resulting in a lower net C sink. Prior to running our simulations, we modified the microbial respiration function to reduce C loss and allow the soil pool to equilibrate over longer time scales, but this modification did not substantially alter the net C uptake. However, Kirschbaum [2004] has demonstrated the importance of multiple decomposition pools (fast, intermediate, and slow) to accurately account for the decomposition of organic matter, which we plan to consider in the future.

[36] The transition of forest from source to sink depends on the severity, time since disturbance, and ecosystem type [Amiro et al., 2010; Gough et al., 2008; Law et al., 2003; Williams et al., 2012; Zhang et al., 2012]. While Amiro et al. [2010] reported that most of the ecosystems transitioned back to a C sink within 10 years of a stand-replacing event, others have suggested a strong C source for several decades following stand replacing disturbances [Campbell et al., 2004; Law et al., 2003]. Our study suggests that most of our sites take decades to transition from C source to a sink indicating that time since disturbance and proportional allocation of C to different product pools is crucial in determining the C sources and sink of terrestrial ecosystems. Where Johnson and Curtis [2001] found that whole tree harvesting had a minimal effect on soil C and N, Gough et al. [2007] reported that repeated clear-felling and burning reduced soil fertility resulting in less C storage compared to sites disturbed only once. Given that all of the EC sites used for validation were disturbed once, most of our sites transitioned back to a C sink faster than sites with repeated disturbance where reduced soil fertility could lower the rate of annual C storage for several decades [Gough et al., 2007]. At the clear-cut sites we investigated, time since disturbance and local environmental conditions influenced the transition to C sink. For example, although UMBS, Duke Forest, and Willow Creek, were all clear-cut, C gains at UMBS have been greater than the other sites following disturbance because of the increased time since disturbance compared to Duke Forest and Willow Creek. In the case of Walker Branch, land use transition occurred twice where forest conversion to agriculture during the period 1901–1941 resulted in a continuous loss of C and forest recovery following cropland abandonment in 1942 increased C uptake (Figure 4d).

[37] The sink strength of old growth forest is debatable, as different studies suggest that old growth forests may be a C source or a C sink. While Odum [1969] and Law et al.

**Table 6.** Changes in the Wood Products, Conversion Fluxes, NCE, and NEP During the Course of Pre-20<sup>th</sup> Century (1701–1900) and 20<sup>th</sup> century (1901–2000)

C Fluxes (Tg C yr <sup>−1</sup> )	1701–1900	1901–2000
Wood products	−77.02	−219.7
NEP	13.98	330.14
NCE	−113.48	73.90
Conversion fluxes	−50.45	−36.5



**Figure 6.** Cumulative modeled NCE for the Eastern US during the (a) historical period and (b) 20<sup>th</sup> century. The anthropogenic-disturbed and undisturbed simulations represent simulation with and without anthropogenic disturbance, respectively, but with transient climate, CO<sub>2</sub>, and ozone. Constant CO<sub>2</sub> is a simulation with anthropogenic disturbance, transient climate, and transient ozone holding CO<sub>2</sub> constant at 280 ppmv, while constant O<sub>3</sub> is a simulation with anthropogenic disturbance, transient climate, and CO<sub>2</sub> but with constant ozone.

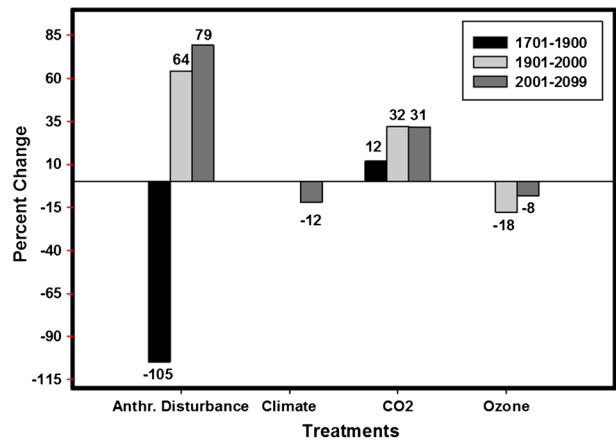
[2004] suggested that old-growth forests are C neutral and C sources, respectively, *Luyssaert et al.* [2008] reported a continuous C sink despite a reduction in C uptake with age. Our cumulative NCE (Figure 4) is consistent with previous findings that undisturbed forest is either C neutral or a small sink [*Luyssaert et al.*, 2008; *Odum*, 1969], while a forest recovering from agricultural abandonment or timber harvest is a strong C sink, depending on the time since disturbance [*Caspersen et al.*, 2000]. Our simulations to isolate recovery following anthropogenic disturbance confirm a substantially increased sequestration rate during the initial recovery period. The increased rate, compared to undisturbed forest, is due to regrowth of younger forests, coupled with CO<sub>2</sub> fertilization during the 20<sup>th</sup> and 21<sup>st</sup> centuries (Figure 4 and Figure 6b).

[38] While the magnitude of the fertilization effect from N deposition in the eastern US is debatable due to uncertainties in estimating the distribution of added N among wood, nonwoody biomass, soil, and leachate [*De Vries et al.*, 2006; *Jenkinson et al.*, 1999; *Magill et al.*, 2000; *Nadelhoffer et al.*, 1999; *Sievering*, 1999], our study showed little or no effect at the temperate forest sites. We found that a neutral or positive effect of N deposition on C sequestration is likely due to variable rates of net nitrogen mineralization and nitrogen uptake by plants which is a function of climate, soil moisture, and plant nitrogen demand. Our results indicate that higher N mineralization and N uptake associated with warmer temperature and moisture conditions have made the system N saturated at Walker Branch compared to other sites considered in this study, negating any effect of adding additional nitrogen. *Garten* [1993] found higher N uptake from isotopically heavy pools of inorganic soil N by plants in valley bottoms at Walker Branch similar to our study but N-uptake rates were highly variable across the ridges. We also did not fertilize the site during the period of agriculture at Walker Branch. N-fertilization studies combined with isotopic labeling in the eastern US indicate that deposition results in relatively little increase in woody biomass accumulation and that the majority ends up in the soil pool [*Currie and Nadelhoffer*, 1999; *Magill et al.*, 1997; *Nadelhoffer*

*et al.*, 1999]. In a study at Harvard forest, *Aber et al.* [1993] found that 75–92% of added N was retained in soil following three years of chronic N addition suggesting that less N was transferred to the vegetation pool. These results suggest that our site-level simulations have adequately captured the influence of N deposition on NEP.

**4.2. Land Use History**

[39] Forest clearing for agriculture and abandonment of agricultural land are the most common land use practices [*Drummond and Loveland*, 2010; *Ramankutty and Foley*, 1999] and have received much attention in C cycle studies because the legacy lasts several decades after the initial change [*Chen et al.*, 2013; *Foster et al.*, 2003]. In the eastern US, approximately half of the area covered by natural vegetation has been cleared in the past three centuries due to agriculture and pasture expansion, urban development, and other land uses [*Smith et al.*, 2004]. Across the region, recovery of forest following agricultural abandonment had a substantial



**Figure 7.** Percent change in NCE during the pre-20<sup>th</sup>, 20<sup>th</sup>, and 21<sup>st</sup> century simulations as a function of anthropogenic disturbance, climate, CO<sub>2</sub>, and ozone. Note that climate-only effects were not explored during the historical period.

**Table 7.** Twentieth and 21<sup>st</sup> Century Simulation Showing the Net Change in Carbon Fluxes (NCE) With (DIST) and Without (UND) Human Disturbance, Climate (CLM), Elevated Carbon Dioxide (CO<sub>2</sub>), and Ozone (OZO)<sup>a</sup>

Experiments	UND	DIST	CLM	CO <sub>2</sub>	OZO
20 <sup>th</sup> century	26.6	73.9	NA	50.2	87.3
21 <sup>st</sup> century (partial annual)	55.5	269.4	301	185	292
21 <sup>st</sup> century (stochastic)	55.5	276.2	300	189.7	299.7

<sup>a</sup>The values corresponding to each factor (CLM, CO<sub>2</sub>, and OZO) are the results of the simulation when those factors were held constant. The net effect of each factor is calculated as the difference between the control (DIST) and factors of interest (UND, CLM, CO<sub>2</sub>, and OZO). The historical simulation (1701–2000) was carried out using land use data sets based on *Hurtt et al.* [2006], while the 21<sup>st</sup> century simulation was carried out with partial annual and stochastic timber harvest. All units in Tg C yr<sup>-1a</sup>.

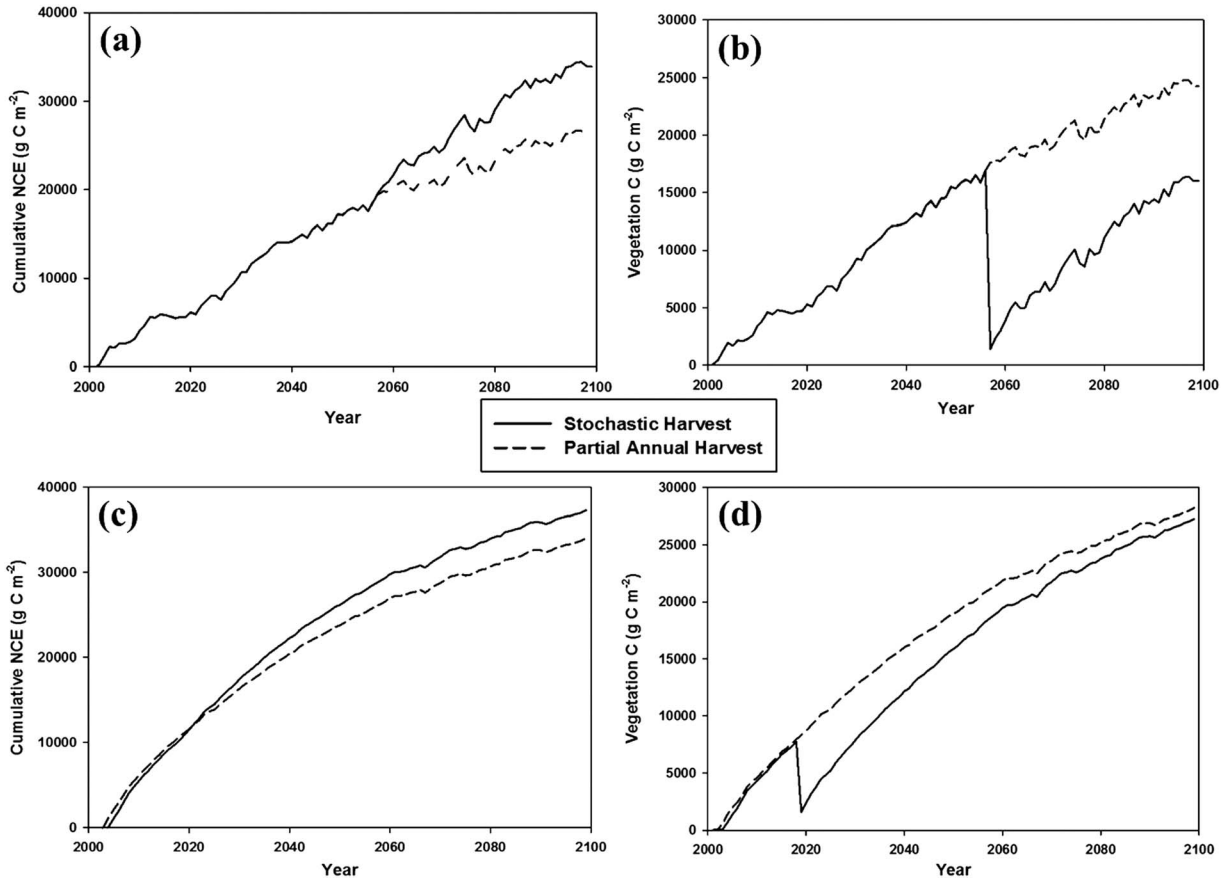
impact on C dynamics, including the transition of the region from C source to sink. The *Hurtt et al.* [2006] data sets used in this study suggest that forest recovery began after reaching the forest minimum during the 1940s, due to westward relocation of agriculture for large-scale mechanized cultivation [*Drummond and Loveland, 2010*].

[40] While our results are consistent with the temporal change in forest area as observed in *Houghton and Hackler* [2000a], there are differences in the change in cropland and pasture area during the historical period (Table 1 and

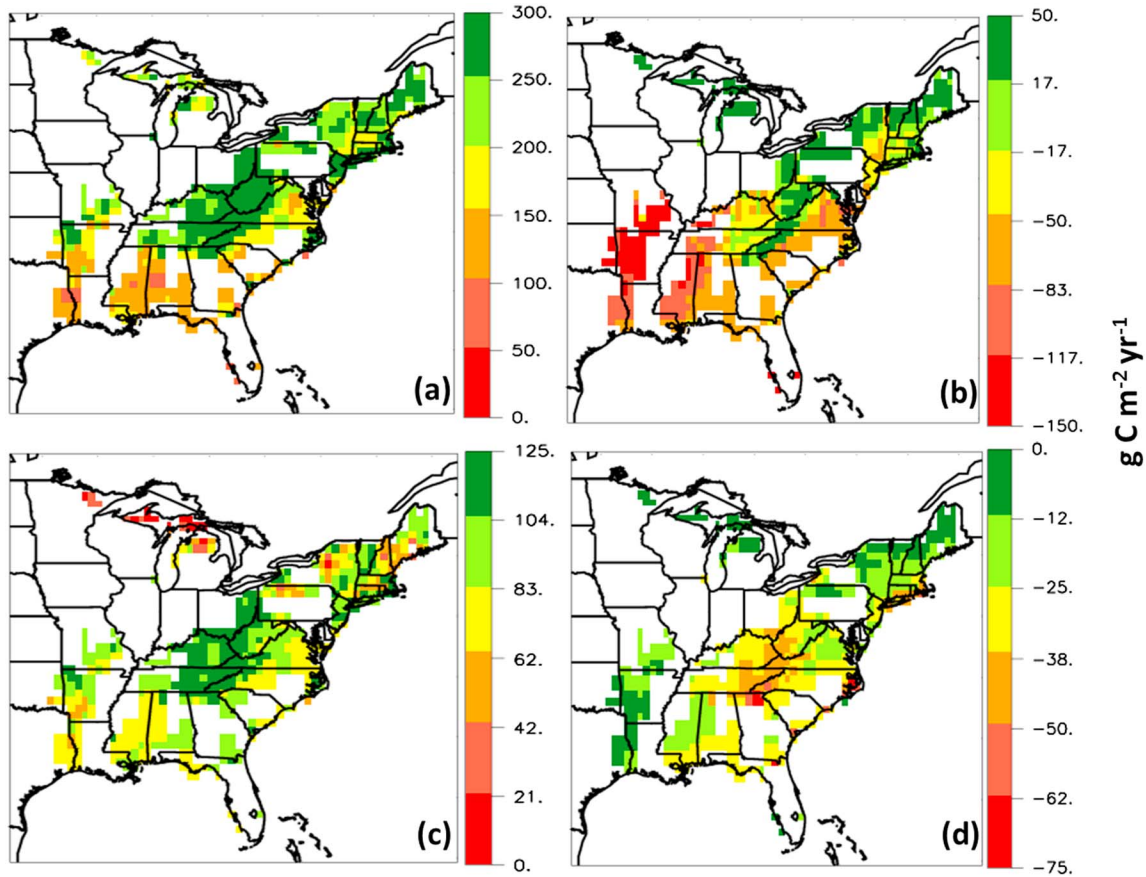
Figure 4). *Houghton and Hackler* [2000a] modified the initial area estimated from *Bailey* [1995], where necessary, so that the areas at the end of 1990 match up with observations resulting in differences in the initial conditions of forest, crop, and pasture. The largest difference occurred in the initial condition of the pastureland (Table 1), where *Hurtt et al.* [2006] estimated pastureland covering  $42.95 \times 10^6$  fewer hectares. Additionally, land use history data sets [*Hurtt et al., 2006*] considered in this study are reconstructed using two global land use history products: The Historical Database of the Global Environment (HYDE) based on global land use and land-cover maps [*Goldewijk, 2001*] and global cropland data sets [*Ramankutty and Foley, 1999*], while results from *Houghton and Hackler* [2000a] were based on historical statistics and rates of change in major land use dividing the conterminous US into seven regions. While similar in total area for the eastern US, *Houghton and Hackler* [2000a] area is approximately 7% larger (Table 1). This difference is due to our aggregation of three of *Houghton and Hackler* [2000a] regions: East North Central, Northeast, and Southeast, in order to compare with *Hurtt et al.* [2006].

### 4.3. Comparison of Forest C Stocks With FIA Observations

[41] Anthropogenic disturbance can have a strong legacy effect on forest C dynamics resulting in changes in both short- and long-term C trajectories [*Foster et al., 2003*].



**Figure 8.** Twenty-first century simulations for two grids showing results of partial vs. stochastic disturbance; (a) cumulative NCE and (b) vegetation C at Madison, MS representing warmer climatic conditions, and (c) cumulative NCE and (d) vegetation C at Arrostook, ME representing cooler climatic conditions.



**Figure 9.** Projected 21<sup>st</sup> century simulation results of changes in NCE ( $\text{g C m}^{-2} \text{yr}^{-1}$ ) as a function of (a) timber harvest, (b) climate, (c)  $\text{CO}_2$  fertilization, and (d) ozone. We only considered grids that are over 50% forested in the year 2000 according to *Hurt et al.* [2006] for our future simulation.

Timber harvest and forest transition to agriculture and pasture varied across the eastern US during the period 1701–2000 as a function of disturbance severity and ecosystem type [Johnson and Curtis, 2001]. Comparison of C stocks of standing trees at a grid level in year 2000 with county level FIA-based observation [Deusen and Heath, 2013] shows that TEM-Hydro2 over-predicted vegetation C at the grid level by 21% (Figure 5). Across the eastern US, the total live C in forests was 14,900 Tg C, which is higher than estimates from Birdsey and Heath [1995] by 38%. In a similar study, Woodbury et al. [2007] found that C stocks in the conterminous US were substantially higher (36%) than previous estimates based on forest inventory data [Turner et al., 1995]. The increase in vegetation C by 36% in Woodbury et al. [2007] was attributed to the use of new allometric equations for calculating total tree C from individual tree diameter data, suggesting that there is disparity in the vegetation C estimates depending on the approach. While our simulated C stock is a function of ecophysiological mechanism, climate, elevated  $\text{CO}_2$ , ozone, and land use history, part of the disparity between the modeled and FIA observed vegetation C might be due to exclusion of historical natural disturbances [Houghton et al., 2000c; McNulty, 2002; Milesi et al., 2003; Zeng et al., 2009]. However, Vanderwel et al. [2013], using FIA data, found that current forest dynamics in the eastern US are not driven by natural

disturbances because catastrophic disturbances only accounted for 0.5% of all plot damage in the eastern US.

#### 4.4. 20<sup>th</sup> Century Response to Disturbance, Elevated $\text{CO}_2$ , and Ozone

[42] Over the course of the 20<sup>th</sup> century, forest recovery following anthropogenic disturbance accounted for 64% of the C sequestered in the region. However, our 20<sup>th</sup> century result must be considered in the context of NCE over the entire historical period, when land use transitions to agriculture and pasture, and timber harvest resulted in a net C loss of 105% compared to the undisturbed simulation with all mature forest. Our estimated NCE of  $73.9 \text{ Tg C yr}^{-1}$  for eastern US forests is consistent with other studies that found a substantial sink over the region and the conterminous US, ranging from 142 to 330  $\text{Tg C yr}^{-1}$ , as a result of recovery from disturbance [Birdsey and Heath, 1995; Houghton et al., 1999; Hurtt et al., 2002; Williams et al., 2012; Xiao et al., 2011].

[43] Zhang et al. [2012] estimated a net C sink of 206  $\text{Tg C yr}^{-1}$  from 1950 to 2010 for the conterminous US and attributed 77% of the biomass accumulation to disturbance and land use change factors similar to our estimate of anthropogenic disturbance accounting for 64% of NCE for the eastern US. Hurtt et al. [2002] conducted a simulation using land use data (crop, pasture, secondary plantation, and natural

vegetation) from 1700 to 1990 that estimated C sequestration at 330 Tg C yr<sup>-1</sup> during the 1980s over the conterminous US. Similarly, *Houghton et al.* [2000c] estimated a net C sink of 350 Tg C yr<sup>-1</sup> during the 1980s using a book-keeping model. However, we estimated a C sink of 105 Tg C yr<sup>-1</sup> during the 1980s, equivalent to 32 and 30% of total C sink in the conterminous US when compared to *Hurt et al.* [2002] and *Houghton et al.* [2000c], respectively. While there is a difference in the spatial extent of the area between these studies (Eastern US vs Conterminous US), the lower estimates of C sink compared to *Houghton et al.* [2000c] could be due to differences in the effect of land use transition on soil C stocks. Below-ground C losses due to land use transition were prescribed as 25% of the total soil C in *Houghton et al.* [2000c], while TEM-Hydro2 uses a dynamic approach to model soil C flux which is a function of litter input, soil temperature, and soil moisture condition. In the eastern US, *Albani et al.*, [2006] estimated a net C sink of 210 and 250 Tg C yr<sup>-1</sup> due to forest regrowth following agricultural abandonment and timber harvest compared to our estimate of 105.4 and 161.8 Tg C yr<sup>-1</sup> during the 1980s and 1990s, respectively. This disparity is primarily due to differences in simulation approach and land use history data set used to drive the model. *Albani et al.* [2006] carried out a simulation using *Ramankutty and Foley* [1999] data sets for the period 1700–1850 and county level data set for the period 1850–present considering the effects of agricultural abandonment and forest harvest. Additionally, our land use history data sets [*Hurt et al.*, 2006] show lack of forest coverage in the upper Midwest resulting in less C sink compared to *Albani et al.* [2006]. This suggests that eastern US forests were a substantial contributor to the C sink due in part to permanent abandonment of agricultural land, fire suppression, and reduced harvest for fuelwood during the latter half of the 20th century [*Albani et al.*, 2006; *Houghton and Hackler*, 2000a; *Houghton et al.*, 2000c; *Hurt et al.*, 2002].

[44] While anthropogenic disturbance and land use history are crucial to accurately estimate the C sink of eastern US forests, other factors such as CO<sub>2</sub> fertilization, climate, N deposition, and tropospheric ozone could substantially influence the C sink. *Caspersen et al.* [2000], using inventory data from a latitudinal gradient in the region, found that recovery from disturbance was the primary driver of C accumulation, and other factors such as CO<sub>2</sub> fertilization contributed little to aboveground NEP. Our results indicate that growth enhancement from CO<sub>2</sub> fertilization accounted for 32% of the increase in NCE during the 20<sup>th</sup> century which is secondary to the effects of recovery following anthropogenic disturbance [*Caspersen et al.*, 2000]. Numerous experimental studies have confirmed that an increase in CO<sub>2</sub> concentration enhances photosynthesis, which in turn increases productivity [*Ainsworth and Long*, 2005; *Curtis and Wang*, 1998; *Houghton*, 2003; *Norby et al.*, 2005; *Nowak et al.*, 2004; *Schimel*, 1995], and prior simulation studies have found that CO<sub>2</sub> fertilization has increased forest productivity in the region [*Aber et al.*, 1995; *Pan et al.*, 2009]. *Pan et al.* [2009] reported similar results with regards to increased C accumulation in recovering forests as compared to undisturbed forests in the mid-Atlantic region. However, their simulations attributed a larger proportion of the increase in NPP to N deposition (17%) compared to CO<sub>2</sub> fertilization (14%), while our results suggested a dominant role of CO<sub>2</sub>

fertilization (32%) during the 20<sup>th</sup> century. We also did not determine the effect of N deposition at the regional scale, which could explain the disparity between our results and those of *Pan et al.* [2009]. Our use of NCE also included conversion fluxes resulting from the decomposition of product pools and is a more inclusive measure of accumulated C sinks over time compared to NEP. Our results show that ozone reduced NCE by 18% during the 20<sup>th</sup> century, indicating that ozone could have a larger effect on regrowing forests, crops, and pasture located near cities where ozone levels are high. Reduction in NPP ranging from 3 to 16% because of increased surface ozone levels has been reported across the US [*Felzer et al.*, 2004; *Ollinger et al.*, 1997], with largest reduction in forest NPP in the southern region of the Northeast [*Ollinger et al.*, 1997], and Midwest agricultural lands [*Felzer et al.*, 2004]. While we did not isolate the effects of changing climate on NCE over the 20<sup>th</sup> century, previous research found that climate had a negative effect on C sequestration in the United States, with the net decrease in C sequestration by 1% during the period 1901–2010 [*Zhang et al.*, 2012]. This work indicates that the effects of climate on NCE over the 20<sup>th</sup> century have been quite small compared to land use change and elevated CO<sub>2</sub> [*Felzer et al.*, 2004; *McGuire et al.*, 2001].

#### 4.5. 21st Century Response to Disturbance, Climate, Elevated CO<sub>2</sub>, and Ozone

[45] Our projections of 21<sup>st</sup> century NCE for present-day forested areas (Figure 7) indicate that we can expect changes in the relative effect of the different factors we examined. With annual or stochastic disturbance in the form of timber harvest, forest recovery will continue to be a substantial contributor to the size of NCE in the future. While C loss does occur during timber harvest, our accounting for the fate of the C in product pools distributes the loss over long time scales as a function of the turnover rate of the pool (Figure S7). In the case of timber harvest, a larger proportion of the disturbed C ends up in long-lived wood products (e.g., 100 year turnover) than would in the case of a disturbance such as wildfire.

[46] Changes in climate and CO<sub>2</sub> fertilization will yield a range of effects on NCE across the region. Our results suggest that future climate and CO<sub>2</sub> fertilization will have a larger positive effect on NCE in the northeast and the southern US, respectively (Figure 8b and Figure 8c). Ozone has a negative effect on NCE during the 21<sup>st</sup> century (8% decrease), but the effect varies depending on location as a function of available soil moisture and proximity to urban areas [*Felzer et al.*, 2004; *Ollinger et al.*, 1997]. While our results are consistent with other studies that predict a C sink with land use change or disturbance during the 21<sup>st</sup> century [*Albani et al.*, 2006; *Heath and Birdsey*, 1993; *Hurt et al.*, 2002], there is a substantial difference in the magnitude of the sink. *Albani et al.* [2006] carried out simulations assuming mature forests for the future resulting in a net sink of 10 Tg C yr<sup>-1</sup>. *Heath and Birdsey* [1993] projected a C sink of 30 Tg C yr<sup>-1</sup> by 2070 assuming that future growing conditions will be similar to past growing conditions, which is less likely under changing climate and altered disturbance regimes. Similarly, *Hurt et al.* [2002] estimated a net C sink of 130 Tg C yr<sup>-1</sup> for the conterminous US by the end of 21<sup>st</sup> century which is much lower than our estimate of 269.4 Tg C

$\text{yr}^{-1}$ . *Hurt et al.* [2002] attributed the reduction in C sequestration rate to forest maturity in the eastern US, while our study was carried out with partial annual and stochastic timber harvest resulting in an increase in C sequestration rate following forest recovery during the latter half of the 21<sup>st</sup> century. In addition, *Hurt et al.* [2002] reported a reduction in C sink assuming no change in land use practices for the future and neglecting the effects of ecophysiological mechanisms such as CO<sub>2</sub> fertilization, climate change, and air pollution. The disparity in results indicates that the role of anthropogenic disturbance in driving NCE is particularly important. Our study only simulates future timber harvest and the fact that we attempt to realistically account for product pools is likely a significant contributor to the disparity between the results of *Hurt et al.* [2002] and this study, as the 100 year product pool will continue to decompose well into the 22<sup>nd</sup> century.

[47] Forest harvest events have a significant effect on short- and long-term C sequestration [*Davis et al.*, 2009], depending on harvesting frequency and harvest rates [*Nunery and Keeton*, 2010]. Previous studies report that partial repeated harvest has the potential to increase C stores [*Davis et al.*, 2012; *Harmon and Marks*, 2002; *Holtmark*, 2012] depending on rotation length and amount of C harvested. While partial annual harvest resulted in a net decrease in NCE by 6.8 Tg C  $\text{yr}^{-1}$  when compared to stochastic harvest, we found no substantial difference in regional NCE between the partial annual (269.4 Tg C  $\text{yr}^{-1}$ ) and stochastic (276.2 Tg C  $\text{yr}^{-1}$ ) timber harvest. However, at the end of 21<sup>st</sup> century, partial annual harvest accumulated more C in vegetation (19,741 g C  $\text{m}^{-2}$ ) compared to stochastic harvest (17,760 g C  $\text{m}^{-2}$ ). In a recent study, *Davis et al.* [2012] report that partial harvest increased net C storage in forest biomass and soils with a harvest intensity of 10–34%. We also find that partial annual harvest at the regional and site levels (Figure 8) increases C storage in the vegetation. However, because the vegetation has grown closer towards mature conditions, the net C sequestration is less than when disturbed once stochastically. While our results are consistent with *Davis et al.* [2012] suggesting that partial harvest increased net C storage in vegetation, there are differences in the approach used to simulate partial harvest. Where *Davis et al.* [2012] simulated partial harvest at a 15 year interval assuming different harvest rates, we simulated future timber harvest based on historical harvest rates using two different approaches: partial annual where we removed the proportion of vegetation C compounded annually and stochastic harvest where we removed the vegetation only once during a 100 year period. We recognize that the effect of ozone in our future simulation is much lower compared to the 20<sup>th</sup> century simulation because we have only considered its effect on forests during the 21<sup>st</sup> century but its effect on forests, crops, and pasture during the 20<sup>th</sup> century. Previous research reported that agricultural crops are more sensitive to ozone [*Reich*, 1987], with the largest reduction in NPP (13% of the total NPP) across the Midwest agricultural lands [*Felzer et al.*, 2004].

[48] Changes in temperature and precipitation have potential impacts on ecosystem structure and function [*Heyder et al.*, 2011; *Walther et al.*, 2002], resulting in subsequent changes in forest productivity, biogeochemical, and water cycles [*Allen et al.*, 2010; *Hanson and Weltzin*, 2000;

*Rustad et al.*, 2012; *Zhao and Running*, 2010]. While increases in temperature and moisture stress associated with climate change can fundamentally decrease forest productivity [*Allen et al.*, 2010], such decreases in productivity can be temporary as plants respond to temperature and moisture stress through acclimation of optimum temperature for plant growth [*Liang et al.*, 2013; *Way and Oren*, 2010]. For example, *Gunderson et al.* [2000] show a clear increase in the optimum temperature of photosynthesis for sugar maples in both growth chambers and open top chambers (OTC), though the actual photosynthetic rate does not increase in the OTC experiments. Although the response of photosynthetic rates to warming differs among species [*Berry and Bjorkman*, 1980], in all cases the optimum temperature increases. In TEM-Hydro2, we found no substantial difference in the NCE with and without acclimation of optimum temperature for photosynthesis, but increasing atmospheric CO<sub>2</sub> during the later half of the 21<sup>st</sup> century increased plant water use efficiency (WUE) from 2.4 g C/kg H<sub>2</sub>O in 2001 to 4.5 g C/kg H<sub>2</sub>O in 2099 equivalent to an increase of 47% with CO<sub>2</sub> fertilization (Figure S8a). *Tian et al.* [2010] found similar results across the southern US with an increase in WUE of 25% during the period 1895–2007, demonstrating that plants have already responded to increased CO<sub>2</sub> concentration. Additionally, increased water use efficiency also affects ozone uptake by plants [*Reich*, 1987], where increased atmospheric CO<sub>2</sub> under water stressed conditions would lead to stomatal closure resulting in decreased ozone uptake by plants. Our results indicate that GPP decline decreased with increasing water stress in areas with low soil moisture content (Figure S8b).

[49] Anthropogenic disturbance has important implications on regional C dynamics; however, several other anthropogenic and natural processes such as urbanization, fire, insect outbreaks, and hurricanes would substantially alter the C dynamics of eastern temperate forests [*Houghton et al.*, 2000a; *Houghton et al.*, 2000c; *Loveland and Acevedo*, 2006; *Zeng et al.*, 2009]. Urbanization has increased dramatically in the eastern US by 9.4% at the expense of agricultural (15.4%) and forest (2.5%) lands [*Loveland and Acevedo*, 2006], with the largest increase in the Southern Coastal Plain (6.2%). *Liu et al.* [2004] report a progressive decline in C sink during the period 1973–2000 due to increased forest clearing and continuing urbanization in the Southeast. While urbanization could release a substantial amount of C to the atmosphere [*Milesi et al.*, 2003], we have held developed land constant to isolate the effects of our focal stressors.

[50] Natural processes such as fire, insect outbreaks, and hurricanes and tropical storms will influence the amount of C stored in forests [*Houghton et al.*, 2000c; *Houghton et al.*, 2000c; *Lovett et al.*, 2006; *McNulty*, 2002; *Zeng et al.*, 2009]. In particular, fire directly influences how much of C remains in the forest. Fire suppression in the US led to an increase in C uptake by 25% following 1926 [*Houghton and Hackler*, 2000a; *Houghton et al.*, 2000c]. However, the relative contribution of forest fire suppression on net C sequestration is less important in the eastern US because their model included the West, where fire is more important. While fire suppression has altered forest structure, with changes leading to increased large, severe fires in the west [*Stephens et al.*, 2009], structural and compositional changes in the east have resulted in mesic conditions that are less prone to burning [*Nowacki and Abrams*, 2008].

Additionally, prescribed fire is an important forest management activity currently being practiced in the southeastern US [Mickler *et al.*, 2002] to reduce hardwood and herbaceous competition in young stands, improve wildlife habitat, and minimize wildfires.

[51] Hurricanes and tropical storms can also release a substantial amount of C to the atmosphere either directly through biomass destruction or indirectly through decreased C sequestration capacity [McNulty, 2002]. Because the intensity of weather and climate extremes such as tropical storms and hurricanes are expected to increase in the future [Zeng *et al.*, 2009], we would expect a difference in C sequestration where the frequency of these other types of disturbance is prevalent [Amiro *et al.*, 2010; Williams *et al.*, 2012]. Tropical storms and hurricanes are less frequent in the northeastern US and have become progressively more frequent toward the southern region along the Atlantic and Gulf coasts with a fourfold increase in tree mortality across the eastern US, but such increase in mortality was only limited to 1–5% of all plots [Vanderwel *et al.*, 2013]. Other key natural processes that would influence the C cycle are the pests and pathogens that have both short- (tree defoliation, loss of vigor, and death) and long-term (change in species composition, forest productivity, and nutrient cycling) effect on forest health [Lovett *et al.*, 2006].

[52] We also recognize that both wet and dry atmospheric N deposition have the potential to alter C uptake of temperate forests. While N deposition during the latter half of the 20<sup>th</sup> century has contributed positively to C sequestration [Holland *et al.*, 1997], Nadelhoffer *et al.* [1999] found no evidence of increased C uptake with N deposition. Additionally, the magnitude of the N-fertilization in the eastern US is debatable because of uncertainties associated with the distribution of added N among woody and nonwoody biomass, and leachate [Nadelhoffer *et al.*, 1999]. Although our site level simulation of N deposition resulted in a net increase in C uptake by 2–8%, we did not isolate the effects of N deposition at the regional scale because regional data sets of the N deposition were not available. While lack of consideration of the N deposition at a regional scale adds uncertainty to our projections of net C sequestration of the eastern temperate forests, the effect of additional N inputs is likely to vary spatially. Previous studies report that high-elevation temperate forests of the eastern US have reached saturation [Aber *et al.*, 1989], and thus additional N would have a negligible effect on net C uptake [Nadelhoffer *et al.*, 1999].

## 5. Model Uncertainty and Bias

[53] The one-layer soil model provides several limitations in terms of decomposition rates, moisture, and temperature effects in our ability to capture below-ground C dynamics following disturbance. Trumbore [1997] suggested that the soil organic matter (SOM) contains three C pools: active, passive, and intermediate/slow. Active pools include fine roots and rapidly decomposed fresh plant litter, while the passive pool includes organic matter with longer turnover times ranging several thousand years. The intermediate or slow pool is poorly defined with turnover times ranging from years to centuries. Because of different turnover times of soil organic matter ranging from days to centuries, it is

possible that TEM-Hydro2 overestimates C efflux using a one-layer soil model.

[54] Most of the issues we have encountered with the one-layer soil model are in arid regions and several steps have been taken to address some of these issues [Felzer *et al.*, 2011]. In particular, one issue in arid regions is the rapid evaporation of water in the absence of adequate precipitation for recharge, leading to insufficient water to support plant growth. To account for this shortcoming, adjustments were made to lower soil evaporation under extremely dry conditions, allowing greater productivity by lowering the optimal temperature for photosynthesis in cold grasslands. While the one-layer physical soil model limits our ability to accurately model the decomposition rates, moisture, and temperature effects in arid regions, we have not encountered such issue for the humid forests of the eastern US [Felzer *et al.*, 2009]. However, to ensure that we did not allow higher than expected rates of microbial decomposition in the eastern US due to varying rates of decomposition, we modified our original temperature and moisture-dependent microbial respiration function allowing the soil pool to equilibrate over longer time scales, but this modification did not substantially alter the NCE at a regional scale.

[55] Another source of uncertainty is the limited forest coverage in areas of the upper-Midwest in our land use land-cover input data sets developed from Hurtt *et al.* [2006]. The data set represents transitions in land use and land cover from 1700 to present, which was developed into cohorts as an input for TEM-Hydro2. In this dynamic cohort approach, a new cohort is formed every time there is a disturbance, with land area within a grid cell subtracted from the undisturbed vegetation and added to the new disturbed cohort. More disturbances result in more cohorts with time, allowing us to track the effect of each disturbance separately. We note that there are regional deficiencies in Hurtt *et al.* [2006], such as an underrepresentation of forests in the Upper Midwest, but these data are still one of the best long-term data sets of land transitions on the continental scale and have been used in many other modeling studies [Gent *et al.*, 2011; Knutson *et al.*, 2006].

[56] Comprehensive uncertainty analysis of the model requires estimation of error resulting from variability in the input variables and model parameters [Crosetto and Tarantola, 2001]. Parameter uncertainty comes from error in measurements used for parameterization, scaling issues when point measurement are upscaled, or from input data estimated through semiempirical analysis such as soil respiration [Zaehle *et al.*, 2005]. The use of Monte Carlo and Bayesian approaches to quantify uncertainty, especially with recent gridded data sets of several ecosystem variables made available by remote sensing, is a powerful tool in model testing and optimization [Gardner *et al.*, 1980; Tang and Zhuang, 2009]. TEM-Hydro2 has 33 biome-dependent parameters and several of these parameters are determined by calibration to target values at specific sites. Sensitivity analysis using Monte Carlo or Bayesian techniques provides a distinct advantage in constraining parameter values, but requires data from multiple sites that are only now becoming available through combination of remote sensing/eddy covariance data sets [Jung *et al.*, 2011; Xiao *et al.*, 2011]. This optimization is the subject of future proposed research.



## 6. Conclusions

[57] A full understanding of the dynamics of C sequestration requires knowledge of land use history, including human activity, as nearly all ecosystems have been subjected to change by humans [Amiro *et al.*, 2010; Magnani *et al.*, 2007; Williams *et al.*, 2012]. Many modeling studies do not account for land use history, due to unavailability of detailed disturbance records or a simplifying assumption that all forests are mature. In the eastern US, terrestrial ecosystems experienced widespread deforestation during the 19<sup>th</sup> century followed by forest regrowth and increased C sequestration in the 20<sup>th</sup> century [Birdsey *et al.*, 2006]. Our 20<sup>th</sup> century simulation showed that forest recovery following agricultural abandonment and timber harvest had a positive effect on the C sequestration rate (NCE), indicating that accounting for anthropogenic disturbance is important for improving future projections. Additionally, the 21<sup>st</sup> century simulation with realistic partial annual and stochastic timber harvest demonstrates the contribution and relative importance of postdisturbance recovery to enhancing C sequestration. It is important to note that the enhancement in NCE is in part due to the nature of the simulated disturbance and the allocation of C to pools with different residence times and the assumption that postdisturbance forest recovery follows a successional pathway that led to the predisturbance forest condition. Also, when accounting for C since the start of disturbance, the net result is recovery of the C lost, unless factors such as CO<sub>2</sub> fertilization enhance the regrowth rates above and beyond what they would have been in the predisturbance period. These results suggest that future C dynamics in eastern US forests may be driven primarily by postdisturbance recovery and CO<sub>2</sub> fertilization if land use change and recovery continue at rates similar to the historical period. However, natural disturbances resulting from more climate extremes will reduce the positive benefits of singular anthropogenic disturbances, and eventually CO<sub>2</sub> fertilization effects will saturate, so there is no long-term benefit from continued climate change.

[58] Future work will focus on developing (i) a multilayer decomposition pool by adopting a microbial/enzyme pool approach [Allison *et al.*, 2010], and using a continuous measure of soil quality [Ågren and Bosatta, 1996], (ii) calibration parameters for other sites in the eastern US to validate the model over a range of biomes, (iii) gridded N deposition data sets to quantify the effects of N deposition at regional level, (iv) development of data sets and algorithms to capture the effect of fire and hurricanes, and (v) uncertainty analysis for the 33 biome-dependent parameters using Bayesian techniques.

[59] **Acknowledgments.** This study was funded by the Department of Energy — Basic Research and Modeling to Support Integrated Assessment - DE-FG02-08ER64648. We also acknowledge the Ecosystems Center, MBL (Jerry Melillo, David Kicklighter) for providing the subcontract to this work. We are also thankful to Timothy Cronin (MIT, Massachusetts), and Dr. Bruce Hargreaves and Dr. Zicheng Yu (Lehigh University) for their suggestions and comments during the course of the study. We are grateful to University of New Hampshire, EOS-WEBSTER Earth Science Information Partner (ESIP) for providing access to land use data sets. We also thank several anonymous reviewers for their suggestion that helped to improve the manuscript.

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