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Simulating the impacts of disturbances on forest carbon cycling in North America: Processes, data, models, and challenges

Shuguang Liu,[1] Ben Bond-Lamberty,[2] Jeffrey A. Hicke,[3] Rodrigo Vargas,[4] Shuqing Zhao,[5] Jing Chen,[6] Steven L. Edburg,[3] Yueming Hu,[7] Jinxun Liu,[8] A. David McGuire,[9] Jingfeng Xiao,[10] Robert Keane,[11] Wenping Yuan,[12] Jianwu Tang,[13] Yiqi Luo,[14] Christopher Potter,[15] and Jennifer Oeding[8]

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[1] Forest disturbances greatly alter the carbon cycle at various spatial and temporal scales. It is critical to understand disturbance regimes and their impacts to better quantify regional and global carbon dynamics. This review of the status and major challenges in representing the impacts of disturbances in modeling the carbon dynamics across North America revealed some major advances and challenges. First, significant advances have been made in representation, scaling, and characterization of disturbances that should be included in regional modeling efforts. Second, there is a need to develop effective and comprehensive process-based procedures and algorithms to quantify the immediate and long-term impacts of disturbances on ecosystem succession, soils, microclimate, and cycles of carbon, water, and nutrients. Third, our capability to simulate the occurrences and severity of disturbances is very limited. Fourth, scaling issues have rarely been addressed in continental scale model applications. It is not fully understood which finer scale processes and properties need to be scaled to coarser spatial and temporal scales. Fifth, there are inadequate databases on disturbances at the continental scale to support the quantification of their effects on the carbon balance in North America. Finally, procedures are needed to quantify the uncertainty of model inputs, model parameters, and model structures, and thus to estimate their impacts on overall model uncertainty. Working together, the scientific community interested in disturbance and its impacts can identify the most uncertain issues surrounding the role of disturbance in the North American carbon budget and develop working hypotheses to reduce the uncertainty.

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1. Introduction

[2] Forest ecosystems store more than 80% of all terrestrial aboveground carbon (C) and more than 70% of all soil organic C worldwide [*Batjes*, 1996; *Jobbágy and Jackson*, 2000]. The magnitude of forest-atmospheric carbon dioxide (CO_2) exchange is about seven times the current level of annual global anthropogenic C emissions. From 1850 to 2000, roughly 28–40% of global anthropogenic CO_2 emissions resulted directly from deforestation [*Houghton*, 2010], whereas recovery from past disturbances is considered to be the dominant driver for some regional terrestrial carbon sinks, contributing to a large portion of the current northern hemisphere terrestrial sink [e.g., *Goodale et al.*, 2002;

[1]U.S. Geological Survey Earth Resources Observation and Science Center, Sioux Falls, South Dakota, USA.
[2]Joint Global Change Research Institute, DOE Pacific Northwest National Laboratory, College Park, Maryland, USA.
[3]Department of Geography, University of Idaho, Moscow, Idaho, USA.
[4]Departamento de Biología de la Conservación, Centro de Investigación Científica y de Educación Superior de Ensenada, Ensenada, Mexico.
[5]College of Urban and Environmental Sciences, Peking University, Beijing, China.
[6]Department of Geography, University of Toronto, Toronto, Ontario, Canada.
[7]College of Information, South China Agricultural University, Guangzhou, China.

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[8]Stinger Ghaffarian Technologies, Sioux Falls, South Dakota, USA.
[9]Alaska Cooperative Fish and Wildlife Research Unit, U.S. Geological Survey, University of Alaska Fairbanks, Fairbanks, Alaska, USA.
[10]Complex Systems Research Center, Institute for the Study of Earth, Oceans, and Space, University of New Hampshire, Durham, New Hampshire, USA.
[11]Missoula Fire Sciences Laboratory, Rocky Mountain Research Station, Missoula, Montana, USA.
[12]College of Global Change and Earth System Science, Beijing Normal University, Beijing, China.
[13]The Ecosystems Center, Marine Biological Laboratory, Woods Hole, Massachusetts, USA.
[14]Department of Botany and Microbiology, University of Oklahoma, Norman, Oklahoma, USA.
[15]National Aeronautics and Space Administration Ames Research Center, Moffett Field, California, USA.

Fang et al., 2001; *Kauppi et al.*, 2006; *Pan et al.*, 2011]. Understanding disturbances is critical for a more accurate calculation of regional carbon fluxes and helpful to better inform policy makers on the importance and uncertainty of disturbances on regulating the regional and global carbon cycle.

[3] A disturbance is defined as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment" [*Pickett and White*, 1985]. Carbon stocks and fluxes of forests are influenced by both natural and human disturbances that alter forest structure and affect fundamental carbon cycle processes [*Franklin et al.*, 2002; *Chambers et al.*, 2007; *Goward et al.*, 2008; *Vargas and Allen*, 2008] and the biogeochemical interactions between forests and the atmosphere [*Schimel et al.*, 2001; *Fang et al.*, 2001; *Kauppi et al.*, 2006; *Masek and Collatz*, 2006; *Zhao et al.*, 2009, 2010a]. For example, it has been estimated that wildland fire disturbances in Canada can change the direction of net forest-atmospheric C exchange in any given year [*J. M. Chen et al.*, 2000; *Kurz and Apps*, 1999; *Bond-Lamberty et al.*, 2007a; *Kurz et al.*, 2008b; *Stinson et al.*, 2011]. *Wiedinmyer and Neff* [2007] estimated that annual fire emissions are about 0.06 Pg C per year from 2002 to 2006 in the United States, which is equivalent to about 4% of U.S. fossil fuel emissions. The average direct C emission from Canadian forest fires was 0.027 Pg C per year from 1959 to 1999 with large interannual variability [*Amiro et al.*, 2001], and this emission was expected to increase under future climate change scenarios [*Amiro et al.*, 2009]. *Chambers et al.* [2007] estimated that about 320 million large trees were killed or damaged along the U.S. Gulf Coast by Hurricane Katrina in 2005, representing a biomass of 0.09–0.11 Pg C transferred from live to dead pools. *Zeng et al.* [2009] analyzed the impacts of historical tropical cyclones on U.S. carbon cycle and found that cyclone damages from 1980 to 1990 offset about 9–18 percent of the C sink in forest trees over the United States. *Vargas and Allen* [2008] have reported the highest annual soil CO_2 efflux with nearly 4000 g C $m^{-2}yr^{-1}$ after hurricane Wilma in 2005. Forest management and conversion also affect carbon cycling at large scales [*Beer et al.*, 2010]. The U.S. Forest Service has estimated that approximately 4.05 million hectares or 1.3% of forest lands are affected by harvesting activities each year across the United States [*Smith and Darr*, 2004]. Insect outbreaks, which have impacted millions of hectares of forest in North America during recent decades, appear to have increased in both extent and severity [*Carroll et al.*, 2004; *Raffa et al.*, 2008] and are likely having larger effects on the carbon balance of North America [e.g., *Kurz et al.*, 2008a].

[4] These observations highlight the importance of including disturbances for a better estimation of the North American carbon budget. To date, however, assessment efforts have not comprehensively considered the full spectrum of disturbance impacts on regional to global carbon budgets, in part, because of the lack of adequate disturbance databases and appropriate models capable of dynamically incorporating disturbance information at regional scales [*Beer et al.*, 2010; *Ciais et al.*, 2010; *Harmon et al.*, 2011]. Therefore, models have rarely included parameters that describe ecosystem responses to disturbances or have made assumptions based on few observations in discrete ecosystems (mainly temperate or boreal) [*Beer et al.*, 2010; *Medvigy et al.*, 2010]. Yet modeling is useful for improving knowledge of the North American carbon budget in several ways: (1) replication of measurements with models suggests sufficient understanding of the simulated processes; (2) model results can fill in the many spatial and temporal gaps in observations; and (3) models can predict future patterns of carbon stocks and fluxes in the context of future global change.

[5] Here we conduct a review with an emphasis on North America as part of a synthesis effort within the North American Carbon program. Our goals are to (1) describe observational evidence of the impacts of various disturbances on forest structure, forest succession, and C cycle, and how disturbances and their impacts are treated and modeled in state-of-the-art carbon cycle models at the stand level; (2) summarize how disturbances and their impacts are scaled up from stand to continental scales; and (3) review major regional- to continental-scale data sets on disturbances and C stocks and fluxes that can be used for quantifying disturbance impacts. Challenges regarding data sets, knowledge, and modeling are discussed in each of the sections. Finally, we suggest a better interaction between the modeling community and the experimental community to identify the most uncertain areas and develop working hypotheses and data-model-fusion methods to reduce the uncertainty associated with disturbance impacts.

2. Process Understanding and Representation

[6] Disturbances alter forest structure and affect forest carbon dynamics in two major ways. First, they transfer carbon from one pool to another (e.g., from live boles to dead coarse woody debris, or from the live biomass pool and surface soil pool to the atmospheric carbon pool through fire consumption). Second, disturbances modify forest soil's physical and chemical factors and microclimatic environments, creating ecological legacies that have long lasting effects on carbon dynamics (Figure 1). Because by definition disturbances always affect the carbon cycle, it is necessary to have a clear understanding of forest structural components before we estimate the impacts of disturbances.

[7] The fundamental components contributing to forest structure and function at the stand level are tree species composition, stem density, leaf area, canopy coverage, size of trees, understory, litter and coarse woody debris (CWD), and soil substrate (Table 1). Forest stand structure is characterized by the vertical distribution of stems, branches, and foliage and the spatial distribution of trees and other structures such as standing dead trees (snags) and CWD on the forest floor [*Harmon et al.*, 1986; *Spies and Franklin*, 1988]. Removal or falling of trees impacts the spatial distribution of trees and thus forest structure such as the creation of canopy gaps [*Runkle*, 1982; *Pickett and White*, 1985; *Canham et al.*, 1990].

2.1. Legacy Impacts of Disturbances

[8] Disturbances are part of the dynamic fabric of ecosystems with strong spatial and temporal variability, creating a spectrum of legacies in forest structure, successional stages, and carbon cycle trajectories (Figure 1). In general, legacy

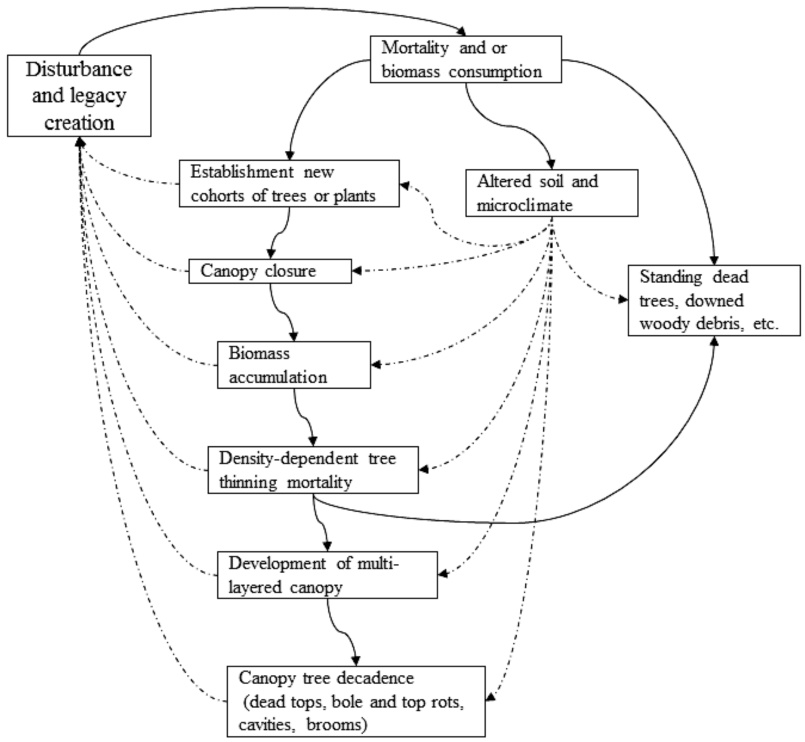

Figure 1. Impact of disturbances on forest ecosystem structural development and the creation of disturbance legacies.

impacts of disturbances on the carbon cycle can be summarized into two categories: mortality and mass transfer, and succession (i.e., changes in heterotrophic respiration, forest succession, and altered soil-climate environment).

2.1.1. Mortality and Mass Transfer

[9] Disturbances might kill trees, resulting in direct and immediate carbon transfer to the atmosphere (in the case of fire) and a shift in structural elements from live to dead pools (e.g., leaves to litter, trees to snags or logs, live roots to coarse woody debris, etc.). Models usually have a set of algorithms dealing with disturbance-induced carbon transfer among pools and their impacts on biogeochemical cycles [e.g., *Parton et al.*, 1987; *Thornton et al.*, 2002; *Liu et al.*, 2004; *Zhao et al.*, 2009]. Most of the accounting procedures are straightforward and similar among different models as the C transferred from any live C pool to its dead C equivalent is generally calculated as the fraction that dies (C transfer coefficient) multiplied by the pre-disturbance live C pool. However, it is a major challenge to accurately define the C transfer coefficients for various disturbances as they vary over time and space (i.e., specifying or simulating the extent and severity of a disturbance). For example, although fire extent and severity can be mapped using remote sensing techniques, linking fire severity with biomass consumption and C transfer coefficients from live to dead C pools has a high degree of uncertainty [*Bond-Lamberty et al.*, 2007c; *Rocha and Shaver*, 2011; *Bond-Lamberty et al.*, 2007b]. In addition, few disturbance models [*Bachelet et al.*, 2005; *Thonicke et al.*, 2001] can predict the spatial and temporal variation of C emissions and C transfer coefficients under future global change scenarios [*Medvigy et al.*, 2010].

[10] Figure 2 details the impacts of various disturbances using a common framework. In essence, this framework systematically specifies the effects of disturbances by assigning coefficients to describe fractions of all C and nutrients pools that (1) are consumed and emitted to the atmosphere, (2) die and fall to the ground, (3) die and remain standing, and (4) are harvested and are laterally transported out of the forest stand. Mass transfer rates from each of the

Table 1. Simplified Representations of Major Structural Elements and C Pools in Typical Forest Carbon Cycle Models

Model Type	Representation of Individuals and C Pools	Key Structural Elements	Live Structural Elements or C Pools	Dead Structural Elements or C Pools	Soil C Pools
Tree	Lumped by trees and pools	Species, age, diameter, height, rooting depth	Leaves, branches, stems, coarse roots, fine roots	Litter, standing dead trees (snags), large woody debris (logs), coarse dead roots, root litter	Soil organic C, and inorganic C
Cohort	Lumped by cohorts and pools	Species, density, age, diameter, and height distributions			
Stand	Lumped by pools	Forest type, tree density, age, canopy height, and leaf area distribution			

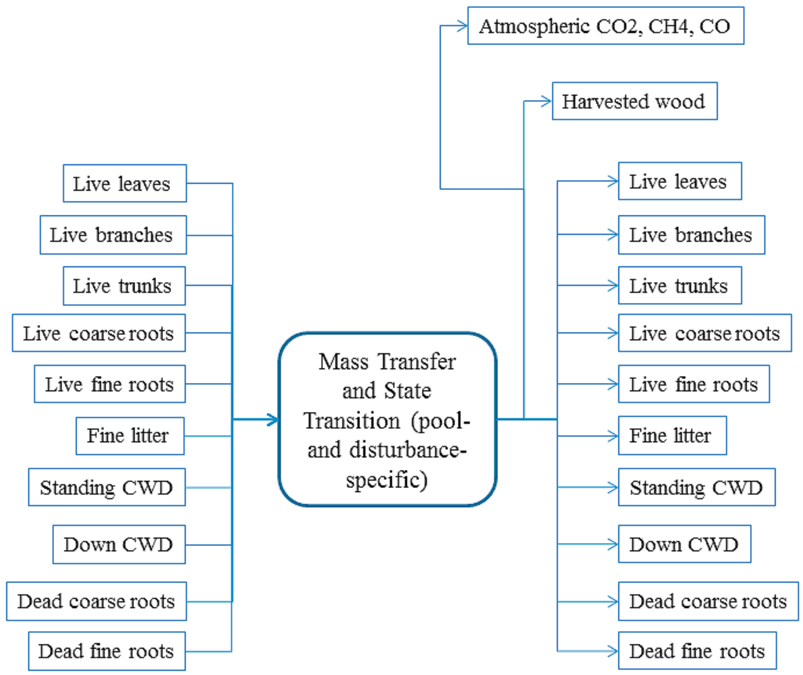

Figure 2. A unified framework for specifying mortality and C transfer among various C pools in a forest system caused by a disturbance. One-to-many relationships usually exist for mass transfer. For example, a portion of live trunks in the forest can be killed by a wind storm, which defines mortality, and the dead materials are transferred to standing and/or down coarse woody debris (CWD), and the rest remains alive.

C pools on the left side of Figure 2 to all the pools on the right side are specified using this scheme. Mass transfer rates effectively describe disturbance intensity or severity, including both mortality (i.e., the reduction of live C pools following disturbance) and the amounts of mass transferred among pools. Simplified, disturbance- or model- specific schemes have been used effectively for different databases and models to focus on the mortality and major disturbance-specific C transfer pathways (e.g., partitioning of fire emissions among CO_2, CH_4 and CO in the work by *French et al.* [2011]). This unified framework is useful to provide a comprehensive overview on the need of quantifying the immediate impacts of various disturbances.

2.1.2. Successional Dynamics

[11] Stand evolution trajectories are often altered dramatically by disturbances [*Johnstone et al.*, 2010] (Figure 1), but natural disturbances rarely eliminate all structural elements from the affected stand [*Franklin et al.*, 2002]. Disturbances can create vastly contrasting quantities and types of living and dead structures that contribute to the ecological legacies associated with structurally diverse starting points for stand structural development [*Johnstone et al.*, 2010]. Such disturbance effects can propagate through the forest for decades at least [*Gough et al.*, 2007] creating lags in heterotrophic respiration caused by delayed mortality or delayed decomposition [*Harmon et al.*, 2011]. Less evident observable effects (e.g., changes in nutrient cycles, belowground processes) are not well known and open challenges and opportunities for basic research and model improvement.

[12] Post-disturbance carbon balance depends on many ecosystem processes including regeneration and vegetation succession, photosynthesis, and respiration [*Goulden et al.*, 2010]. Disturbances may switch forests from a sink to a source of carbon by increasing respiration and reducing leaf biomass and therefore photosynthesis in the period after disturbances (Figure 3). Measurement of net ecosystem C exchange has shown that regenerating temperate forests remained net sources of CO_2 for at least 14 years after logging, due to increased rates of soil respiration [*Olsson et al.*, 1996; *Yanai et al.*, 2003; *Clark et al.*, 2004]. *Amiro et al.* [2010] analyzed more than 180 site-years of eddy-covariance measurements of carbon fluxes made at forest chronosequences in North America, and showed that net ecosystem production (NEP) exhibited a carbon loss from all ecosystems following a stand-replacing disturbance, becoming a carbon sink by 20 years for all ecosystems, and by 10 years for most.

2.2. Modeling Forest Carbon Dynamics and Impacts of Disturbances

2.2.1. Modeling Approaches

[13] Various process-based models have been developed over the past several decades for simulating forest carbon dynamics. The effects of stand information, interannual climate variability, disturbance history, and vegetation ecophysiology on carbon fluxes and stocks are integrated by these ecosystem process models with various complexities. These models can generally be placed into two major categories: ecosystem compartment models and demography models. It is worthwhile to point out that process models can also be categorized as either diagnostic or prognostic models [*Knorr et al.*, 2010; *King et al.*, 2011].

[14] Many compartment models have been developed over the past three decades [*Parton et al.*, 1987; *Running*

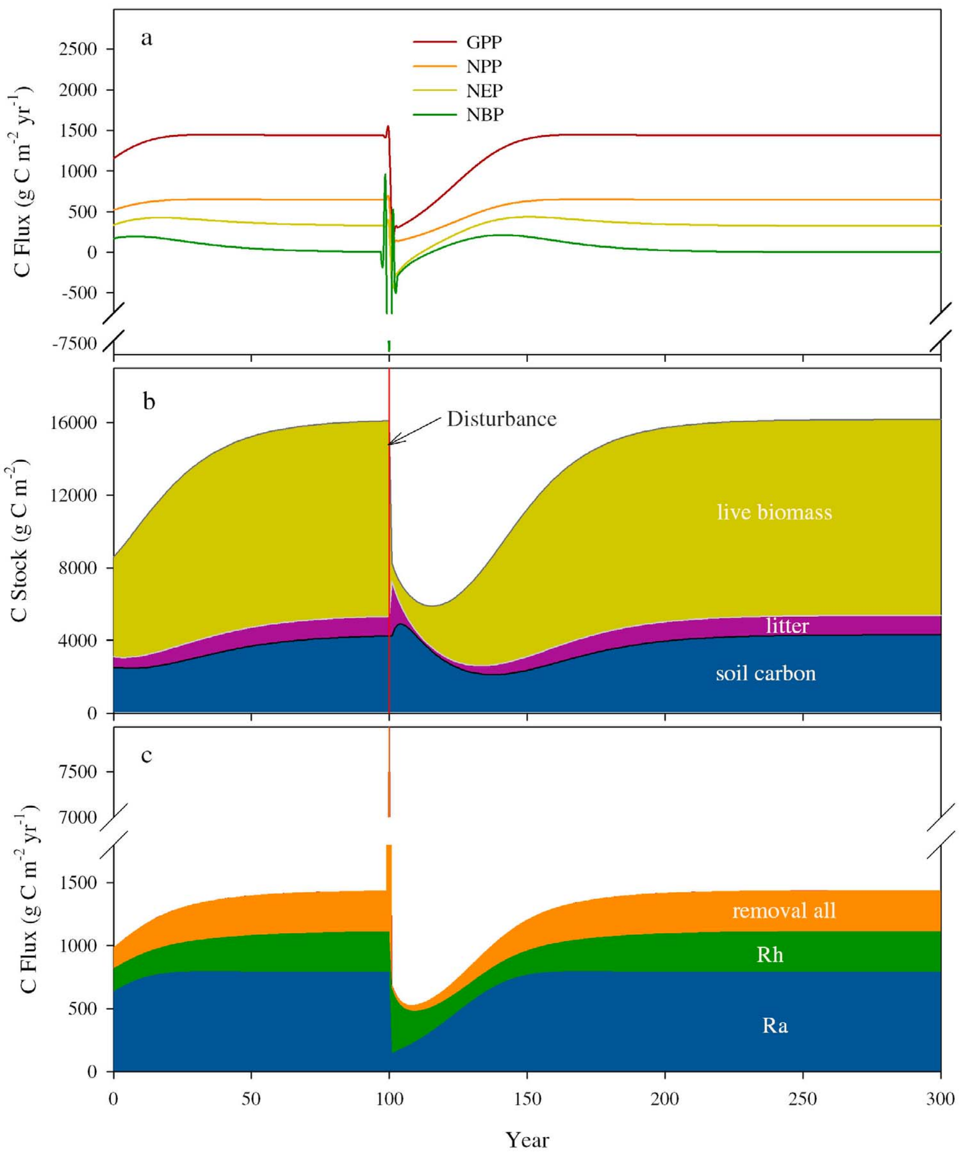

Figure 3. Theoretical carbon stock and flux changes of a forest ecosytem following a stand-replacing disturbance event. (a) Changes of gross primary productivity (GPP), net primary productivity (NPP), net ecosystem productivity (NEP) and net biome productivity (NBP) following disturbance. (b) Changes of three major carbon pools as affected by disturbance; the ecosystem lose a significant amount of C during and after the disturbance, but will have net carbon gain after about 20 years due to forest regrowth. (c) Changes of ecosystem autotrophic respiration (Ra), heterotrophic respiration (Rh), and removals (e.g., logging, fire removal, insect consumption, erosion, etc.). Ra = GPP-NPP; Rh = NPP-NEP; removal all = NEP-NBP.

and Gower, 1991; *Bond-Lamberty et al.*, 2005; *W. Chen et al.*, 2000; *Chen et al.*, 2003; *Raich et al.*, 1991; *McGuire*, 1992; *Liu et al.*, 2003]. These biogeochemical and ecophysiological models use general stand information (see Table 1) and meteorological data to simulate energy, carbon, water, and nitrogen cycling in various details. One key commonality of these compartment models is that the carbon pools of a stand are organized by biomass compartments such as leaves, branches, stems, roots, and CWD and the structural information such as diameter at the breast height (DBH), tree height, and density are not explicitly considered in model representations. Most of the models consider both forest growth recovery under the influence of climate and atmospheric (CO_2 and nitrogen) changes and the interaction between growth variation and heterotrophic respiration variation. This type of model is needed because during the long life span of forests, climate and atmospheric changes are considerable and the impacts of these changes on forest carbon cycle cannot be ignored [*Pan et al.*, 2010; *Norby et al.*, 2001]. These models represent the foundation of ecosystem carbon modeling efforts because of their generalized approach to ecosystem carbon dynamics, and have been extensively examined and applied to simulate biogeochemical processes of forests associated with disturbance

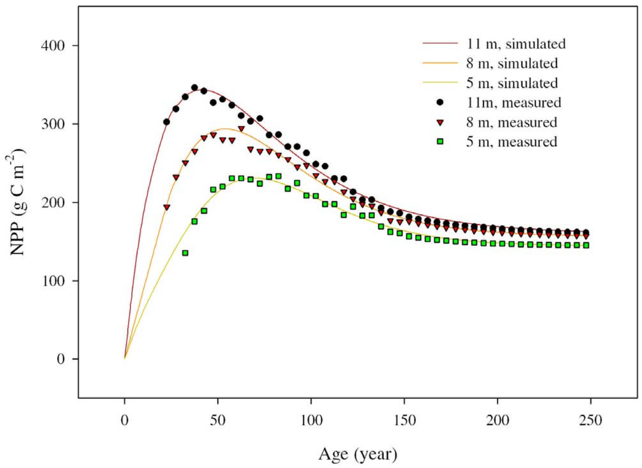

Figure 4. Variation of NPP with forest stand age under various site conditions, for black spruce forests in Ontario, Canada [*Chen et al.*, 2002].

[*W. Wang et al.*, 2009; *Law et al.*, 2003; *Tatarinov and Cienciala*, 2006; *Brugnach*, 2005].

[15] In contrast, ecosystem demography models, which are also referred to as gap models, used a different modeling structure targeted to simulate the impacts of disturbances on forest composition and structure. They explicitly consider species composition, mortality, age structure, height, and disturbances (see Table 1). Since the conception and development of the classic JABOWA model [*Botkin et al.*, 1972], many such models have been developed, including SORTIE [*Pacala et al.*, 1996], FIRE-BGC [*Keane et al.*, 1996], LINKAGES [*Pastor and Post*, 1986], FORCLIM [*Bugmann*, 1994], HYBRID [*Friend et al.*, 1997], LANDIS [*Mladenoff*, 2004], FVS [*Dixon*, 2002], and ED [*Hurtt et al.*, 1998; *Moorcroft et al.*, 2001]. They have been widely used to simulate the impacts of management practices, disturbances, and global change on long-term dynamics of forest structure, biomass, and composition [*Shugart et al.*, 1992; *Hurtt et al.*, 1998; *Bugmann*, 2001; *Norby et al.*, 2001; *Dixon*, 2002]. All forest gap models are built upon the notion that a forest stand is a composite of many small horizontally homogeneous patches of land, and these patches are simulated separately with possibly different species composition, age, and/or successional stage. This abstraction and modeling strategy made it possible to consider the establishment, growth, and mortality of mixed-species, mixed-age forests [*Bugmann*, 2001; *Norby et al.*, 2001; *Wullschleger et al.*, 2001].

2.2.2. Understanding and Representation of Major C Cycle Processes

[16] Initially, disturbances kill some or most of the photosynthetic organs (i.e., leaves) in a forest, instantly reducing its gross carbon uptake capability. The evolution of photosynthetic activity of a forest following disturbances can be modeled from stand structural information (e.g., species composition and leaf area index (LAI)), soil moisture, temperature, nutrients, and microclimate using a variety of approaches. Major approaches for photosynthesis modeling include (1) the Farquhar's leaf-level biochemical equations, in which Rubisco concentration and stomatal conductance are key parameters, applied to the canopy level through the use of LAI based on big-leaf (Biome-BGC [*Kimball et al.*, 1997]), two-leaf [*De Pury and Farquhar*, 1997; *Wang and Leuning*, 1998], or multilayer [*Bonan*, 1995] upscaling methodologies; (2) stand-specific maximum photosynthesis rate (prescribed or derived from in situ measurement or satellite observations, [*Zhao et al.*, 2010a] multiplied by scalars of LAI, temperature, soil moisture, and/or nutrients; (3) light-use efficiency approaches that rely heavily on LAI or normalized difference vegetation index (NDVI), moisture, and temperature [*Potter et al.*, 1998; *Hicke et al.*, 2002; *Yuan et al.*, 2007]; and (4) data-driven and statistical-based approaches in which the predictive models are derived from eddy covariance flux measurements and explanatory variables such as land cover, enhanced vegetation index (EVI), land surface temperature (LST), moisture index, and LAI [e.g., *Xiao et al.*, 2010, 2011]. Net primary production is partitioned into biomass compartments, in some models, following tree-specific dynamic allocation patterns possibly adjusted by nutrients and forest development stage [*Running and Gower*, 1991]. The growth rate of a recovering forest varies greatly with the time since disturbance [*Gower et al.*, 1996; *Chen et al.*, 2002] (Figure 4). This rapid change in NPP with age is the main cause of the measured NEP variation with age for boreal forests [*Coursolle et al.*, 2006] and temperate forests [*Law et al.*, 2003].

[17] Fire disturbance has other near-instantaneous effects, in particular the combustion of biomass; the loss of this C to the atmosphere exerts a significant radiative forcing [*Randerson et al.*, 2006]. In many high-latitude forests and tundra, the depth of burning (in the thick organic horizon) is a key factor in estimating carbon losses and subsequent ecosystem- to biome-scale climate feedbacks, and one likely to be affected by changes in fire intensity [*Turetsky et al.*, 2011]. Significant efforts have been directed toward this area as part of the North American Carbon Program [e.g., *Balshi et al.*, 2007], and *French et al.* [2011] provide a comprehensive review of methods used to model carbon emissions. In addition, fires generate black carbon [*Czimczik et al.*, 2003; *Kane et al.*, 2007], a long-lived though not indefinite [*Ohlson et al.*, 2009] carbon pool in boreal forests. Black carbon accumulation can significantly change the composition of recalcitrance of soil organic matter, in ways that remain poorly understood [*Kane et al.*, 2010] and rarely modeled.

[18] The impacts of disturbances on heterotrophic respiration, primarily originating from the soil and CWD pools, are difficult to quantify [*Trumbore*, 2006; *Harmon et al.*, 2011]. The size of the soil C pool is determined by the balance between C input from litterfall (including woody debris) and root mortality/exudation and the release of C during decomposition. Soil C decomposition depends on many factors, including the size of the soil C pools, chemical quality of the substrate, soil microclimate, and soil properties (temperature, moisture, soil texture, pH, nutrient status, etc.) [*Trumbore et al.*, 1996; *Liski et al.*, 1999; *Davidson and Janssens*, 2006]. Disturbances usually not only transfer live materials to the dead structural components but also alter the subsequent size of soil organic C pools as well as soil and microclimate conditions, affecting heterotrophic respiration for several decades after disturbance. Decomposition of C on the forest floor and in the soil profile can be enhanced for years after disturbances because soils become warmer and possibly wetter due to reduced

evapotranspiration in boreal forests, for example; such effects have been observed in the field [*Yi et al.*, 2010] and modeled at the landscape scale [*Bond-Lamberty et al.*, 2009]. In addition, uprooting of trees by windthrow can accelerate the decomposition of partially protected C in deep soil layers [*Vargas et al.*, 2010]. Litter fall and rhizodeposition dramatically decrease shortly after disturbance, and labile soil carbon pools would therefore decrease significantly, leading to decrease in heterotrophic respiration. Finally, it is important to understand how disturbances and heterotrophic respiration are simulated in models and how elemental equations representing these processes are constructed. For example, it is critical to assess whether the global convergence of temperature sensitivity of ecosystem respiration (Q_{10}) (~1.4 [*Bond-Lamberty and Thomson*, 2010a; *Mahecha et al.*, 2010]) is consistent after disturbances across ecosystems. Disturbance effects on heterotrophic respiration are particularly important to constrain; *Amiro et al.* [2010] and *Goulden et al.* [2010] both found that the carbon dynamics following disturbance is primarily driven by gross primary productivity, while heterotrophic respiration was relatively time-invariant.

[19] CWD evolution is an aspect of forest structural changes during forest recovery or succession. The size and decay classes of CWD at a forest site can be linked to histories of forest disturbance, management, and forest succession [*Gough et al.*, 2007]. Major disturbances can destroy the old stands, creating large-size classes of debris (snags and logs) in early decay classes, and initiate a new stand [*Oliver*, 1980; *Harmon et al.*, 1986] (Figure 1). These large-size classes of CWD will gradually degrade into rotting organic matter during forest stand development. Through measurements of woody debris pools along numerous chronosequences, investigators have developed a paradigm of a U-shaped curve that characterizes the long-term CWD dynamics in unmanaged disturbed forests [*Spies and Franklin*, 1988; *Currie and Nadelhoffer*, 2002]. In this U-shaped curve, CWD from the previously disturbed stands decays slowly, while that originating from the new stand gradually accumulates after a lag of several decades [*Harmon et al.*, 1986]. In addition, woody decay after disturbance does not often follow a monotonic trend, since wood debris pools standing in the air will be different from the pools fallen on the ground in terms of decomposition rates, resulting in a few pulses of decomposition many years after the disturbance [*Harmon et al.*, 2011].

[20] Finally, a novel aspect of forest recovery after disturbances is the ability of plants to use old nonstructural carbon compounds (NSC) for metabolic activities [*Vargas et al.*, 2009]. After disturbances plants are under stress with a limited capacity to photosynthesize and to take up nutrients and water, which may further reduce gross primary productivity (GPP). Thus, the possibility that plants allocate older stored carbon for metabolic activities provides a new dimension of the fate and the implied role of stored carbon in plants that could be incorporated in the next generation of models. Failure to account for the mobilization of older stored carbon for plant metabolic activities can lead to inaccurate estimates of above and below-ground NPP, and has implications for our understanding of plant recovery and resilience adaptations [*Langley et al.*, 2002].

2.2.3. Modeling the Impacts of Harvest

[21] Many modeling studies have investigated the effects of harvest on the carbon cycle at regional to continental scales [e.g., *Hurtt et al.*, 2002; *Liu et al.*, 2003; *Zhao et al.*, 2010a; *Albani et al.*, 2006; *Shevliakova et al.*, 2009]. The effects of harvesting practices on aboveground biomass C reduction are straightforward, but its impacts on soil carbon dynamics are poorly understood. Harvesting results in structural damages to forest canopy and soils, and can increase litter C stock at the forest floor and in soil temporarily. But overall it enhances soil C loss because of structural damages to forest canopy and the soil. In the years following disturbances, soil C loss may exceed C gain in the aboveground biomass [*Kowalski et al.*, 2004]. *Pennock and van Kessel* [1997] showed that soil C was reduced between 5 and 20 t C/ha over 20 years following clear-cutting, which is a significant loss compared to the accumulated C in the biomass of the maturing forest.

[22] Soil C dynamics are related to the intensity of harvesting and recovery of productivity. Whole-tree harvesting can cause a small decrease whereas conventional harvesting (leaving the non-timber materials on site) results in a small increase of soil C [*Johnson and Curtis*, 2001; *Tang et al.*, 2009]. Nevertheless, the small changes usually diminish over time without a lasting effect [*Johnson and Curtis*, 2001; *Tang et al.*, 2009]. *Tang et al.* [2005] found that forest thinning did not change soil respiration because thinning caused combined effects of a decrease in root respiration, an increase in soil organic matter, and changes in soil temperature and water content. *Jandl et al.* [2007] analyzed the effects of harvesting, thinning, and control of natural disturbances on soil C dynamics, and found that soil C storage can be enhanced by increasing C input to the soil through enhanced forest productivity. At the same time, minimizing the impacts of disturbances on forest structure and soil reduces the risk of unintended C loss.

[23] Selective harvesting (or thinning) is a centerpiece of silvicultural practices in the world to promote desired tree species, stem quality, and ecosystem services. For example, the areal extent of partial cutting is 61 percent of that of clear-cutting in the United States [*Masek et al.*, 2011]. Although selective cutting is a widespread forest management practice, the effects of selective cutting on carbon budget have largely been ignored over large areas. It is difficult to use process models to assess such effects at regional to continental scales because of data scarcity and technical limitations [*Franklin et al.*, 2009]. Realizing the importance of selective cutting in the simulation of regional C dynamics, *Liu et al.* [2003] calculated the area of selective cutting from clear-cut area (detected from remote sensing) and the ratio of clear-cut and selective-cut at regional scale from surveys, and then randomly allocated the total selective-cut area to grid cells on landscape.

2.2.4. Modeling the Impacts of Insect Outbreaks

[24] Herbivorous insects have serious impacts on forests either through the consumption of leaves or fluids (e.g., defoliation) or through consumption of phloem (e.g., by bark beetles). Defoliators feed on tree leaves, causing reductions in leaf area and primary productivity [*Cook et al.*, 2008; *Hogg et al.*, 2008]. Some insects such as the forest tent caterpillar are responsible for widespread defoliation that rarely results in whole tree mortality [*Volney and Fleming*, 2000]. However, other defoliators like the eastern spruce

budworm in northeastern North America can result in widespread tree mortality following multiple years of severe attacks [*Fleming et al.*, 2002; *Samman and Logan*, 2000]. For example, the mountain pine beetle (*Dendroctonus ponderosae* Hopkins, Coleoptera: Curculionidae, Scolytinae), a native insect of the pine forests of western North America, has recently affected 130,000 km^2 in British Columbia [*Kurz et al.*, 2008a]. Other bark beetles that have caused damage over large regions include spruce beetle and *Ips* spp. in western North America, and southern pine beetle in the southern U.S. [*U.S. Department of Agriculture (USDA)*, 2009; *Raffa et al.*, 2008].

[25] Several factors require consideration for modeling the impacts of insect outbreaks on the carbon cycle, including the type, extent and severity of insect disturbance and the consequences of tree mortality. The type of insect disturbance (e.g., bark beetle or defoliator) determines which carbon cycle process is affected. Consequences of tree mortality, such as subsequent needledrop, snagfall, and seedling establishment, need to be represented. The spatial extent and severity of outbreaks need to be prescribed in the model.

[26] Several studies have investigated impacts of insect outbreaks to the C cycle at the stand scale. For instance, *Hogg* [2001] investigated the impact of forest tent caterpillars on growth and dieback dynamics of trembling aspen using a modified version of the FOREST-BGC ecosystem model, and found that this insect was a key factor in controlling the growth and dieback of aspen. *Schäfer et al.* [2009] conducted a similar study on gypsy moth defoliation using the 4C-A model. Only 50% of the foliage reemerged after the disturbance, which reduced productivity by 75%. *Seidl et al.* [2008] examined spruce bark beetle disturbances on 1 ha stands using the patch model PICUS in Europe, with insect damage calculated as a function of the infestation risk, infestation damage, spatial distribution of mortality, and population dynamics. Biotic disturbances were found to be important mechanisms controlling future responses of productivity to climate change in this study. *Pfeifer et al.* [2010] used the Forest Vegetation Simulator (FVS) to investigate stand-level responses to mountain pine beetle outbreaks in central Idaho, USA. The prescribed insect-caused tree mortality in this study resulted in substantial reductions in carbon stocks and fluxes following the outbreak, depending on the extent of tree mortality. *Pfeifer et al.* [2010] also found that stands generally recovered 25 years following the outbreaks, and that recovery rate was strongly governed by the size of surviving trees.

[27] Several studies have addressed regional effects of insect outbreaks. *Kurz and Apps* [1999] used the Carbon Budget Model of the Canadian Forest Sector version 2 (CMB-CFS2) to investigate carbon fluxes in the forests of Canada from 1929 to 1989. The area affected was derived from aerial surveys by converting the area affected into the effective area of mortality through multipliers specific to particular insect pest species. The study concluded that the large increases in insect outbreaks in the late 20th century, in conjunction with increased wildfire, caused Canadian forests to switch from a net carbon sink to a net carbon source. *Kurz et al.* [2008a] used CMB-CFS3 to quantify the impacts of an ongoing mountain pine beetle outbreak in British Columbia. They used historical observations and predictions of the future trajectory of the outbreak to determine that this disturbance has caused the region to become a carbon source that will continue for 20 years. *Hicke et al.* [2007] modeled net primary productivity using satellite-derived estimates and the Carnegie-Ames-Stanford-Approach light-use efficiency model in North America from 1982 through 1998. They found significant increases in productivity in eastern North America and suggested that this increase occurred as forests recovered following outbreaks of spruce budworm that had occurred in previous decades. Finally, *Albani et al.* [2010] used the Ecosystem Demography model to investigate the impact of the hemlock woolly adelgid on carbon cycling in the eastern U.S. and found that this insect had a small overall impact on regional carbon cycling due to the low amount of hemlock in eastern forests.

[28] These studies suggest that some insect outbreaks may have profound impacts on carbon dynamics in North America, but that the impacts of climate and atmospheric changes on forest insects and diseases are difficult to predict. Under changing conditions of ozone and ambient CO_2 concentration, the population of insects and the frequency of diseases increased in a FACE experiment in North America with aspen (*Populus tremuloides*) and mixed aspen–birch (*Betula papyrifera*) stands [*Percy et al.*, 2002; *Loya et al.*, 2003]. In addition, forest productivity was suppressed either because of damage or the detrimental effect of ozone. The reduced production significantly lowered the rate of soil C formation.

[29] The impacts of insects and diseases on forest carbon dynamics are usually ignored in large-scale model simulations of carbon dynamics. Aerial survey databases exist and can be used for defining when and where historical outbreaks occur [*Law et al.*, 2003]. However, such data have limitations because they are not collected with the goal of driving process models. Predictive models of insect outbreaks exist for some processes for a few insect species (e.g., winter mortality [*Régnière and Bentz*, 2007]), but integrated prognostic models generally have not been developed. An additional and rarely explored complication is the potential interactions between disturbances, e.g., how insect-stressed stands might be more vulnerable to fire [*Kulakowski and Veblen*, 2006].

[30] Significant gaps in our understanding of the impact of insect and disease outbreaks on carbon cycling include (1) the method of prescribing insect and diseases outbreaks in a carbon cycle model; (2) adequate field observations for model evaluation; and (3) representation of significant disturbance-related processes in carbon models. First, prescribing insect outbreaks within a modeling framework requires careful consideration. Observations quantifying outbreak extent exist, but contain many uncertainties and lack rigorous evaluation with ground observations. Converting these data into actual area of mortality or carbon is key to accurately specifying the extent of tree mortality [*Kurz and Apps*, 1999]. In addition to prescribing historical outbreaks, complete insect or disease prognostic models are currently lacking. Ideally, such models would include host tree susceptibility and population dynamics, both of which are not well understood. Second, although field observations of carbon cycle consequences of outbreaks exist [e.g., *Amiro et al.*, 2010], additional studies are needed across a broader range of insect/disease and forest types and mortality severity. Particularly useful are studies that observe all

component carbon fluxes and that provide a control site for comparison. Finally, a complete representation of processes affected by outbreaks within carbon models may be lacking. Tree mortality is rarely 100% within a stand (grid cell), so the ability to track tree cohorts through time at a subgrid scale facilitates simulations. Modifications in canopy structure due to snags also have an impact on light and water interception, and thus on carbon stocks and fluxes. Seedling establishment is another process controlling postoutbreak carbon stocks and fluxes [*Pfeifer et al.*, 2010]. The responses of these processes are important for accurately modeling forest carbon stocks and fluxes following an insect or disease disturbance.

2.2.5. Modeling the Impacts of Wildfire

[31] Wildland fire plays a critical role in the structure and function of forest ecosystems in many regions in North America. It is the primary disturbance in most western North American forests and it is the primary stand-renewing agent in the Canadian boreal forest [*Weber and Stocks*, 1998]. The role of fire in ecosystem C dynamics is complex and complicated, however. Combustion emissions are often balanced by long-term C sequestration in young, vigorous trees growing in the absence of competition. Nitrogen and phosphorus released by the consumption of duff and coarse woody debris can be immediately utilized by surviving and colonizing plants, increasing the potential for C sequestration, yet subsequent growth will be affected by nitrogen losses as well [*Harden et al.*, 2003]. Soil carbon lost during fire events can be very difficult to replace if fire frequencies increase [*Turetsky et al.*, 2011]. However, the amount of C lost to fire is difficult to estimate because of the challenges in quantifying pre-fire forest structure and biomass conditions, severity of fire, the impacts of fire (e.g., consumption) on diverse structural components [*Amiro*, 2001].

[32] Fire severity or the long- and short-term ecological effects of fire have been explored and quantified in field studies [e.g., *Kasischke and Johnstone*, 2005; *Zhu et al.*, 2006; *Turetsky et al.*, 2011]. Low severity fires produce few C emissions but may immediately stimulate plant growth and C storage by removing competition and releasing sequestered nutrients. Few models provide comprehensive fire severity estimates because fire effects are manifested at all scales of simulation [*Dalziel and Perera*, 2009]. The LANDSUM model [*Keane et al.*, 2006], for example, can generate generalized burn severity (low, medium and high) probability maps based on stand-level terrain and vegetation conditions, while the FireBGC landscape model provides comprehensive mechanistic simulations of tree mortality, fuel consumption, smoke emissions, and carbon cycling at the tree level [*Keane et al.*, 1996]. Some landscape models of fire and vegetation may oversimplify the effects of wildland fire on carbon cycling by generalizing fire severity into ordinal categories, while other sophisticated models simulate fire behavior and model its effect on individual trees and fuel consumption [*Keane et al.*, 2004].

[33] Generalized combustion and/or mortality ratios for tree, shrub, grass, surface fine litter, and soil organic matter have been estimated based on field data from over 80 burns (collected by C. Key et al., USGS, manuscript in review, 2011) are available for empirical model development, but complex mechanistic models need fine-scale, process driven parameters. To validate and parameterize ecosystem models, the USDA-USGS Monitoring Trend of Burn Severity (MTBS) project provides important remote sensing based estimates of burn severity based on an index called Differenced Normalized Burn Ratio (DNBR) and an index called Composite Burn Index (CBI), which is a commonly collected ground-based variable to estimate postfire effects. However, it should be noted that the use of the DNBR family of indices to map fire severity requires collection of field data for algorithm development in specific forest types, and has been found to not perform well for some forest systems, particularly in Alaskan boreal forests [*French et al.*, 2008].

[34] Fire management, such as wildfire suppression and fuel reduction treatments, are additional important activities that affect fire behavior and subsequent C dynamics. For example, the continued suppression of wildfires may increase C storage, but the inevitable catastrophic wildfire that cannot be suppressed will undoubtedly release more C into the atmosphere and cause the most ecological damage because of high accumulated fuel loadings and low fuel moistures [*Stocks et al.*, 1996]. Moreover, fire-prone ecosystems may sequester less carbon the longer fire is excluded from them because photosynthetic gains are offset by high respiration [*Keane et al.*, 2002]. Forest models should have the ability to simulate individual tree growth and fuel accumulation to account for fire management effects on the C cycle [*Bugmann*, 2001].

2.2.6. Modeling the Impacts of Storms

[35] Both ice and wind storms reduce NEP mainly through a reduction in assimilation capacity and an increase in heterotrophic respiration from CWD decomposition [*Schulze et al.*, 1999; *Tremblay et al.*, 2005; *McCarthy et al.*, 2006; *Lindroth et al.*, 2009]. Storm damages include windthrow or ice-break of stems or branches, crown reduction, increased mortality, and changes in site conditions (light, temperature, etc.). The severity of damage varies by tree traits (species, diameter, height, etc.), slope, aspect, frequency of storms, and wind speed [*McCarthy et al.*, 2006; *Zeng et al.*, 2009]. Spatially explicit individual tree-based forest models (e.g., SORTIE) can be especially useful to simulate the effects of storms on the basic demographic processes (i.e., recruitment, growth and mortality) that regulate forest community and carbon dynamics [*Tremblay et al.*, 2005].

[36] Storm damage, and subsequent management (e.g., salvage harvesting) may dramatically change forest structure resulting in increased amounts of CWD on the forest floor [e.g., *Vargas and Allen*, 2008]. No organic matter is consumed, but these disturbances substantially increase organic matter consumption rates since most of biomass materials lay on the ground, subject to microbial decomposition. The CWD deposited in the ground usually has high nutrient ratios and is available for rapid decomposition, limited only by climate; in hot humid regions decomposition could occur in less than 1 year, resulting in large short-term C losses after the disturbance [*Vargas et al.*, 2010], whereas in temperate and boreal regions decomposition would be slower resulting in different heterotrophic respiration rates [*Harmon et al.*, 2011].

[37] Only a few studies have attempted to directly quantify how carbon fluxes are affected by storms over large areas [*Chambers et al.*, 2007; *McNulty*, 2002; *Luo et al.*, 2003; *Zeng et al.*, 2009]. *McNulty* [2002] estimated that a

single storm can convert the equivalent of 10% of the total annual U.S. carbon sequestration to dead and downed biomass. *Chambers et al.* [2007] estimated that an amount equivalent to 50–140% of the net annual U.S. carbon sink in forest trees was lost because of Katrina. *Zeng et al.* [2009] evaluated the impacts of historical tropical cyclones from 1851 to 2000 on forest and carbon cycle over the continental U.S. They found that hurricane-induced release of CO2 potentially offset the carbon sink in forest trees by 9–18% over the entire United States over the period 1980–1990, and U.S. forests after 1900 experienced twice the impact before 1900 because of more active tropical cyclones and a larger extent of forested areas. *Lindroth et al.* [2009] estimated that the Lothar storm in 1999 reduced the European carbon balance by ca. 16 million tons C, which was 30% of the NBP in Europe. All these studies demonstrated that the impact of increased forest damage by more frequent storms must be considered to explain partially the large interannual variability of the terrestrial carbon sink.

3. Scaling Up From Sites to Regions

[38] Individual disturbance events usually result in substantial short-term ecosystem carbon loss locally. These carbon losses may be offset by carbon uptake in other areas where recovery is taking place. The overall net carbon flux from forests to the atmosphere resulting from disturbance depends on the spatial extent, severity, and heterogeneity of disturbances (e.g., fire suppression, logging, and insect outbreaks) within the region. *Goodale et al.* [2002] found over 80% of the estimated forest sink in the Northern Hemisphere occurred in only one-third of the forest area (i.e., regions affected by fire suppression, agricultural abandonment, and plantation forestry), and that carbon accumulation from the regrowth of forests in boreal regions can be offset by fire and other disturbances that vary considerably from year to year. Therefore regional modeling estimates face the challenge of including disturbances and the influence of interannual variability.

3.1. Scaling Approaches and Practices

[39] Many modeling efforts at landscape to global scales have attempted to incorporate disturbance information into the simulation of carbon dynamics at regional scales. These efforts differ substantially in the types of disturbances considered and the modeling approaches used [*Hurtt et al.*, 2002; *Liu et al.*, 2003; *Masek and Collatz*, 2006; *Zhao et al.*, 2010a; *McGuire et al.*, 2001; *Balshi et al.*, 2007; *Yi et al.*, 2010]. These upscaling approaches can be classified broadly into two categories: paint pixels by process models and by data-driven statistical models.

3.1.1. Paint Pixels by Process Models

[40] All the upscaling practices in this category apply site-scale models to simulate carbon dynamics for each pixel (or by pixel group) within the study areas. There is an explicit fundamental rule associated with this approach: the site-scale models should be applied to site scale, meaning the cell size should be compatible with field scale. Unfortunately, this rule is not often observed in many applications for two main practical reasons. First, computation becomes prohibitive when the total number of simulation units or pixels becomes too big over large areas with a small cell size. Second, we usually do not have high-resolution supporting data layers of soil, climate, land cover change, and disturbances over large areas.

3.1.1.1. Cell Size of Modeling and Characterization of Disturbances

[41] The influence of the spatial resolution of disturbance information on the simulation of terrestrial carbon dynamics is not well understood and is often ignored, as various grid cell sizes have been used [*Hurtt et al.*, 2002; *Liu et al.*, 2003; *Masek and Collatz*, 2006; *Zhao et al.*, 2010a; *McGuire et al.*, 2001; *Balshi et al.*, 2007; *Yi et al.*, 2010]. Many modeling studies used the resolution of grid cell given by climatological data sets (e.g., 0.5° or 1°), and the organization of disturbance information on landscape using such coarse resolution is challenging. An improved approach is the use of "cohorts" or joint frequency distribution (JFD) table, where each cohort or JFD represents all the cells (landscape units) of a unique combination of soil, climate, vegetation, and disturbance history [*Liu et al.*, 2003; *Balshi et al.*, 2007; *McGuire et al.*, 2010]. The use of JFD or cohorts can save simulation time while retaining all the spatially explicit information.

[42] A few studies have investigated the importance of including fine-scale land cover and disturbance data layers. *Turner et al.* [2000] investigated the scale of mapping spatial heterogeneity in land cover on NPP and NEP in the central Cascades Mountains of western Oregon, and found that NPP and NEP was 12% lower and 4% lower at 1000 m compared to 25 m. *Zhao et al.* [2010b] quantified and evaluated the impact of land cover change and disturbances at various spatial resolutions (250 m, 500 m, 1 km, 2 km, and 4 km) on the magnitude and spatial patterns of regional carbon sequestration in four counties in Georgia and Alabama using the General Ensemble biogeochemical Modeling System (GEMS). This study found a threshold of 1 km for accurately characterizing land disturbances and estimating regional terrestrial carbon sequestration. *Dalziel and Perera* [2009] found fire disturbance patterns and forest community structure interact at a range of spatial scales because tree species vary in their fuel value and in their tolerance to fire damage. With increasing cell size, minor landscape features and processes such as rare forests (e.g., wetlands) and disturbances (e.g., selective harvesting and windthrow) can be missed and not included in modeling [*Zhao et al.*, 2010b].

[43] These findings have important implications for continental to global-scale carbon modeling efforts: what spatial resolution is adequate for characterizing disturbances to support carbon modeling? As carbon fluxes among different land cover types differ greatly and are nonlinear functions of many stand-structural and environmental parameters, the validity of this 1 km threshold value might be related to the heterogeneity and the level of fragmentation of the land surface. For the relatively homogenous boreal landscape, up to 45% correction is needed for LAI derived at 1 km resolution [*Chen et al.*, 1999] because of mixed land-water pixels, which are the norm at high latitudes. As many global LAI and GPP products are currently produced at about 1 km resolution ([*Garrigues et al.*, 2008] MODIS), corrections to these products by subpixel cover type fractions or other measures will be useful. Some such efforts have already been reported for NPP [*Simic et al.*, 2004] and ET [*El*

Maayar and Chen, 2006]. New algorithms or procedures need to be added into models to improve the quantification of disturbance impacts as more cross-scale understandings become available.

3.1.1.2. Adequate Characterization and Modeling of Disturbance in Time

[44] The temporal interval between two consecutive disturbance maps is also an important consideration in both disturbance mapping and incorporation of disturbance information into simulation models. Some disturbance maps are generated based on remotely sensed information from optical sensors. If the time interval is longer than the time needed for ecosystem recovery (optically), these maps will miss some disturbances. *Zhao et al.* [2009], using GEMS, evaluated the impacts of the length of time interval between two consecutive land use change maps on estimating regional carbon sequestration in the southeastern United States. The results of this study indicate that ignoring detailed fast-changing dynamics of land cover change and disturbances in the region can lead to a significant overestimation of carbon uptake as the regional carbon sequestration rate increased from 0.27 to 0.69, 0.80 and 0.97 Mg C ha^{-1} yr^{-1} when land use change mapping frequency shifted from 1 year to 5 years, 10 years, and static (no land cover change or disturbances), respectively.

[45] These results suggest that it is essential to incorporate fast-changing detailed dynamics of disturbances into local to global carbon cycle studies. Otherwise, it is difficult to accurately quantify the geographic distribution, magnitudes, and mechanisms of terrestrial carbon sinks and sources at the local to global scales. The critical time interval (number of years between two consecutive maps) depends on a number of factors including the type and severity of disturbances and the speed of ecosystem recovery optically. In general, annual maps of land cover and disturbances are useful with respect to simulating interannual variability in carbon dynamics. Shorter time intervals of disturbance mapping may be useful for capturing short-lived processes such as defoliation or for comparison with atmospheric inversion analyses of carbon exchange. From a practical standpoint, the time interval of disturbance mapping should be optimized by considering the speed of ecosystem recovery after disturbance. Longer time intervals can be used in slow-recovering regions, and shorter ones in the fast recovering regions. Disturbances span across multiple temporal and spatial scales where the most extremes (i.e., LIDs) are limited in frequency but may have the largest impact on ecosystems. The use of the concept "extreme events" is populating the ecological and biogeoscience literature because of the potential link between these events and climate change. However, it is appropriate to rethink the concept of disturbances especially for those related to extreme events at large geographical distances (LIDs) [*Turner and Dale*, 1998]. These events are infrequent with respect to human scales or the life span of organisms in the environment, and may have large consequences on the dynamics of energy and matter of natural and human-modified ecosystems.

3.1.1.3. Model Initialization or Spin-Up

[46] Explicit modeling of disturbance over large areas poses challenges for traditional model 'spin-up' procedures. Model spin-up is already computationally costly [*Bond-Lamberty et al.*, 2005] and numerically uncertain (relative to field data), as it constitutes a classic initial value problem [*Luo et al.*, 2003; *White et al.*, 2006]. Explicitly modeling disturbances during spin-up perturbs all ecosystem carbon pools, including the stable soil compartments whose rate of change typically determines the spin-up termination [*Pietsch and Hasenauer*, 2006]. Disturbances thus extend the spin-up phase, potentially forever; imposing an upper limit on spin-up time can result in a simulation cell whose carbon balance is strongly negative or positive at the end of model initialization. The use of real and hindcasted fire histories ameliorate this problem [*Mouillot and Field*, 2005; *Balshi et al.*, 2007]. However, they do not completely solve the problem of initial conditions.

[47] To fully quantify disturbance effects on carbon sink dynamics, we need to quantify three sets of parameters respectively related to carbon influx, ecosystem carbon residence time, and initial values of all carbon pools. The three sets of parameters can adequately define disequilibrium of carbon cycles caused by disturbances [*Luo and Weng*, 2011]. The traditional, spin-up approach in combination with some historical data could not accurately quantify the degree of dynamic disequilibrium in land carbon cycle. To estimate all the three sets of parameters to quantify disturbance effects, we need to use data assimilation techniques, which have recently applied to a few ecosystems [*Weng and Luo*, 2011]. Finally, it has been discussed that the steady state assumption in process-based models, whenever it's adopted, may lead to erroneous parameter estimates when the considered ecosystem is not in steady state [*Carvalhais et al.*, 2008]. The conditions of steady state required by most models to run may not be appropriate under a disturbance regime since direct and indirect effects generate nonsteady state conditions in the ecosystem [*Carvalhais et al.*, 2010].

3.1.1.4. Emerging Approaches to Address Scaling Issues

[48] Work on upscaling C dynamics from sites to large areas has been dominated by ecosystem-scale compartment models because of their simplified lumped treatment of trees, ease of parameterization, and lower computation load. With increases in computing power, however, more demography models are being used for this purpose, including some major regional to continental applications in North America and Europe [*Hurtt et al.*, 2002; *Dixon*, 2002]. For example, the Forest Vegetation Simulator (FVS), a national system of forest demography models maintained by the USDA Forest Service that can be dynamically linked with the national forest inventory system (FIA) [*Dixon*, 2002], has been widely used for regional and national applications [*DeRose and Long*, 2009; *Crookston and Dixon*, 2005]. The Ecosystem Demography (ED) model has been used at the regional to global scales to explicitly account for the impacts of various disturbances including fire and fire suppression [*Hurtt et al.*, 2002] and insect outbreaks [*Albani et al.*, 2010]. Overall, demography models provide several advantages over the compartment models including explicit representation of demographic processes (e.g., seed advection, seed mixing, sapling survival, competitive exclusion and plant mortality). They separate the lumped tree compartments (as in the compartment models) into cohorts organized by species or plant functional type and age, providing a better

framework to simulate the impacts of various disturbances on the structure and functions of forests.

[49] In reality, it is always necessary to reach a balance among model complexity, cell size, and the size of the study area because of the constraints in input data layers and computation resources. For example, gap models simulate tree growth, survival, and mortality on gap-sized forest plots (e.g., 0.01–10 ha in size). Direct applications of these models wall-to-wall to each plot-scale cell (pixel) over large areas are prohibitive. To facilitate the scaling of gap-processes to large areas, coarser vegetation characteristics such as plant functional types by age cohort have to be used within each cell instead of species-level information [*Hurtt et al.*, 2002] (see Table 1), and this need resulted in the development of many dynamic global vegetation models (DGVMs) including HYBRID [*Friend et al.*, 1997], IBIS [*Foley et al.*, 1996], LPJ [*Haxeltine and Prentice*, 1996], SDGVM [*Woodward et al.*, 1998], VECODE [*Brovkin et al.*, 1997], and LM3V [*Shevliakova et al.*, 2009]. Forest disturbances and age structure and management are not simulated by most DGVMs. Validation of DGVMs most frequently focus on carbon fluxes from FLUXNET [*Thornton et al.*, 2002; *Schwalm et al.*, 2010], and future validation effort needs to use a broad range of data (e.g., height, basal area, and volume increment) [*Hurtt et al.*, 1998; *Desai et al.*, 2007; *Bellassen et al.*, 2011].

[50] Another emerging need is to merge the so-called diagnostic and prognostic modeling approaches to improve our understanding of the consequences of disturbances and the confidence in predictive upscaling. Diagnostic approaches rely heavily on remote sensing and field observations [*Potter*, 1993; *Frolking et al.*, 2009; *Xiao et al.*, 2010, 2011]. For example, the impacts of disturbances on GPP or NPP can be robustly "seen" or inferred from remotely sensed data [*Potter*, 1993; *Hicke et al.*, 2003; *Zhao and Running*, 2010; *Yuan et al.*, 2007; *Xiao et al.*, 2010]. The purpose of diagnostic modeling has been to quantify and understand the impacts of disturbances and other stressors on C stocks and fluxes using prescribed data layers, while the purpose of prognostic modeling has been on predicting disturbances (occurrence, extent, and severity) and their consequences. In order to increase confidence in prognostic models, these models must have effective hindcasting capability of disturbance history (fire, insects, harvest, etc.) so they can spin-up through a realistic representation of disturbances. This capability is critically needed and currently not well implemented in most models.

[51] Disturbance regimes in a region can be represented in models using statistical methods. A disturbance regime is usually defined by its frequency, severity, and spatial coverage. Most natural disturbances, such as fire, storms, and insect outbreaks are stochastic processes, which are usually characterized by probability distributions. Thus we can construct probability distributions of frequency, severity, and spatial coverage for different types of disturbances from regional databases. The constructed probability distributions can be used as a disturbance generator in an ecosystem model to assess carbon sink dynamics in a region [*Albani et al.*, 2010; *Hurtt et al.*, 2002; *Luo and Weng*, 2011; *Zeng et al.*, 2009].

3.1.2. Paint Pixels by Data-Driven Statistical Models

[52] In addition to process-based modeling, data-driven and statistical-based approaches have been used to estimate forest carbon dynamics and examine the impacts of disturbances. In contrast to the process-based modeling approach, data-driven approaches rely heavily on in situ and/or remotely sensed data or observations. Data-driven approaches often employ statistical or artificial intelligence methods to derive empirical models directly from observations, and these derived models are then used to estimate C stocks and fluxes.

[53] *Xiao et al.* [2010, 2011] produced continuous gross primary productivity (GPP) and net ecosystem carbon exchange (NEE) estimates with high spatial (1km) and temporal (8 day) resolutions for temperate North America over the period 2000–2006 from eddy covariance measurements and satellite observations using piecewise regression models. This approach makes use of eddy flux data from towers encompassing a wide range of ecosystem and climate types, disturbance history, and uses satellite observations such as EVI, LAI, and LST before and after disturbances to account for disturbance effects. *Xiao et al.* [2010, 2011] used these continuous flux estimates to assess the magnitude, distribution, and interannual variability of the recent U.S. terrestrial carbon sinks, concluding that the dominant sources of the recent interannual variation in U.S. carbon sinks included extreme climate events (e.g., drought) and disturbances (e.g., wildfires, hurricanes). Similar regional efforts are needed across the whole of North America with process-based models, data-driven and statistical-based approaches.

3.2. Beyond Forests

[54] While the main focus of this paper is on forest ecosystems, we realize that several issues are broader than forests per se. First, it is necessary to distinguish NEE and NEP and their spatial and temporal dependence [*Chapin et al.*, 2006]. For example, harvest creates an apparent C sink at the stand-level, but that will be gradually returned to the atmosphere through decomposition of wood products somewhere else (in the region, continent, or other parts of the globe) [e.g., *Skog*, 2008]. Many life-cycle analyses have been made to account for the fate of harvested wood [e.g., *Eriksson et al.*, 2007]. However, these activities are often done with regional and national timber harvest numbers and not directly linked with biogeochemical or demography models. Along the same line of wood harvest, to our knowledge, no studies have investigated the magnitude, spatial distribution, and consequences of salvage logging after fire/insects disturbances over large areas. Second, land cover transitions (i.e., deforestation and reforestation) or woody encroachments in the western U.S. [*Barger et al.*, 2011] are important aspects of forest landscape disturbances. A holistic landscape perspective is needed to capture such kind of disturbances [*Liu et al.*, 2003; *Zhao et al.*, 2010a], and this requires the models be able to simulate C dynamics not only in forests but also in other ecosystems including crops and grasslands [e.g., *Wang et al.*, 2005]. Third, erosion of soils and residues after disturbances can have a significant impact on on- and off-site carbon dynamics and ecosystem recovery [*Liu et al.*, 2003; *Smith et al.*, 2007]. *Webster et al.* [1990] showed that forest logging disturbance has increased C export from

stands, has accelerated turnover of benthic particulate organic matter, and is depleting benthic material. These changes are related primarily to the decline of woody debris dams in the disturbed streams. Nevertheless, the impact of disturbance-induced erosion and its impact of C dynamics are rarely mapped and quantified.

3.3. Regional Considerations

[55] Many gaps exist between countries at the moment in terms of modeling development and application, and characterization of disturbances over large areas (i.e., across all North America [Canada-USA-Mexico]). Thus, it may not be possible to comprehensively test models on Mexican ecosystems at present because the lack and accessibility to databases about disturbances and ecosystems responses. However, a wide North American effort can be made in the near future. For example, an initiative of a network of eddy covariance towers at different Mexican ecosystems is underway (MexFlux currently has eight operating sites; R. Vargas personal communication, 2011). Mexico also has high beta diversity so there are many ecosystems that are also present in Canada and the U.S. but there are also many others that are only present in Mexico. Most importantly, most models have not been tested and parameterized for these ecosystems (e.g., tropical forests wet versus dry) so there is a large opportunity for interaction and research across North America.

[56] North American boreal forests have a number of attributes that make them, in some ways, more easily modeled than their temperate or tropical counterparts: vegetation diversity is minimal [*Shugart et al.*, 1992]; most stands are even-aged as a result of frequent fires [*Kurz and Apps*, 1999]; and nitrogen deposition is low [*Reay et al.*, 2008]. There are a number of unique challenges in modeling disturbances in the boreal forest, associated with the frequent fires and poor drainage of a young, post-glacial landscape [*Camill et al.*, 2009; *Grosse et al.*, 2011]. Most process models are ill-equipped to simulate such ecosystems [*Trettin et al.*, 2001]; problematic aspects (from the models' points of view) include a high and fluctuating water table; significant methane production and consumption; anoxic soil and low soil redox potentials that limit decomposition; and the dominance of nonvascular plants. Dedicated wetland models [*Wang et al.*, 2007; *Frolking et al.*, 2001; *Mitsch et al.*, 1988] incorporate many of the hydrological and biogeochemical complexities of wetlands but are of limited applicability in well-drained systems. In contrast, general-purpose process models frequently lack mechanisms to simulate biotic and abiotic processes in poorly drained soils [*Peng and Apps*, 1999; *Zhuang et al.*, 2003; *Yarie and Billings*, 2002; *Thornley and Cannell*, 2004]. One solution is to extend these biogeochemical process models from upland forest ecosystems to poorly drained ones and even continually inundated wetlands [*Zhang et al.*, 2002; *Potter et al.*, 2001; *Pietsch et al.*, 2003; *Brown et al.*, 2010; *Bond-Lamberty et al.*, 2007a].

4. Databases Over Large Areas

[57] A number of efforts have focused on the characterization of various disturbances from landscape to global scales [*Frolking et al.*, 2009; *Kennedy et al.*, 2007; *Rollins*, 2009; *Masek et al.*, 2008; *Goward et al.*, 2008; *Hurtt et al.*, 2006; *Huang et al.*, 2009; *French et al.*, 2011]. As new data products on forest disturbance emerge, they will be integrated into biogeochemical models to generate more robust estimates of forest carbon stocks and fluxes over large areas.

4.1. Type, Extent, Intensity, Timing, and Spatial Resolution

[58] Land cover and change maps are the very basic information required for modeling the spatial and temporal changes of C stocks and fluxes over large areas. Major national and international efforts have been designated to map land cover change at regional to continental scales. There are two types of land cover and land use change database available at the moment. The first include data sets compiled from pre-existing maps, regional and national ground surveys, and highly generalized biogeographic maps [*Waisanen and Bliss*, 2002; *Hurtt et al.*, 2006]. For example, *Hurtt et al.* [2006] has developed a global gridded data set describing land-use transitions, wood harvest activity, and resulting secondary lands for the past three centuries. The second type of database is derived from remotely sensed data. With more remote sensing data sources (e.g., Landsat, MODIS, SPOT, MERIS), better processing techniques, and increasing capacity [*Xian and Homer*, 2010; *Kennedy et al.*, 2007; *Masek et al.*, 2008; *Huang et al.*, 2009; *Friedl et al.*, 2010], it is possible to map land cover change in more detail over large areas. Annual land cover and change information are being generated globally using MODIS data [*Hansen et al.*, 2003; *Friedl et al.*, 2010]. The U.S. Geological Survey (USGS) has been developing National Land Cover Database (NLCD) from Landsat at 30 m resolution for the United States at five-year intervals [*Xian and Homer*, 2010]. USGS is also generating high-quality land cover change information for the United Stated from 1970s to present using Landsat data [*Loveland et al.*, 2002] and has been used to quantify the impacts of land use change and disturbances on C dynamics [e.g., *Liu et al.*, 2003].

[59] Disturbances have been mapped and monitored separately by disturbance type. Severe storms can cause extensive tree mortality and damage to forest structure [*Zeng et al.*, 2009; *Lindroth et al.*, 2009]. Few data sets are available characterizing the frequency, extent, strength/severity, and consequences of large storms at regional and continental scales. *Zeng et al.* [2009] developed a data set on historical tropical cyclones from 1851 to 2000 over the continental U.S., and evaluated the impacts on forest mortality and carbon cycle. However, this data set has not been released to the public. The Canadian Large Fire Database (LFDB) from the Canadian Forest Service [*Stocks et al.*, 2002] provides quantitative information for large fires across Canada. The LFDB was constructed from provincial and territorial fire reports with information on start location, area burned, fire start date, and ignition source (human, lightning, unknown). Quantitative information on large fires across Alaska can be obtained from the historical large fire database for Alaska from the Bureau of Land Management, Alaska Forest Service; this database represents a compilation of fires in Alaska between 1942 and 2007, with point and boundary location information for fires. USGS LANDFIRE project is also producing consistent and comprehensive maps and data on vegetation, wildland fuel, and fire regimes across the United

States [*Rollins*, 2009]. More information on fire disturbances in North America can be found in the works by *French et al.* [2011] and *Kasischke et al.* [2011].

[60] Efforts are also underway to map disturbances synoptically. MODIS has been used to generate disturbance index maps including extent, severity, and timing of disturbances [*Mildrexler et al.*, 2009]. North American forest disturbances are mapped from a decadal Landsat record [*Goward et al.*, 2008; *Masek et al.*, 2008] and from stacks of Landsat images that have much shorter time intervals [*Kennedy et al.*, 2007; *Huang et al.*, 2009]. While these efforts provide a complete picture on all the disturbances happened on the landscape, additional effort is needed to attribute the detected disturbances to causes because different disturbance types can generate totally different impacts on forest structure, recovery, and carbon stocks and fluxes.

[61] Complementary to remote sensing, ground-based monitoring programs, such as the Forest Inventory and Analysis (FIA) program of the USDA Forest Service (http://fia.fs.fed.us/[*Woodall et al.*, 2010]) or similar monitoring systems in Mexico and Canada, provide valuable information on stand age, biomass, mortality, partial and clear-cutting, and other disturbances (e.g., fire, wind, and harvest). Although based on spatially discrete sampling plots, these programs can provide critical information on disturbances at the county or state/province level, which can then be used to constrain model simulations or spatially explicit mapping efforts.

[62] Insect and disease outbreaks are mapped by the USDA Forest Service Aerial Detection Survey program [*USDA*, 2009]. Surveys are available from one to several decades, depending on region. Damage is recorded by observers in planes that identify polygons and estimate causal agent (e.g., bark beetle), tree species, and number of trees affected. Tree mortality as well as defoliation is noted. Although a rich data source, these surveys are subjectively developed, produce polygons that include unaffected as well as affected trees, and do not cover all forested areas every year. Canadian insect surveys are similar in design. Regional and national maps describing the extent and severity of outbreaks are available but are limited to recent years and must be converted from polygon to gridded data before suitable for use in modeling. While mapping of insect outbreaks across Canada and the U.S. has undergone significant improvement over the past 2 decades, prior to this time, data to quantify the aerial extent of insect disturbances is generally limited to major insect species in the U.S., with more detailed information being available for Canada back to 1975.

4.2. Stand Age

[63] Stand age, directly reset by stand-replacing disturbances such as harvesting and severe fires, is likely the most available surrogate variable for forest carbon dynamics. It is an important parameter to determine the balance between the carbon gain through growth and carbon loss through respiration. Forest age maps are particularly useful for upscaling from site-level measurements (flux, biomass, soil carbon) to large regions. *Chen et al.* [2003] developed forest age maps for Canada, collaborating with *Pan et al.* [2010], they developed the North American Forest Stand Age database using forest inventory, large fire polygons, and remotely sensed data. This database is the first continental forest age map of North America, and provides stand age information for each 1 km cell across Canada and the lower 48 states of U.S., but future efforts should include Mexico to truly represent all North America. The CONAFOR (Comisión Nacional Forestal; htpp://www.conafor.gob.mx) in Mexico has conducted an extensive forest survey including stand age and harvest [*Masek et al.*, 2011], but the full database is yet not open to the public. These maps can be used to determine the year of disturbance for each pixel, and thus provide a possibility to estimate the direct carbon emission at the time of disturbance and to model the full carbon dynamics after the disturbance as a result of growth recovery and its influence on the soil carbon pools. They will be a valuable data set for large-scale carbon modeling and will potentially improve the accuracy of carbon cycle simulations.

4.3. Standing Biomass or Carbon Pools

[64] In addition to disturbances, it is also important to monitor the spatial distribution and temporal changes of forest structure, recovery, and carbon accumulation for two purposes. First, such data sets are necessary for calculating the immediate and long-term impacts of disturbances on carbon emissions and transfer among different C pools. Second, they can provide detailed information on forest recovery, which can be used to calibrate and validate model simulations. A few data sets depicting forest biomass have been developed for the United States and Canada. *Zhang and Kondragunta* [2006] developed a forest biomass data set at a spatial resolution of 1 km for the conterminous U.S. using foliage-based generalized allometric models and MODIS data. The following components were included in the data set: foliage biomass, branch biomass, and above-ground biomass. *Blackard et al.* [2008] developed a forest biomass for the conterminous U.S., Alaska, and Puerto Rico using nationwide forest inventory data and MODIS data at a spatial resolution of 250m (http://fsgeodata.fs.fed.us/raster-gateway/biomass/), with uncertainty estimates for above-ground biomass at each grid cell. Scientists at the Woods Hole Research Center have generated maps of canopy height and standing carbon stock for the conterminous United States (http://www.whrc.org/nbcd/). Ron Hall and others have developed a national forest biomass map for Canada using forest inventory data and remote sensing (http://www.gofc-gold.uni-jena.de/documents/missoula09/9_Hall%20ECV%20 biomass%20canadav2.pdf). County-level maps of forest biomass in the eastern U.S. [*Brown et al.*, 1999] and carbon stocks in the western U.S. [*Hicke et al.*, 2007] have been produced using forest inventory data. Future effort should drive producing biomass maps for the entire North America with a higher temporal repetitive cycle. In addition, it is critical to supply uncertainty estimates for all biomass maps.

4.4. Carbon Fluxes

[65] A number of publicly available databases (as opposed to meta-analyses) have been assembled for documenting observations of carbon fluxes in ecosystems, particularly forests, across the globe; such databases, increasingly available and updated continuously on the Internet, may provide valuable constraints on modeled ecosystem function. For example, *Luyssaert et al.* [2007] assembled a high-quality

database of forest NEE and other flux measurements. In a similar vein, a global compendium of soil respiration studies was published by *Bond-Lamberty and Thomson* [2010b], including seasonal to annual fluxes, temperature sensitivities, and a variety of ancillary data. Finally, FLUXNET data, although highly constrained in their spatial coverage, are valuable and frequently used for model-data comparisons [e.g., *Stöckli et al.*, 2008; *Baldocchi et al.*, 2001; *Schwalm et al.*, 2010]. Recently there has been a compilation of site level carbon fluxes and corresponding model outputs for selected sites across North America under the organization of the North American Carbon Program [e.g., *Schwalm et al.*, 2010]. Gridded flux fields derived from FLUXNET observations using upscaling methods provide spatially continuous estimates of ecosystem carbon fluxes [*Yuan et al.*, 2007; *Xiao et al.*, 2010, 2011], and these flux fields can be used to evaluate ecosystem models over broad regions. For instance, the continuous flux fields derived from AmeriFlux and MODIS data streams for the United States, referred to as EC-MOD [*Xiao et al.*, 2010, 2011], have been used to evaluate modeled GPP and NEE from a water-centric ecosystem model at the continental scale [*Sun et al.*, 2011].

4.5. Issues With Current Databases

[66] There is a wealth of untapped information for use in regional modeling efforts, and there is a huge opportunity for regional models to take advantage of existing data sets. As more data become available, they will contribute to the improvement of regional C simulations and reduction of uncertainty. However, development of most data sets is at present not well organized across disciplines and regions. We do not have a systematic set of defined variables that can be readily mapped or predicted to satisfy the needs for carbon simulations and accounting at regional to global scales. Disturbance intensity is usually not available, or, when available, is not well linked to its impacts on carbon storage of forest ecosystems. Information on uncertainties in disturbance severity is critical for quantifying uncertainty in modeled carbon dynamics, but rarely provided. At present, not all major disturbances are mapped at the continental scale with adequate spatial and temporal resolution. Future effort should focus on (1) defining a set of variables to map or predict for supporting the need of C science and management; (2) mapping all major disturbances systematically across North America at appropriate spatial resolution and temporal frequency; and (3) mapping mortality and carbon transfer coefficients (see Figure 2) directly in addition to mapping the properties of disturbances such as type, timing, extent, and severity.

[67] There are gaps among the modeling, experimentalist, and remote sensing communities. All need each other to test hypotheses, generate data, and advance our understanding of disturbances at multiple spatial and temporal scales. Experimentalists cannot test disturbances over and over because: (1) they are infrequent, (2) they usually reduce the metabolic state of an ecosystem and reduce the ecosystem services, (3) it is expensive to do, and (4) they are difficult to replicate in space and time. However, with limited information experimentalists have proposed hypotheses (e.g., for nitrogen cycling, ecosystem recovery, etc). These hypotheses have been tested (usually) at small spatial and temporal scales. However, modelers, working with experimentalists and remote sensing community, have the advantage of using the experimental data as a baseline, and then test the performance of the model, and help in developing future hypotheses for disturbances.

5. Uncertainty

[68] The very nature of many physical systems results in significant and sometimes inevitable uncertainty [*Roe and Baker*, 2007]. Nonetheless, quantifying and constraining uncertainty is necessary to understand the strengths and limits of carbon-cycling models [*Oreskes et al.*, 1994], and to produce meaningful policy recommendations.

[69] Uncertainty comes from three sources: input data, model parameter, and model structure. Big uncertainties exist in carbon modeling at the regional to continental scales because some major processes or feedback mechanisms were missing in the models [*Beer et al.*, 2010] and some key data sets were not available [*Ciais et al.*, 2010]. To our knowledge, no study has been performed to comprehensively quantify uncertainty of carbon stocks and fluxes from uncertainty sources, to error propagation, and to error attribution at the regional to continental scales. Nevertheless, various studies have emerged to account for different components of the uncertainty. For example, *Liu* [2009] and *O'Hagan* [2011] illustrated how to incorporate input data uncertainties using statistical distributions and Monte Carlo approaches. Model parameter uncertainties have been addressed using various model-data fusion techniques at the site scale by applying them on eddy covariance observations and/or other biometric measurements [*Rayner et al.*, 2005; *Y. P. Wang et al.*, 2009; *Liu et al.*, 2008; *Chen et al.*, 2008; *Richardson et al.*, 2010; *Ricciuto et al.*, 2011]. Model structure uncertainty have been assessed by model intercomparisons [*Friedlingstein et al.*, 2006; *Heimann et al.*, 1998; *Schwalm et al.*, 2010], quantifying the improvement of model fit after a given component is switched on [*Zaehle et al.*, 2006; *Bellassen et al.*, 2011], and forcing a model using measurements instead of model outputs [*Demarty et al.*, 2007].

[70] Stochastic, nonlinear disturbances make uncertainty quantification considerably more difficult, as, for example, most algorithms for parameter-space searches will not handle gracefully stochastic disturbance-induced changes in model state [e.g., *Williams et al.*, 2005]. Bootstrap techniques have been used to produce uncertainty estimates for many regional-scale analyses [*Bond-Lamberty et al.*, 2007b; *Saleska et al.*, 2003]. Modern data assimilation techniques, in which observed data and models are combined to find the model representation most consistent with observations [*Rayner et al.*, 2005], allow new possibilities. In particular, the 'systemic shock' of disturbances can uniquely constrain the model and thus its uncertainty; for example, the effect of major volcanic eruptions on atmospheric CO_2 has been used to examine the temperature sensitivity of soil respiration [*Jones and Cox*, 2001]. Thus while disturbances are challenging with respect to model uncertainty, they also offer unique opportunities.

[71] Uncertainty exists in every step of the effort to simulate the impacts of disturbances on carbon dynamics. Both measurement/observations and models are subject to errors. Procedures are needed to quantify the uncertainty of model inputs or data layers, model parameters, and model structures,

and their impacts on model simulations. Working together, modelers and data layer developers can identify the most uncertain areas and develop working hypotheses to reduce the uncertainty.

6. Summary

[72] Disturbances such as wildfire, insect/disease outbreaks, blowdowns, hurricanes, logging, and thinning are prevalent at many spatial and temporal scales. They impact the structure of ecosystems, communities, or populations and change their resources, substrate availability, and/or the physical environment. Understanding disturbances and their impacts is critical for a better quantification of regional carbon stocks and fluxes to better inform policy makers. However, there are major challenges because of the heterogeneity of the disturbances in time and space and the complexity of the responses of forests to disturbances.

[73] First, there are significant advances in process understanding and representation, scaling, and characterization of disturbances using remote sensing and monitoring networks (i.e., databases), and these advances should be included in regional modeling efforts. There is a wealth of untapped information for use in improving regional modeling efforts, including synthesis results of FLUXNET observations and fast-emerging geospatial data layers on disturbances, ecosystem properties, and C stocks and fluxes. The advance of computational technology also offers new opportunities. This includes improved representation of processes (e.g., demographic or gap processes at species or plant functional type level rather than lumped to ecosystem level) that was not previously possible, and improved spatial and temporal resolutions for regional and continental modeling.

[74] Second, there is an urgent need to develop effective and comprehensive process-based procedures or algorithms that can be used to quantify the immediate and long-term impacts of disturbances on forest succession, soils, microclimate, and cycles of carbon, water, and nutrients. Although many models have been developed over the past three decades, they are originally designed for specific ecosystems within certain regions, and most of them lack systematic calibration and validation over North America. Relevant observations can be from FLUXNET, Long-term Ecological Research stations, etc. It is critical to evaluate all aspects of model performance not only on the carbon cycle but also on the simulations of vegetation succession, alterations of soil and microclimate, and water and nutrients dynamics because adequate simulations of carbon dynamics rely on the correct quantification of the changes of soil and vegetation conditions.

[75] Third, our capability to simulate the occurrences and severity of disturbances under climate and management changes is very limited, even though climate change and management practices will alter disturbance regimes. It is important to develop relationships between disturbance regimes and climate change and/or land use to improve our capability in quantifying carbon sequestration and its spatial and temporal patterns at the continental scale under global climate change scenarios.

[76] Fourth, scaling challenges have rarely been addressed at the continental scale. We do not understand which processes and properties are critical at a given temporal or spatial scale, and which can be simplified. Previous and current model simulations at the continental scale did not incorporate a full suite of disturbances information, due to the lack of spatially explicit information on disturbance and model limitations to account for disturbance effects, and therefore provided little insight on the relative importance of various disturbances at the continent and regional scales on the carbon cycle. We may take statistical approaches to quantify disturbance regimes with probability distributions of disturbance frequency, severity, and spatial coverage at continental scales. Those probability distributions can be used as a generator of disturbances in ecosystem models to predict regional-scale impacts of disturbance.

[77] Fifth, we do not have continentally consistent disturbance databases to support model simulations of the impacts of disturbances on C dynamics in North America. Combining freely available Landsat imagery with other information may provide some data layers in the near future, but major issues remain to be addressed as to what should be mapped and what variables should be quantified. It is necessary to coordinate the regional efforts mapping the occurrence and severity of disturbances to generate wall-to-wall maps to characterize and monitor the occurrences and properties of major disturbances across North America. International standards for disturbance databases should be developed with explicit inclusion of uncertainty measurements, and adequate spatial and temporal resolutions. Another prominent issue is to develop explicit and quantifiable links with model simulations; current databases can rarely be directly used by models to quantify the immediate transfer of carbon among different pools, the alterations of forest succession, soils, and microclimate, and eventually the dynamics of carbon in vegetation and soils.

[78] Finally, uncertainty exists in every step of the effort to simulate the impacts of disturbances on carbon dynamics. Both measurement/observations and models are subject to errors. Procedures are needed to quantify the uncertainty of model inputs or data layers, model parameters, and model structures, and their impacts on model simulations. Working together, modelers and data layer developers can identify the most uncertain areas and develop working hypotheses to reduce the uncertainty.

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References

Albani, M., D. Medvigy, G. C. Hurtt, and P. R. Moorcroft (2006), The contributions of land-use change, CO_2 fertilization, and climate variability to the Eastern US carbon sink, *Global Change Biol.*, *12*(12), 2370–2390, doi:10.1111/j.1365-2486.2006.01254.x.

Albani, M., P. R. Moorcroft, A. M. Ellison, D. A. Orwig, and D. R. Foster (2010), Predicting the impact of hemlock woolly adelgid on carbon dynamics of eastern United States forests, *Can. J. For. Res.*, *40*(1), 119–133, doi:10.1139/X09-167.

Amiro, B. D. (2001), Paired-tower measurements of carbon and energy fluxes following disturbance in the boreal forest, *Global Change Biol.*, *7*(3), 253–268, doi:10.1046/j.1365-2486.2001.00398.x.

Amiro, B. D., J. B. Todd, B. M. Wotton, K. A. Logan, M. D. Flannigan, B. J. Stocks, J. A. Mason, D. L. Martell, and K. G. Hirsch (2001), Direct carbon emissions from Canadian forest fires, 1959–1999, *Can. J. For. Res.*, *31*(3), 512–525, doi:10.1139/x00-197.
Amiro, B. D., A. Cantin, M. D. Flannigan, and W. J. de Groot (2009), Future emissions from Canadian boreal forest fires, *Can. J. For. Res.*, *39*(2), 383–395, doi:10.1139/X08-154.
Amiro, B. D., et al. (2010), Ecosystem carbon dioxide fluxes after disturbance in forests of North America, *J. Geophys. Res.*, *115*, G00K02, doi:10.1029/2010JG001390.
Bachelet, D., J. Lenihan, R. Neilson, R. Drapek, and T. Kittel (2005), Simulating the response of natural ecosystems and their fire regimes to climatic variability in Alaska, *Can. J. For. Res.*, *35*(9), 2244–2257, doi:10.1139/x05-086.
Baldocchi, D., et al. (2001), FLUXNET: A new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities, *Bull. Am. Meteorol. Soc.*, *82*(11), 2415–2434, doi:10.1175/1520-0477(2001)082<2415:FANTTS>2.3.CO;2.
Balshi, M. S., et al. (2007), The role of historical fire disturbance in the carbon dynamics of the pan-boreal region: A process-based analysis, *J. Geophys. Res.*, *112*, G02029, doi:10.1029/2006JG000380.
Barger, N., S. Archer, J. Campbell, C. Huang, J. Morton, and A. Knapp (2011), Woody plant proliferation in North American drylands: A synthesis of impacts on Ecosystem Carbon Balance, *J. Geophys. Res.*, *116*, G00K07, doi:10.1029/2010JG001506.
Batjes, N. H. (1996), Total carbon and nitrogen in the soils of the world, *Eur. J. Soil Sci.*, *47*(2), 151–163, doi:10.1111/j.1365-2389.1996.tb01386.x.
Beer, C., et al. (2010), Terrestrial gross carbon dioxide uptake: Global distribution and covariation with climate, *Science*, *329*(5993), 834–838, doi:10.1126/science.1184984.
Bellassen, V., G. le Maire, O. Guin, J. F. Dhôte, P. Ciais, and N. Viovy (2011), Modelling forest management within a global vegetation model-Part 2: Model validation from a tree to a continental scale, *Ecol. Modell.*, *222*(1), 57–75, doi:10.1016/j.ecolmodel.2010.08.038.
Blackard, J. A., et al. (2008), Mapping U.S. forest biomass using nationwide forest inventory data and moderate resolution information, *Remote Sens. Environ.*, *112*(4), 1658–1677, doi:10.1016/j.rse.2007.08.021.
Bonan, G. B. (1995), Land-atmosphere CO_2 exchange simulated by a land surface process model coupled to an atmospheric general circulation model, *J. Geophys. Res.*, *100*(D2), 2817–2831, doi:10.1029/94JD02961.
Bond-Lamberty, B., and A. Thomson (2010a), Temperature-associated increases in the global soil respiration record, *Nature*, *464*(7288), 579–582, doi:10.1038/nature08930.
Bond-Lamberty, B., and A. M. Thomson (2010b), A global database of soil respiration data, *Biogeosciences*, *7*, 1915–1926, doi:10.5194/bg-7-1915-2010.
Bond-Lamberty, B., S. T. Gower, D. E. Ahl, and P. E. Thornton (2005), Reimplementation of the Biome-BGC model to simulate successional change, *Tree Physiol.*, *25*(4), 413–424.
Bond-Lamberty, B., S. T. Gower, and D. E. Ahl (2007a), Improved simulation of poorly drained forests using Biome-BGC, *Tree Physiol.*, *27*(5), 703–715.
Bond-Lamberty, B., S. D. Peckham, D. E. Ahl, and S. T. Gower (2007b), The dominance of fire in determining carbon balance of the central Canadian boreal forest, *Nature*, *450*(7166), 89–92, doi:10.1038/nature06272.
Bond-Lamberty, B., S. D. Peckham, D. E. Ahl, and S. T. Gower (2007c), Fire as the dominant driver of central Canadian boreal forest carbon balance, *Nature*, *450*(7166), 89–92, doi:10.1038/nature06272.
Bond-Lamberty, B., S. D. Peckham, S. T. Gower, and B. E. Ewers (2009), Effects of fire on regional evapotranspiration in the central Canadian boreal forest, *Global Change Biol.*, *15*(5), 1242–1254, doi:10.1111/j.1365-2486.2008.01776.x.
Botkin, D. B., J. F. Janak, and J. R. Wallis (1972), Some ecological consequences of a computer model of forest growth, *J. Ecol.*, *60*(3), 849–872, doi:10.2307/2258570.
Brovkin, V., A. Ganopolski, and Y. Svirezhev (1997), A continuous climate-vegetation classification for use in climate-biosphere studies, *Ecol. Modell.*, *101*(2–3), 251–261, doi:10.1016/S0304-3800(97)00049-5.
Brown, S. L., P. Schroeder, and J. S. Kern (1999), Spatial distribution of biomass in forests of the eastern USA, *For. Ecol. Manage.*, *123*(1), 81–90, doi:10.1016/S0378-1127(99)00017-1.
Brown, M., T. A. Black, Z. Nesic, V. N. Foord, D. L. Spittlehouse, A. L. Fredeen, N. J. Grant, P. J. Burton, and J. A. Trofymow (2010), Impact of mountain pine beetle on the net ecosystem production of lodgepole pine stands in British Columbia, *Agric. For. Meteorol.*, *150*(2), 254–264, doi:10.1016/j.agrformet.2009.11.008.
Brugnach, M. (2005), Process level sensitivity analysis for complex ecological models, *Ecol. Modell.*, *187*(2–3), 99–120, doi:10.1016/j.ecolmodel.2005.01.044.
Bugmann, H. (1994), On the ecology of mountainous forests in a changing climate: A simulation study, Ph.D. thesis, Swiss Fed. Inst. of Technol., Zurich.
Bugmann, H. (2001), A review of forest gap models, *Clim. Change*, *51*(3–4), 259–305, doi:10.1023/A:1012525626267.
Camill, P., A. Barry, E. Williams, C. Andreassi, J. Limmer, and D. Solick (2009), Climate-vegetation-fire interactions and their impact on long-term carbon dynamics in a boreal peatland landscape in northern Manitoba, Canada, *J. Geophys. Res.*, *114*, G04017, doi:10.1029/2009JG001071.
Canham, C. D., J. S. Denslow, W. J. Platt, J. R. Runkle, T. A. Spies, and P. S. White (1990), Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests, *Can. J. For. Res.*, *20*(5), 620–631, doi:10.1139/x90-084.
Carroll, A. L., S. W. Taylor, J. Régnière, and L. Safranyik (2004), Effects of climate change on range expansion by the mountain pine beetle in British Columbia, in *Mountain Pine Beetle Symposium: Challenges and Solutions*, edited by J. E. Brooks, T. L. Shore and J. E. Stone, pp. 223–232, Pac. For. Cent., Kelowna, B. C.
Carvalhais, N., et al. (2008), Implications of the carbon cycle steady state assumption for biogeochemical modeling performance and inverse parameter retrieval, *Global Biogeochem. Cycles*, *22*, GB2007, doi:10.1029/2007GB003033.
Carvalhais, N., M. Reichstein, P. Ciais, G. J. Collatz, M. D. Mahecha, L. Montagnani, D. Papale, S. Rambal, and J. Seixas (2010), Identification of vegetation and soil carbon pools out of equilibrium in a process model via eddy covariance and biometric constraints, *Global Change Biol.*, *16*(10), 2813–2829, doi:10.1111/j.1365-2486.2010.02173.x.
Chambers, J. Q., J. I. Fisher, H. Zeng, E. L. Chapman, D. B. Baker, and G. C. Hurtt (2007), Hurricane Katrina's carbon footprint on U.S. Gulf Coast forests, *Science*, *318*(5853), 1107, doi:10.1126/science.1148913.
Chapin, F. S., G. M. Woodwell, W. H. Schlesinger, and E. D. Schulze (2006), Reconciling carbon-cycle concepts, terminology, and methods, *Ecosystems*, *9*, 1041, doi:10.1007/s10021-005-0105-7.
Chen, J. M., J. Liu, J. Cihlar, and M. L. Goulden (1999), Daily canopy photosynthesis model through temporal and spatial scaling for remote sensing applications, *Ecol. Modell.*, *124*(2–3), 99–119, doi:10.1016/S0304-3800(99)00156-8.
Chen, J. M., W. Chen, J. Liu, J. Cihlar, and S. Gray (2000), Annual carbon balance of Canada's forests during 1895–1996, *Global Biogeochem. Cycles*, *14*(3), 839–849, doi:10.1029/1999GB001207.
Chen, J. M., W. Ju, J. Cihlar, D. Price, J. Liu, W. Chen, J. Pan, A. Black, and A. Barr (2003), Spatial distribution of carbon sources and sinks in Canada's forests, *Tellus, Ser. B*, *55*(2), 622–641, doi:10.1034/j.1600-0889.2003.00036.x.
Chen, M., S. Liu, L. L. Tieszen, and D. Y. Hollinger (2008), An improved state-parameter analysis of ecosystem models using data assimilation, *Ecol. Modell.*, *219*(3–4), 317–326, doi:10.1016/j.ecolmodel.2008.07.013.
Chen, W., J. Chen, and J. Cihlar (2000), An integrated terrestrial ecosystem carbon-budget model based on changes in disturbance, climate, and atmospheric chemistry, *Ecol. Modell.*, *135*(1), 55–79, doi:10.1016/S0304-3800(00)00371-9.
Chen, W., J. M. Chen, D. T. Price, and J. Cihlar (2002), Effects of stand age on net primary productivity of boreal black spruce forests in Ontario, Canada, *Can. J. For. Res.*, *32*(5), 833–842, doi:10.1139/x01-165.
Ciais, P., et al. (2010), Can we reconcile atmospheric estimates of the Northern terrestrial carbon sink with land-based accounting?, *Curr. Opin. Environ. Sustainability*, *2*(4), 225–230, doi:10.1016/j.cosust.2010.06.008.
Clark, K. L., H. L. Gholz, and M. S. Castro (2004), Carbon dynamics along a chronosequence of slash pine plantations in North Florida, *Ecol. Appl.*, *14*(4), 1154–1171, doi:10.1890/02-5391.
Cook, B. D., P. V. Bolstad, J. G. Martin, F. A. Heinsch, K. J. Davis, W. Wang, A. R. Desai, and R. M. Teclaw (2008), Using light-use and production efficiency models to predict photosynthesis and net carbon exchange during forest canopy disturbance, *Ecosystems*, *11*(1), 26–44, doi:10.1007/s10021-007-9105-0.
Coursolle, C., et al. (2006), Late-summer carbon fluxes from Canadian forests and peatlands along an eastwest continental transect, *Can. J. For. Res.*, *36*, 783–800, doi:10.1139/x05-270.
Crookston, N. L., and G. E. Dixon (2005), The forest vegetation simulator: A review of its structure, content, and applications, *Comput. Electron. Agric.*, *49*(1), 60–80, doi:10.1016/j.compag.2005.02.003.
Currie, W. S., and K. J. Nadelhoffer (2002), The imprint of land-use history: Patterns of carbon and nitrogen in downed woody debris at the Harvard Forest, *Ecosystems*, *5*(5), 446–460, doi:10.1007/s10021-002-1153-x.
Czimczik, C. I., C. M. Preston, M. W. I. Schmidt, and E.-D. Schulze (2003), How surface fire in Siberian Scots pine forests affects soil organic carbon in the forest floor: Stocks, molecular structure, and con-

version to black carbon (charcoal), *Global Biogeochem. Cycles*, *17*(1), 1020, doi:10.1029/2002GB001956.

Dalziel, B. D., and A. H. Perera (2009), Tree mortality following boreal forest fires reveals scale-dependant interactions between community structure and fire intensity, *Ecosystems*, *12*(6), 973–981, doi:10.1007/s10021-009-9272-2.

Davidson, E. A., and I. A. Janssens (2006), Temperature sensitivity of soil carbon decomposition and feedbacks to climate change, *Nature*, *440*(7081), 165, doi:10.1038/nature04514.

Demarty, J., F. Chevallier, A. D. Friend, N. Viovy, S. Piao, and P. Ciais (2007), Assimilation of global MODIS leaf area index retrievals within a terrestrial biosphere model, *Geophys. Res. Lett.*, *34*, L15402, doi:10.1029/2007GL030014.

De Pury, D. G. G., and G. D. Farquhar (1997), Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models, *Plant Cell Environ.*, *20*(5), 537–557, doi:10.1111/j.1365-3040.1997.00094.x.

DeRose, R. J., and J. N. Long (2009), Wildfire and spruce beetle outbreak: Simulation of interacting disturbances in the central Rocky Mountains, *Ecoscience*, *16*(1), 28–38, doi:10.2980/16-1-3160.

Desai, A. R., P. R. Moorcroft, P. V. Bolstad, and K. J. Davis (2007), Regional carbon fluxes from an observationally constrained dynamic ecosystem model: Impacts of disturbance, CO_2 fertilization, and heterogeneous land cover, *J. Geophys. Res.*, *112*, G01017, doi:10.1029/2006JG000264.

Dixon, G. E. (2002), Essential FVS: A user's guide to the Forest Vegetation Simulator, internal report, 219 pp., For. Manage. Serv. Cent., Fort Collins, Colo.

El Maayar, M., and J. Chen (2006), Spatial scaling of evapotranspiration as affected by heterogeneities in vegetation, topography, and soil texture, *Remote Sens. Environ.*, *102*(1–2), 33–51, doi:10.1016/j.rse.2006.01.017.

Eriksson, E., A. R. Gillespie, L. Gustavsson, O. Langvall, M. Olsson, R. Sathre, and J. Stendahl (2007), Integrated carbon analysis of forest management practices and wood substitution, *Can. J. For. Res.*, *37*(3), 671–681, doi:10.1139/X06-257.

Fang, J., A. Chen, C. Peng, S. Zhao, and L. Ci (2001), Changes in forest biomass carbon storage in China between 1949 and 1998, *Science*, *292*(5525), 2320–2322, doi:10.1126/science.1058629.

Fleming, R. A., J. N. Candau, and R. S. McAlpine (2002), Landscape-scale analysis of interactions between insect defoliation and forest fire in central Canada, *Clim. Change*, *55*(1–2), 251–272, doi:10.1023/A:1020299422491.

Foley, J. A., I. C. Prentice, N. Ramankutty, S. Levis, D. Pollard, S. Sitch, and A. Haxeltine (1996), An integrated biosphere model of land surface processes, terrestrial carbon balance, and vegetation dynamics, *Global Biogeochem. Cycles*, *10*(4), 603–628, doi:10.1029/96GB02692.

Franklin, J. F., et al. (2002), Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example, *For. Ecol. Manage.*, *155*(1–3), 399–423, doi:10.1016/S0378-1127(01)00575-8.

Franklin, O., K. Aoki, and R. Seidl (2009), A generic model of thinning and stand density effects on forest growth, mortality and net increment, *Ann. For. Sci.*, *66*(8), 815, doi:10.1051/forest/2009073.

French, N. H. F., E. S. Kasischke, R. J. Hall, K. A. Murphy, D. L. Verbyla, E. E. Hoy, and J. L. Allen (2008), Using Landsat data to assess fire and burn severity in the North American boreal forest region: An overview and summary of results, *Int. J. Wildland Fire*, *17*(4), 443–462, doi:10.1071/WF08007.

French, N. H. F., et al. (2011), Model comparisons for estimating carbon emissions from North American wildland fire, *J. Geophys. Res.*, *116*, G00K05, doi:10.1029/2010JG001469.

Friedl, M. A., D. Sulla-Menashe, B. Tan, A. Schneider, N. Ramankutty, A. Sibley, and X. Huang (2010), MODIS Collection 5 global land cover: Algorithm refinements and characterization of new datasets, *Remote Sens. Environ.*, *114*(1), 168–182, doi:10.1016/j.rse.2009.08.016.

Friedlingstein, P., et al. (2006), Climate-carbon cycle feedback analysis: Results from the C4MIP model intercomparison, *J. Clim.*, *19*(14), 3337–3353, doi:10.1175/JCLI3800.1.

Friend, A. D., A. K. Stevens, R. G. Knox, and M. G. R. Cannell (1997), A process-based, terrestrial biosphere model of ecosystem dynamics (Hybrid v3.0), *Ecol. Modell.*, *95*(2–3), 249–287, doi:10.1016/S0304-3800(96)00034-8.

Frolking, S., N. T. Roulet, T. R. Moore, P. J. H. Richard, M. Lavoie, and S. D. Muller (2001), Modeling northern peatland decomposition and peat accumulation, *Ecosystems*, *4*(5), 479–498, doi:10.1007/s10021-001-0105-1.

Frolking, S., M. W. Palace, D. B. Clark, J. Q. Chambers, H. H. Shugart, and G. C. Hurtt (2009), Forest disturbance and recovery: A general review in the context of spaceborne remote sensing of impacts on aboveground biomass and canopy structure, *J. Geophys. Res.*, *114*, G00E02, doi:10.1029/2008JG000911.

Garrigues, S., et al. (2008), Validation and intercomparison of global Leaf Area Index products derived from remote sensing data, *J. Geophys. Res.*, *113*, G02028, doi:10.1029/2007JG000635.

Goodale, C. L., et al. (2002), Forest carbon sinks in the Northern Hemisphere, *Ecol. Appl.*, *12*(3), 891–899, doi:10.1890/1051-0761(2002)012[0891:FCSITN]2.0.CO;2.

Gough, C. M., C. S. Vogel, K. H. Harrold, K. George, and P. S. Curtis (2007), The legacy of harvest and fire on ecosystem carbon storage in a north temperate forest, *Global Change Biol.*, *13*(9), 1935–1949, doi:10.1111/j.1365-2486.2007.01406.x.

Goulden, M. L., A. M. S. McMillan, G. C. Winston, A. V. Rocha, K. L. Manies, J. W. Harden, and B. P. Bond-Lamberty (2010), Patterns of NPP, GPP, respiration, and NEP during boreal forest succession, *Global Change Biol.*, *17*(2), 855–871, doi:10.1111/j.1365-2486.2010.02274.x.

Goward, S. N., et al. (2008), Forest disturbance and North American carbon flux, *Eos Trans. AGU*, *89*(11), 105, doi:10.1029/2008EO110001.

Gower, S. T., R. E. McMurtrie, and D. Murty (1996), Aboveground net primary production decline with stand age: Potential causes, *Trends Ecol. Evol.*, *11*(9), 378–382, doi:10.1016/0169-5347(96)10042-2.

Grosse, G., et al. (2011), Vulnerability of high-latitude soil organic carbon in North America to disturbance, *J. Geophys. Res.*, *114*, G00K06, doi:10.1029/2010JG001507.

Hansen, M. C., R. S. DeFries, J. R. G. Townshend, M. Carroll, C. Dimiceli, and R. A. Sohlberg (2003), Global percent tree cover at a spatial resolution of 500 meters: First results of the MODIS vegetation continuous fields algorithm, *Earth Interact.*, *7*, 1–15, doi:10.1175/1087-3562(2003)007<0001:GPTCAA>2.0.CO;2.

Harden, J. W., M. C. Mack, H. Veldhuis, and S. T. Gower (2003), Fire dynamics and implications for nitrogen cycling in boreal forests, *J. Geophys. Res.*, *108*(D3), 8223, doi:10.1029/2001JD000494.

Harmon, M. E., et al. (1986), Ecology of coarse woody debris in temperate ecosystems, in *Advances in Ecological Research*, edited by A. MacFadyen and E. D. Ford, pp. 133–302, Academic, Orlando, Fla., doi:10.1016/S0065-2504(08)60121-X.

Harmon, M. E., B. Bond-Lamberty, J. Tang, and R. Vargas (2011), Heterotrophic respiration in disturbed forests: A review with examples from North America, *J. Geophys. Res.*, *116*, G00K04, doi:10.1029/2010JG001495.

Haxeltine, A., and I. C. Prentice (1996), BIOME3: An equilibrium terrestrial biosphere model based on ecophysiological constraints, resource availability, and competition among plant functional types, *Global Biogeochem. Cycles*, *10*(4), 693–709, doi:10.1029/96GB02344.

Heimann, M., et al. (1998), Evaluation of terrestrial carbon cycle models through simulations of the seasonal cycle of atmospheric CO_2: First results of a model intercomparison study, *Global Biogeochem. Cycles*, *12*(1), 1–24, doi:10.1029/97GB01936.

Hicke, J. A., G. P. Asner, J. T. Randerson, C. Tucker, S. Los, R. Birdsey, J. C. Jenkins, and C. Field (2002), Trends in North American net primary productivity derived from satellite observations, 1982–1998, *Global Biogeochem. Cycles*, *16*(2), 1018, doi:10.1029/2001GB001550.

Hicke, J. A., G. P. Asner, E. S. Kasischke, N. H. F. French, J. T. Randerson, G. James Collatz, B. J. Stocks, C. J. Tucker, S. O. Los, and C. B. Field (2003), Postfire response of North American boreal forest net primary productivity analyzed with satellite observations, *Global Change Biol.*, *9*(8), 1145–1157, doi:10.1046/j.1365-2486.2003.00658.x.

Hicke, J. A., J. C. Jenkins, D. S. Ojima, and M. Ducey (2007), Spatial patterns of forest characteristics in the western United States derived from inventories, *Ecol. Appl.*, *17*(8), 2387–2402, doi:10.1890/06-1951.1.

Hogg, E. H. (2001), Modelling aspen responses to climatic warming and insect defoliation in western Canada, in *Sustaining Aspen in Western Landscapes: Symposium Proceedings, Grand Junction, Colorado, 13–15 June 2000, Proc. RMRS-P-18*, edited by W. D. Shepperd, et al., pp. 325–338, USDA For. Serv., Fort Collins, Colo.

Hogg, E. H., J. P. Brandt, and M. Michaelian (2008), Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests, *Can. J. For. Res.*, *38*(6), 1373–1384, doi:10.1139/X08-001.

Houghton, R. A. (2010), How well do we know the flux of CO_2 from land-use change?, *Tellus, Ser. B*, *62*(5), 337–351, doi:10.1111/j.1600-0889.2010.00473.x.

Huang, C., et al. (2009), Development of time series stacks of Landsat images for reconstructing forest disturbance history, *Int. J. Digital Earth*, *2*, 195–218, doi:10.1080/17538940902801614.

Hurtt, G. C., P. R. Moorcroft, S. W. P. And, and S. A. Levin (1998), Terrestrial models and global change: Challenges for the future, *Global Change Biol.*, *4*(5), 581–590, doi:10.1046/j.1365-2486.1998.t01-1-00203.x.

Hurtt, G. C., S. W. Pacala, P. R. Moorcroft, J. Caspersen, E. Shevliakova, R. A. Houghton, and B. Moore Iii (2002), Projecting the future of the U.S. carbon sink, *Proc. Natl. Acad. Sci. U. S. A.*, *99*(3), 1389–1394, doi:10.1073/pnas.012249999.

Hurtt, G. C., S. Frolking, M. G. Fearon, B. Moore, E. Shevliakova, S. Malyshev, S. W. Pacala, and R. A. Houghton (2006), The underpinnings of land-use history: Three centuries of global gridded land-use transitions, wood-harvest activity, and resulting secondary lands, *Global Change Biol.*, *12*(7), 1208–1229, doi:10.1111/j.1365-2486.2006.01150.x.

Jandl, R., M. Lindner, L. Vesterdal, B. Bauwens, R. Baritz, F. Hagedorn, D. W. Johnson, K. Minkkinen, and K. A. Byrne (2007), How strongly can forest management influence soil carbon sequestration?, *Geoderma*, *137*(3–4), 253–268, doi:10.1016/j.geoderma.2006.09.003.

Jobbágy, E. G., and R. B. Jackson (2000), The vertical distribution of soil organic carbon and its relation to climate and vegetation, *Ecol. Appl.*, *10*(2), 423–436, doi:10.1890/1051-0761(2000)010[0423:TVDOSO]2.0.CO;2.

Johnson, D. W., and P. S. Curtis (2001), Effects of forest management on soil C and N storage: Meta analysis, *For. Ecol. Manage.*, *140*(2–3), 227–238, doi:10.1016/S0378-1127(00)00282-6.

Johnstone, J. F., T. N. Hollingsworth, F. S. Chapin, and M. C. Mack (2010), Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest, *Global Change Biol.*, *16*(4), 1281–1295, doi:10.1111/j.1365-2486.2009.02051.x.

Jones, C. D., and P. M. Cox (2001), Constraints on the temperature sensitivity of global soil respiration from the observed interannual variability in atmospheric CO_2, *Atmos. Sci. Lett.*, *2*(1–4), CII–CVIII.

Kane, E. S., E. S. Kasischke, D. W. Valentine, M. R. Turetsky, and A. D. McGuire (2007), Topographic influences on wildfire consumption of soil organic carbon in interior Alaska: Implications for black carbon accumulation, *J. Geophys. Res.*, *112*, G03017, doi:10.1029/2007JG000458.

Kane, E. S., W. C. Hockaday, M. R. Turetsky, C. A. Masiello, D. W. Valentine, B. P. Finney, and J. A. Baldock (2010), Topographic controls on black carbon accumulation in Alaskan black spruce forest soils: Implications for organic matter dynamics, *Biogeochemistry*, *100*(1–3), 39–56, doi:10.1007/s10533-009-9403-z.

Kasischke, E. S., and J. F. Johnstone (2005), Variation in postfire organic layer thickness in a black spruce forest complex in interior Alaska and its effects on soil temperature and moisture, *Can. J. For. Res.*, *35*(9), 2164–2177, doi:10.1139/x05-159.

Kasischke, E. S., T. Loboda, L. Giglio, N. H. F. French, E. E. Hoy, B. de Jong, and D. Riano (2011), Quantifying burned area for North American forests: Implications for direct reduction of carbon stocks, *J. Geophys. Res.*, *116*, G04003, doi:10.1029/2011JG001707.

Kauppi, P. E., J. H. Ausubel, J. Y. Fang, A. S. Mather, R. A. Sedjo, and P. E. Waggoner (2006), Returning forests analyzed with the forest identity, *Proc. Natl. Acad. Sci. U. S. A.*, *103*(46), 17,574–17,579, doi:10.1073/pnas.0608343103.

Keane, R. E., P. Morgan, and S. W. Running (1996), 1996 FIRE-BGC–A mechanistic ecological process model for simulating fire succession on coniferous forest landscapes of the northern Rocky Mountains, *Res. Pap. INT-RP-484*, Intermt. Res. Stn., Ogden, Utah.

Keane, R. E., K. C. Ryan, T. T. Veblen, C. D. Allen, J. Logan, and B. Hawkes (2002), Cascading effects of fire exclusion in rocky mountain ecosystems: A literature review, *Gen. Tech. Rep. RMRS-GTR-91*, Rocky Mt. Res. Stn., Fort Collins, Colo.

Keane, R. E., G. J. Cary, I. D. Davies, M. D. Flannigan, R. H. Gardner, S. Lavorel, J. M. Lenihan, C. Li, and T. S. Rupp (2004), A classification of landscape fire succession models: Spatial simulations of fire and vegetation dynamics, *Ecol. Modell.*, *179*(1), 3–27, doi:10.1016/j.ecolmodel.2004.03.015.

Keane, R. E., L. M. Holsinger, and S. D. Pratt (2006), Simulating historical landscape dynamics using the landscape fire succession model LANDSUM version 4.0, *Gen. Tech. Rep. RMRS-GTR-171CD*, Rocky Mt. Res. Stn., Fort Collins, Colo.

Kennedy, R. E., W. B. Cohen, and T. A. Schroeder (2007), Trajectory-based change detection for automated characterization of forest disturbance dynamics, *Remote Sens. Environ.*, *110*(3), 370–386, doi:10.1016/j.rse.2007.03.010.

Kimball, J. S., P. E. Thornton, M. A. White, and S. W. Running (1997), Simulating forest productivity and surface-atmosphere carbon exchange in the BOREAS study region, *Tree Physiol.*, *17*(8–9), 589–599.

King, D. A., D. P. Turner, and W. D. Ritts (2011), Parameterization of a diagnostic carbon cycle model for continental scale application, *Remote Sens. Environ.*, *115*(7), 1653–1664, doi:10.1016/j.rse.2011.02.024.

Knorr, W., T. Kaminski, M. Scholze, N. Gobron, B. Pinty, R. Giering, and P. P. Mathieu (2010), Carbon cycle data assimilation with a generic phenology model, Carbon cycle data assimilation with a generic phenology model, *J. Geophys. Res.*, *115*, G04017, doi:10.1029/2009JG001119.

Kowalski, A. S., et al. (2004), Paired comparisons of carbon exchange between undisturbed and regenerating stands in four managed forest in Europe, *Global Change Biol.*, *10*(10), 1707–1723, doi:10.1111/j.1365-2486.2004.00846.x.

Kulakowski, D., and T. T. Veblen (2006), The effect of fires on susceptibility of subalpine forests to 19th century spruce beetle outbreak in western Colorado, *Can. J. For. Res.*, *36*(11), 2974–2982, doi:10.1139/x06-182.

Kurz, W. A., and M. J. Apps (1999), A 70-year retrospective analysis of carbon fluxes in the Canadian Forest Sector, *Ecol. Appl.*, *9*(2), 526–547, doi:10.1890/1051-0761(1999)009[0526:AYRAOC]2.0.CO;2.

Kurz, W. A., C. C. Dymond, G. Stinson, G. J. Rampley, E. T. Neilson, A. L. Carroll, T. Ebata, and L. Safranyik (2008a), Mountain pine beetle and forest carbon feedback to climate change, *Nature*, *452*(7190), 987–990, doi:10.1038/nature06777.

Kurz, W. A., G. Stinson, and G. Rampley (2008b), Could increased boreal forest ecosystem productivity offset carbon losses from increased disturbances?, *Philos. Trans. R. Soc. B*, *363*(1501), 2259–2268, doi:10.1098/rstb.2007.2198.

Langley, J. A., B. G. Drake, and B. A. Hungate (2002), Extensive belowground carbon storage supports roots and mycorrhizae in regenerating scrub oaks, *Oecologia*, *131*(4), 542–548, doi:10.1007/s00442-002-0932-6.

Law, B. E., O. J. Sun, J. Campbell, S. Van Tuyl, and P. E. Thornton (2003), Changes in carbon storage and fluxes in a chronosequence of ponderosa pine, *Global Change Biol.*, *9*(4), 510–524, doi:10.1046/j.1365-2486.2003.00624.x.

Lindroth, A., F. Lagergren, A. Grelle, L. Klemedtsson, O. Langvall, P. Weslien, and J. Tuulik (2009), Storms can cause Europe-wide reduction in forest carbon sink, *Global Change Biol.*, *15*(2), 346–355, doi:10.1111/j.1365-2486.2008.01719.x.

Liski, J., H. Ilvesniemi, A. Mäkelä, and C. J. Westman (1999), CO_2 emissions from soil in response to climatic warming are overestimated: The decomposition of old soil organic matter is tolerant of temperature, *Ambio*, *28*(2), 171–174.

Liu, S. (2009), Quantifying the spatial details of carbon sequestration potential and performance, in *Science and Technology of Carbon Sequestration*, *Geophys. Monogr. Ser.*, vol. 183, edited by B. McPherson and E. Sundquist, pp. 117–128, AGU, Washington D. C.

Liu, S., N. Bliss, E. Sundquist, and T. G. Huntington (2003), Modeling carbon dynamics in vegetation and soil under the impact of soil erosion and deposition, *Global Biogeochem. Cycles*, *17*(2), 1074, doi:10.1029/2002GB002010.

Liu, S., T. R. Loveland, and R. Kurtz (2004), Contemporary carbon dynamics in terrestrial ecosystems in the Southeastern Plains of the United States, *Environ. Manage*, *33*, S442–S456, doi:10.1007/s00267-003-9152-z.

Liu, S., P. Anderson, G. Zhou, B. Kauffman, F. Hughes, D. Schimel, V. Watson, and J. Tosi (2008), Resolving model parameter values from carbon and nitrogen stock measurements in a wide range of tropical mature forests using nonlinear inversion and regression trees, *Ecol. Modell.*, *219*(3–4), 327–341, doi:10.1016/j.ecolmodel.2008.07.025.

Loveland, T. R., T. L. Sohl, S. V. Stehman, A. L. Gallant, K. L. Sayler, and D. E. Napton (2002), A strategy for estimating the rates of recent United States land cover changes, *Photogramm. Eng. Remote Sens.*, *8*, 1091–1099.

Loya, W. M., K. S. Pregitzer, N. J. Karberg, J. S. King, and C. P. Giardina (2003), Reduction of soil carbon formation by tropospheric ozone under increased carbon dioxide levels, *Nature*, *425*(6959), 705–707, doi:10.1038/nature02047.

Luo, Y., and E. Weng (2011), Dynamic disequilibrium of the terrestrial carbon cycle under global change, *Trends Ecol. Evol.*, *26*(2), 96–104, doi:10.1016/j.tree.2010.11.003.

Luo, Y., L. W. White, J. G. Canadell, E. H. DeLucia, D. S. Ellsworth, A. Finzi, J. Lichter, and W. H. Schlesinger (2003), Sustainability of terrestrial carbon sequestration: A case study in Duke Forest with inversion approach, *Global Biogeochem. Cycles*, *17*(1), 1021, doi:10.1029/2002GB001923.

Luyssaert, S., et al. (2007), CO_2 balance of boreal, temperate, and tropical forests derived from a global database, *Global Change Biol.*, *13*(12), 2509–2537, doi:10.1111/j.1365-2486.2007.01439.x.

Mahecha, M. D., et al. (2010), Global convergence in the temperature sensitivity of respiration at ecosystem level, *Science*, *329*(5993), 838–840, doi:10.1126/science.1189587.

Masek, J. G., and G. J. Collatz (2006), Estimating forest carbon fluxes in a disturbed southeastern landscape: Integration of remote sensing, forest inventory, and biogeochemical modeling, *J. Geophys. Res.*, *111*, G01006, doi:10.1029/2005JG000062.

Masek, J. G., C. Huang, R. Wolfe, W. Cohen, F. Hall, J. Kutler, and P. Nelson (2008), North American forest disturbance mapped from a decadal Landsat record, *Remote Sens. Environ.*, *112*(6), 2914–2926, doi:10.1016/j.rse.2008.02.010.

Masek, J. G., et al. (2011), Recent rates of forest harvest and conversion in North America, *J. Geophys. Res.*, *116*, G00K03, doi:10.1029/2010JG001471.

McCarthy, H. R., R. Oren, H. S. Kim, K. H. Johnsen, C. Maier, S. G. Pritchard, and M. A. Davis (2006), Interaction of ice storms and management practices on current carbon sequestration in forests with potential mitigation under future CO_2 atmosphere, *J. Geophys. Res.*, *111*, D15103, doi:10.1029/2005JD006428.

McGuire, A. D. (1992), Interactions between carbon and nitrogen dynamics in estimating net primary productivity for potential vegetation in North America, *Global Biogeochem. Cycles*, *6*(2), 101–124, doi:10.1029/92GB00219.

McGuire, A. D., et al. (2001), Carbon balance of the terrestrial biosphere in the twentieth century: Analyses of CO_2, climate and land use effects with four process-based ecosytem models, *Global Biogeochem. Cycles*, *15*(1), 183–206, doi:10.1029/2000GB001298.

McGuire, A. D., R. W. Ruess, A. Lloyd, J. Yarie, J. S. Clein, and G. P. Juday (2010), Vulnerability of white spruce tree growth in interior Alaska in response to climate variability: Dendrochronological, demographic, and experimental perspectives, *Can. J. For. Res.*, *40*, 1197–1209, doi:10.1139/X09-206.

McNulty, S. G. (2002), Hurricane impacts on US forest carbon sequestration, *Environ. Pollut.*, *116*, suppl. 1, 17–24, doi:10.1016/S0269-7491(01)00242-1.

Medvigy, D., S. C. Wofsy, J. W. Munger, and P. R. Moorcroft (2010), Responses of terrestrial ecosystems and carbon budgets to current and future environmental variability, *Proc. Natl. Acad. Sci. U. S. A.*, *107*(18), 8275–8280, doi:10.1073/pnas.0912032107.

Mildrexler, D., M. Zhao, and S. Running (2009), Testing a MODIS Global Disturbance Index across North America, *Remote Sens. Environ.*, *113*(10), 2103–2117.

Mitsch, W. J., M. Straskraba, and S. E. Jørgensen (Eds.) (1988), *Wetland Modelling*, *Dev. Environ. Modell.*, vol. 12, 227 pp., Elsevier, Amsterdam.

Mladenoff, D. J. (2004), LANDIS and forest landscape models, *Ecol. Modell.*, *180*(1), 7–19, doi:10.1016/j.ecolmodel.2004.03.016.

Moorcroft, P. R., G. C. Hurtt, and S. W. Pacala (2001), A method for scaling vegetation dynamics: The ecosystem demography model (ED), *Ecol. Monogr.*, *71*(4), 557–586, doi:10.1890/0012-9615(2001)071[0557:AMFSVD]2.0.CO;2.

Mouillot, F., and C. B. Field (2005), Fire history and the global carbon budget: A 1° × 1° fire history reconstruction for the 20th century, *Global Change Biol.*, *11*(3), 398–420, doi:10.1111/j.1365-2486.2005.00920.x.

Norby, R., K. Ogle, P. Curtis, F.-W. Badeck, A. Huth, G. Hurtt, T. Kohyama, and J. Peñuelas (2001), Aboveground growth and competition in forest gap models: An Analysis for studies of climatic change, *Clim. Change*, *51*(3–4), 415–447, doi:10.1023/A:1012510619424.

O'Hagan, A. (2011), Probabilistic uncertainty specification: Overview, elaboration techniques and their application to a mechanistic model of carbon flux, *Environ. Modell. Software*, doi:10.1016/j.envsoft.2011.03.003, in press.

Ohlson, M., B. Dahlberg, T. Økland, K. J. Brown, and R. Halvorsen (2009), The charcoal carbon pool in boreal forest soils, *Nat. Geosci.*, *2*(10), 692–695, doi:10.1038/ngeo617.

Oliver, C. D. (1980), Forest development in North America following major disturbances, *For. Ecol. Manage.*, *3*, 153–168, doi:10.1016/0378-1127(80)90013-4.

Olsson, B. A., H. Staaf, H. Lundkvist, J. Bengtsson, and K. Rosén (1996), Carbon and nitrogen in coniferous forest soils after clear-felling and harvests of different intensity, *For. Ecol. Manage.*, *82*(1–3), 19–32, doi:10.1016/0378-1127(95)03697-0.

Oreskes, N., K. Shrader-Frechette, and K. Belitz (1994), Verification, validation, and confirmation of numerical models in the earth sciences, *Science*, *263*(5147), 641–646, doi:10.1126/science.263.5147.641.

Pacala, S. W., C. D. Canham, J. Saponara, J. A. Silander Jr., R. K. Kobe, and E. Ribbens (1996), Forest models defined by field measurements: Estimation, error analysis and dynamics, *Ecol. Monogr.*, *66*(1), 1–43, doi:10.2307/2963479.

Pan, Y., J. M. Chen, R. Birdsey, K. McCullough, L. He, and F. Deng (2010), Age structure and disturbance legacy of North American forests, *Biogeosci. Discuss*, *7*(1), 979–1020.

Pan, Y., et al. (2011), A large and persistent carbon sink in the world's forests, *Science*, *333*(6045), 988–993, doi:10.1126/science.1201609.

Parton, W. J., D. S. Schimel, C. V. Cole, and D. S. Ojima (1987), Analysis of factors controlling soil organic-matter levels in great-plains grasslands, *Soil Sci. Soc. Am. J.*, *51*(5), 1173–1179, doi:10.2136/sssaj1987.03615995005100050015x.

Pastor, J., and W. M. Post (1986), Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles, *Biogeochemistry*, *2*(1), 3–27, doi:10.1007/BF02186962.

Peng, C., and M. J. Apps (1999), Modelling the response of net primary productivity (NPP) of boreal forest ecosystems to changes in climate and fire disturbance regimes, *Ecol. Modell.*, *122*(3), 175–193, doi:10.1016/S0304-3800(99)00137-4.

Pennock, D. J., and C. van Kessel (1997), Clear-cut forest harvest impacts on soil quality indicators in the mixedwood forest of Saskatchewan, Canada, *Geoderma*, *75*(1–2), 13–32, doi:10.1016/S0016-7061(96)00075-4.

Percy, K. E., et al. (2002), Altered performance of forest pests under atmospheres enriched by CO_2 and O_3, *Nature*, *420*(6913), 403–407, doi:10.1038/nature01028.

Pfeifer, E. M., J. A. Hicke, and A. J. H. Meddens (2010), Observations and modeling of aboveground tree carbon stocks and fluxes following a bark beetle outbreak in the western United States, *Global Change Biol.*, *17*(1), 339–350, doi:10.1111/j.1365-2486.2010.02226.x.

Pickett, S. T. A., and P. S. White (Eds.) (1985), *The Ecology of Natural Disturbance and Patch Dynamics*, Academic, San Diego, Calif.

Pietsch, S. A., and H. Hasenauer (2006), Evaluating the self-initialization procedure for large-scale ecosystem models, *Global Change Biol.*, *12*(9), 1658–1669, doi:10.1111/j.1365-2486.2006.01211.x.

Pietsch, S. A., H. Hasenauer, J. Kučera, and J. Čermák (2003), Modeling effects of hydrological changes on the carbon and nitrogen balance of oak in floodplains, *Tree Physiol.*, *23*(11), 735–746.

Potter, C. S. (1993), Terrestrial ecosystem production: A process model based on global satellite and surface data, *Global Biogeochem. Cycles*, *7*(4), 811–841, doi:10.1029/93GB02725.

Potter, C. S., E. A. Davidson, S. A. Klooster, D. C. Nepstad, G. H. De Negreiros, and V. Brooks (1998), Regional application of an ecosystem production model for studies of biogeochemistry in Brazilian Amazonia, *Global Change Biol.*, *4*(3), 315–333, doi:10.1046/j.1365-2486.1998.00154.x.

Potter, C., J. Bubier, P. Crill, and P. Lafleur (2001), Ecosystem modeling of methane and carbon dioxide fluxes for boreal forest sites, *Can. J. For. Res.*, *31*(2), 208–223, doi:10.1139/cjfr-31-2-208.

Raffa, K. F., B. H. Aukema, B. J. Bentz, A. L. Carroll, J. A. Hicke, M. G. Turner, and W. H. Romme (2008), Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions, *BioScience*, *58*(6), 501–517, doi:10.1641/B580607.

Raich, J. W., E. B. Rastetter, J. M. Melillo, D. W. Kicklighter, P. A. Steudler, B. J. Peterson, A. L. Grace, B. Moore, and C. J. Vorosmarty (1991), Potential net primary productivity in South America: Application of a global model, *Ecol. Appl.*, *1*(4), 399–429, doi:10.2307/1941899.

Randerson, J. T., et al. (2006), The impact of boreal forest fire on climate warming, *Science*, *314*(5802), 1130–1132, doi:10.1126/science.1132075.

Rayner, P. J., M. Scholze, W. Knorr, T. Kaminski, R. Giering, and H. Widmann (2005), Two decades of terrestrial carbon fluxes from a carbon cycle data assimilation system (CCDAS), *Global Biogeochem. Cycles*, *19*, GB2026, doi:10.1029/2004GB002254.

Reay, D. S., F. Dentener, P. Smith, J. Grace, and R. A. Feely (2008), Global nitrogen deposition and carbon sinks, *Nat. Geosci.*, *1*(7), 430–437, doi:10.1038/ngeo230.

Régnière, J., and B. Bentz (2007), Modeling cold tolerance in the mountain pine beetle, Dendroctonus ponderosae, *J. Insect Physiol.*, *53*(6), 559–572, doi:10.1016/j.jinsphys.2007.02.007.

Ricciuto, D. M., A. W. King, D. Dragoni, and W. M. Post (2011), Parameter and prediction uncertainty in an optimized terrestrial carbon cycle model: Effects of constraining variables and data record length, *J. Geophys. Res.*, *116*, G01033, doi:10.1029/2010JG001400.

Richardson, A. D., et al. (2010), Estimating parameters of a forest ecosystem C model with measurements of stocks and fluxes as joint constraints, *Oecologia*, *164*(1), 25–40, doi:10.1007/s00442-010-1628-y.

Rocha, A. V., and G. R. Shaver (2011), Postfire energy exchange in arctic tundra: The importance and climatic implications of burn severity, *Global Change Biol.*, *17*(9), 2831–2841, doi:10.1111/j.1365-2486.2011.02441.x.

Roe, G. H., and M. B. Baker (2007), Why is climate sensitivity so unpredictable?, *Science*, *318*(5850), 629–632, doi:10.1126/science.1144735.

Rollins, M. G. (2009), LANDFIRE: A nationally consistent vegetation, wildland fire, and fuel assessment, *Int. J. Wildland Fire*, *18*(3), 235–249, doi:10.1071/WF08088.

Runkle, J. R. (1982), Patterns of disturbance in some old-growth mesic forests of eastern North America, *Ecology*, *63*(5), 1533–1546, doi:10.2307/1938878.

Running, S. W., and S. T. Gower (1991), FOREST-BGC, A general model of forest ecosystem processes for regional applications. II. Dynamic carbon allocation and nitrogen budgets, *Tree Physiol.*, *9*(1–2), 147–160, doi:10.1093/treephys/9.1-2.147.

Saleska, S. R., et al. (2003), Carbon in Amazon Forests: Unexpected seasonal fluxes and disturbance-induced losses, *Science*, *302*(5650), 1554–1557, doi:10.1126/science.1091165.

Samman, S., and J. A. Logan (2000), Assessment and response to bark beetle outbreaks in the Rocky Mountain area: Report to Congress from Forest Health Protection, Washington Office, Forest Service, U.S. Department of Agriculture, *Gen. Tech. Rep. RMRS-GTR-62*, Rocky Mt. Res. Stn., Fort Collins, Colo.

Schäfer, K. V. R., K. L. Clark, N. Skowronski, and E. P. Hamerlynck (2009), Impact of insect defoliation on forest carbon balance as assessed with a canopy assimilation model, *Global Change Biol.*, *16*, 546–560, doi:10.1111/j.1365-2486.2009.02037.x.

Schimel, D. S., et al. (2001), Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems, *Nature*, *414*(6860), 169–172, doi:10.1038/35102500.

Schulze, E. D., et al. (1999), Productivity of forests in the eurosiberian boreal region and their potential to act as a carbon sink–A synthesis, *Global Change Biol.*, *5*(6), 703–722, doi:10.1046/j.1365-2486.1999.00266.x.

Schwalm, C. R., et al. (2010), A model-data intercomparison of CO_2 exchange across North America: Results from the North American Carbon Program site synthesis, *J. Geophys. Res.*, *115*, G00H05, doi:10.1029/2009JG001229.

Seidl, R., W. Rammer, D. Jager, and M. J. Lexer (2008), Impact of bark beetle (*Ips typographus* L.) disturbance on timber production and carbon sequestration in different management strategies under climate change, *For. Ecol. Manage.*, *256*(3), 209–220, doi:10.1016/j.foreco.2008.04.002.

Shevliakova, E., S. W. Pacala, S. Malyshev, G. C. Hurtt, P. C. D. Milly, J. P. Caspersen, L. T. Sentman, J. P. Fisk, C. Wirth, and C. Crevoisier (2009), Carbon cycling under 300 years of land use change: Importance of the secondary vegetation sink, *Global Biogeochem. Cycles*, *23*, GB2022, doi:10.1029/2007GB003176.

Shugart, H. H., R. Leemans, and G. B. Bonan (Eds.) (1992), *A Systems Analysis of the Global Boreal Forest*, 565 pp., Cambridge Univ. Press, Cambridge, U. K., doi:10.1017/CBO9780511565489.

Simic, A., J. M. Chen, J. Liu, and F. Csillag (2004), Spatial scaling of net primary productivity using subpixel information, *Remote Sens. Environ.*, *93*(1–2), 246–258, doi:10.1016/j.rse.2004.07.008.

Skog, K. E. (2008), Sequestration of carbon in harvested wood products for the United States, *For. Prod. J.*, *58*, 56–72.

Smith, S. V., S. H. Bullock, A. Hinojosa-Corona, E. Franco-Vizcaíno, M. Escoto-Rodríguez, T. G. Kretzschmar, L. M. Farfán, and J. M. Salazar-Ceseña (2007), Soil erosion and significance for carbon fluxes in a mountainous Mediterranean-climate watershed, *Ecol. Appl.*, *17*(5), 1379–1387, doi:10.1890/06-0615.1.

Smith, W. B., and D. Darr (2004), U.S. forest resource facts and historical trends, *Rep. FS-801*, U.S. Dep. of Agric. For. Serv., Washington, D. C.

Spies, T. A., and J. F. Franklin (1988), Old-growth and forest dynamics in the Douglas-fir region of western Oregon and Washington, *Nat. Areas J.*, *8*(3), 190–201.

Stinson, G., et al. (2011), An inventory-based analysis of Canada's managed forest carbon dynamics, 1990 to 2008, *Global Change Biol.*, *17*(6), 2227–2244, doi:10.1111/j.1365-2486.2010.02369.x.

Stöckli, R., D. M. Lawrence, G.-Y. Niu, K. W. Oleson, P. E. Thornton, Z.-L. Yang, G. B. Bonan, A. S. Denning, and S. W. Running (2008), Use of FLUXNET in the Community Land Model development, *J. Geophys. Res.*, *113*, G01025, doi:10.1029/2007JG000562.

Stocks, B. J., B. S. Lee, and D. L. Martell (1996), Some potential carbon budget implications of fire management in the boreal forest, in *Forest Ecosystems, Forest Management, and the Global Carbon Cycle*, *NATO ASI Ser., Ser. I*, vol. 40, edited by M. J. Apps and D. T. Price, pp. 89–96, Springer, New York.

Stocks, B. J., et al. (2002), Large forest fires in Canada, 1959–1997, *J. Geophys. Res.*, *107*, 8149, doi:10.1029/2001JD000484. [Printed *108*(D1), 2003].

Sun, G., et al. (2011), Upscaling key ecosystem functions across the conterminous United States by a water-centric ecosystem model, *J. Geophys. Res.*, *116*, G00J05, doi:10.1029/2010JG001573.

Tang, J., Y. Qi, M. Xu, L. Misson, and A. H. Goldstein (2005), Forest thinning and soil respiration in a ponderosa pine plantation in the Sierra Nevada, *Tree Physiol.*, *25*(1), 57–66, doi:10.1093/treephys/25.1.57.

Tang, J., P. V. Bolstad, and J. G. Martin (2009), Soil carbon fluxes and stocks in a Great Lakes forest chronosequence, *Global Change Biol.*, *15*(1), 145–155, doi:10.1111/j.1365-2486.2008.01741.x.

Tatarinov, F. A., and E. Cienciala (2006), Application of BIOME-BGC model to managed forests. 1. Sensitivity analysis, *For. Ecol. Manage.*, *237*(1–3), 267–279, doi:10.1016/j.foreco.2006.09.085.

Thonicke, K., S. Venevsky, S. Sitch, and W. Cramer (2001), The role of fire disturbance for global vegetation dynamics: Coupling fire into a dynamic global vegetation model, *Glob. Ecol. Biogeogr.*, *10*(6), 661–677, doi:10.1046/j.1466-822X.2001.00175.x.

Thornley, J. H. M., and M. G. R. Cannell (2004), Long-term effects of fire frequency on carbon storage and productivity of boreal forests: A modeling study, *Tree Physiol.*, *24*(7), 765–773.

Thornton, P. E., et al. (2002), Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests, *Agric. For. Meteorol.*, *113*(1–4), 185–222, doi:10.1016/S0168-1923(02)00108-9.

Tremblay, M., C. Messier, and D. J. Marceau (2005), Analysis of deciduous tree species dynamics after a severe ice storm using SORTIE model simulations, *Ecol. Modell.*, *187*(2–3), 297–313, doi:10.1016/j.ecolmodel.2005.01.038.

Trettin, C. C., B. Song, M. F. Jurgensen, and C. Li (2001), Existing soil carbon models do not apply to forested wetlands, *Gen. Tech. Rep. SRS-46*, South. Res. Stn., Asheville, N. C.

Trumbore, S. E. (2006), Carbon respired by terrestrial ecosystems–Recent progress and challenges, *Global Change Biol.*, *12*(2), 141–153, doi:10.1111/j.1365-2486.2006.01067.x.

Trumbore, S. E., O. A. Chadwick, and R. Amundson (1996), Rapid exchange between soil carbon and atmospheric carbon dioxide driven by temperature change, *Science*, *272*(5260), 393–396, doi:10.1126/science.272.5260.393.

Turetsky, M. R., E. S. Kane, J. W. Harden, R. D. Ottmar, K. L. Manies, E. Hoy, and E. S. Kasischke (2011), Recent acceleration of biomass burning and carbon losses in Alaskan forests and peatlands, *Nat. Geosci.*, *4*(1), 27–31, doi:10.1038/ngeo1027.

Turner, D. P., W. B. Cohen, and R. E. Kennedy (2000), Alternative spatial resolutions and estimation of carbon flux over a managed forest landscape in western Oregon, *Landscape Ecol.*, *15*(5), 441–452, doi:10.1023/A:1008116300063.

Turner, M. G., and V. H. Dale (1998), Comparing large, infrequent disturbances: What have we learned?, *Ecosystems*, *1*(6), 493–496, doi:10.1007/s100219900045.

U.S. Department of Agriculture (USDA) (2009), Major forest insect and disease conditions in the United States 2008 Update, *Rep. FS-933*, For. Serv., Washington, D. C.

Vargas, R., and M. F. Allen (2008), Diel patterns of soil respiration in a tropical forest after Hurricane Wilma, *J. Geophys. Res.*, *113*, G03021, doi:10.1029/2007JG000620.

Vargas, R., S. E. Trumbore, and M. F. Allen (2009), Evidence of old carbon used to grow new fine roots in a tropical forest, *New Phytol.*, *182*(3), 710–718, doi:10.1111/j.1469-8137.2009.02789.x.

Vargas, R., N. Hasselquist, E. B. Allen, and M. F. Allen (2010), Effects of a hurricane disturbance on aboveground forest structure, arbuscular mycorrhizae and belowground carbon in a restored tropical forest, *Ecosystems*, *13*(1), 118–128, doi:10.1007/s10021-009-9305-x.

Volney, W. J. A., and R. A. Fleming (2000), Climate change and impacts of boreal forest insects, *Agric. Ecosyst. Environ.*, *82*(1–3), 283–294, doi:10.1016/S0167-8809(00)00232-2.

Waisanen, P. J., and N. B. Bliss (2002), Changes in population and agricultural land in conterminous United States counties, 1790 to 1997, *Global Biogeochem. Cycles*, *16*(4), 1137, doi:10.1029/2001GB001843.

Wang, Q., M. Watanabe, and Z. Ouyang (2005), Simulation of water and carbon fluxes using BIOME-BGC model over crops in China, *Agric. For. Meteorol.*, *131*(3–4), 209–224, doi:10.1016/j.agrformet.2005.06.002.

Wang, S., J. M. Chen, W. M. Ju, X. Feng, M. Chen, P. Chen, and G. Yu (2007), Carbon sinks and sources in China's forests during 1901–2001, *J. Environ. Manage.*, *85*(3), 524–537, doi:10.1016/j.jenvman.2006.09.019.

Wang, W., K. Ichii, H. Hashimoto, A. R. Michaelis, P. E. Thornton, B. E. Law, and R. R. Nemani (2009), A hierarchical analysis of terrestrial ecosystem model Biome-BGC: Equilibrium analysis and model calibration, *Ecol. Modell.*, *220*(17), 2009–2023, doi:10.1016/j.ecolmodel.2009.04.051.

Wang, Y. P., and R. Leuning (1998), A two-leaf model for canopy conductance, photosynthesis and partitioning of available energy I: Model description and comparison with a multi-layered model, *Agric. For. Meteorol.*, *91*(1–2), 89–111, doi:10.1016/S0168-1923(98)00061-6.

Wang, Y. P., C. M. Trudinger, and I. G. Enting (2009), A review of applications of model-data fusion to studies of terrestrial carbon fluxes at different scales, *Agric. For. Meteorol.*, *149*(11), 1829–1842, doi:10.1016/j.agrformet.2009.07.009.

Weber, M. G., and B. J. Stocks (1998), Forest fires and sustainability in the boreal forests of Canada, *Ambio*, *27*(7), 545–550.
Webster, J. R., S. W. Golladay, E. F. Benfield, D. J. D'Angelo, and G. T. Peters (1990), Effects of forest disturbance on particulate organic matter budgets of small streams, *J. N. Am. Benthol. Soc.*, *9*(2), 120–140, doi:10.2307/1467446.
Weng, E. S., and Y. Q. Luo (2011), Relative information contributions of model vs. data to contstraints of short- and long-term forecasts of forest carbon dynamics, *Ecol. Appl.*, doi:10.1890/09-1394.1.
White, L., F. White, Y. Luo, and T. Xu (2006), Estimation of parameters in carbon sequestration models from net ecosystem exchange data, *Appl. Math. Comput.*, *181*(2), 864–879, doi:10.1016/j.amc.2006.02.014.
Wiedinmyer, C., and J. C. Neff (2007), Estimates of CO_2 from fires in the United States: Implications for carbon management, *Carbon Balance Manage.*, *2*(1), doi:10.1186/1750-0680-2-10.
Williams, M., P. A. Schwarz, B. E. Law, J. Irvine, and M. R. Kurpius (2005), An improved analysis of forest carbon dynamics using data assimilation, *Global Change Biol.*, *11*(1), 89–105, doi:10.1111/j.1365-2486.2004.00891.x.
Woodall, C. W., B. L. Conkling, M. C. Amacher, J. W. Coulston, S. Jovan, C. H. Perry, B. Schulz, G. C. Smith, and S. W. Wolf (2010), The Forest Inventory and Analysis Database Version 4.0: Database description and users manual for Phase 3, *Gen. Tech. Rep. NRS-61*, North. Res. Stn., Newtown Square, Pa.
Woodward, F. I., M. R. Lomas, and R. A. Betts (1998), Vegetation-climate feedbacks in a greenhouse world, *Philos. Trans. R. Soc. London B*, *353*, 29–39, doi:10.1098/rstb.1998.0188.
Wullschleger, S. D., R. B. Jackson, W. S. Currie, A. D. Friend, Y. Luo, F. Mouillot, Y. Pan, and G. Shao (2001), Below-ground processes in gap models for simulating forest response to global change, *Clim. Change*, *51*(3–4), 449–473, doi:10.1023/A:1012570821241.
Xian, G., and C. Homer (2010), Updating the 2001 National Land Cover Database Impervious Surface Products to 2006 using Landsat Imagery Change Detection Methods, *Remote Sens. Environ.*, *114*(8), 1676–1686, doi:10.1016/j.rse.2010.02.018.
Xiao, J., et al. (2010), A continuous measure of gross primary production for the conterminous United States derived from MODIS and AmeriFlux data, *Remote Sens. Environ.*, *114*(3), 576–591, doi:10.1016/j.rse.2009.10.013.
Xiao, J., et al. (2011), Assessing net ecosystem carbon exchange of U.S. terrestrial ecosystems by integrating eddy covariance flux measurements and satellite observations, *Agric. For. Meteorol.*, *151*, 60–69.
Yanai, R. D., W. S. Currie, and C. L. Goodale (2003), Soil carbon dynamics after forest harvest: An ecosystem paradigm reconsidered, *Ecosystems*, *6*(3), 197–212, doi:10.1007/s10021-002-0206-5.
Yarie, J., and S. Billings (2002), Carbon balance of the taiga forest within Alaska: Present and future, *Can. J. For. Res.*, *32*(5), 757–767, doi:10.1139/x01-075.
Yi, S., A. D. McGuire, E. S. Kasischke, J. W. Harden, K. L. Manies, M. Mack, and M. Turetsky (2010), A dynamic organic soil biogeochemical model for simulating the effects of wildfire on soil environmental and carbon dynamics of black spruce forests, *J. Geophys. Res.*, *115*, G04015, doi:10.1029/2010JG001302.
Yuan, W., et al. (2007), Deriving a light use efficiency model from eddy covariance flux data for predicting daily gross primary production across biomes, *Agric. For. Meteorol.*, *143*(3–4), 189–207, doi:10.1016/j.agrformet.2006.12.001.
Zaehle, S., S. Sitch, I. C. Prentice, J. Liski, W. Cramer, M. Erhard, T. Hickler, and B. Smith (2006), The importance of age-related decline in forest NPP for modeling regional carbon balances, *Ecol. Appl.*, *16*(4), 1555–1574, doi:10.1890/1051-0761(2006)016[1555:TIOADI]2.0.CO;2.
Zeng, H., J. Q. Chambers, R. I. Negrón-Juárez, G. C. Hurtt, D. B. Baker, and M. D. Powell (2009), Impacts of tropical cyclones on U.S. forest tree mortality and carbon flux from 1851 to 2000, *Proc. Natl. Acad. Sci. U. S. A.*, *106*(19), 7888–7892, doi:10.1073/pnas.0808914106.
Zhang, X., and S. Kondragunta (2006), Estimating forest biomass in the USA using generalized allometric models and MODIS land products, *Geophys. Res. Lett.*, *33*, L09402, doi:10.1029/2006GL025879.
Zhang, Y., C. Li, C. C. Trettin, H. Li, and G. Sun (2002), An integrated model of soil, hydrology, and vegetation for carbon dynamics in wetland ecosystems, *Global Biogeochem. Cycles*, *16*(4), 1061, doi:10.1029/2001GB001838.
Zhao, M., and S. W. Running (2010), Drought-induced reduction in global terrestrial net primary production from 2000 through 2009, *Science*, *329*(5994), 940–943, doi:10.1126/science.1192666.
Zhao, S., S. Liu, Z. Li, and T. L. Sohl (2009), Ignoring detailed fast-changing dynamics of land use overestimates regional terrestrial carbon sequestration, *Biogeosciences*, *6*(8), 1647–1654, doi:10.5194/bg-6-1647-2009.
Zhao, S., S. Liu, Z. Li, and T. L. Sohl (2010a), Federal land management, carbon sequestration, and climate change in the Southeastern U.S.—A case study with Fort Benning, *Environ. Sci. Technol.*, *44*(3), 992–997, doi:10.1021/es9009019.
Zhao, S., S. Liu, Z. Li, and T. L. Sohl (2010b), A spatial resolution threshold of land cover in estimating terrestrial carbon sequestration in four counties in Georgia and Alabama, USA, *Biogeosciences*, *7*(1), 71–80, doi:10.5194/bg-7-71-2010.
Zhu, Z., C. H. Key, D. Ohlen, and N. Benson (2006), Evaluate sensitivities of burn-severity mapping algorithms for different ecosystems and fire histories in the United States, edited, final report to the Joint Fire Science Program, 35 pp., U.S. Geol. Surv., Reston, Va.
Zhuang, Q., A. D. McGuire, K. P. O'Neill, J. W. Harden, V. E. Romanovsky, and J. Yarie (2003), Modeling soil thermal and carbon dynamics of a fire chronosequence in interior Alaska, *J. Geophys. Res.*, *108*(D1), 8147, doi:10.1029/2001JD001244.

B. Bond-Lamberty, Joint Global Change Research Institute, DOE Pacific Northwest National Laboratory, College Park, MD 20740, USA.

J. Chen, Department of Geography, University of Toronto, Toronto, ON M5S 3G3, Canada.

S. L. Edburg and J. A. Hicke, Department of Geography, University of Idaho, Moscow, ID 83844, USA.

Y. Hu, College of Information, South China Agricultural University, Guangzhou 510642, China.

R. Keane, Missoula Fire Sciences Laboratory, Rocky Mountain Research Station, Missoula, MT 59808, USA.

J. Liu, S. Liu, and J. Oeding, U.S. Geological Survey Earth Resources Observation and Science Center, 47914 252nd St., Sioux Falls, SD 57198, USA. (sliu@usgs.gov)

Y. Luo, Department of Botany and Microbiology, University of Oklahoma, Norman, OK 73019, USA.

A. D. McGuire, U.S. Geological Survey, Alaska Cooperative Fish and Wildlife Research Unit, University of Alaska Fairbanks, Fairbanks, AK 99775, USA.

C. Potter, National Aeronautics and Space Administration Ames Research Center, Moffett Field, CA 94035, USA.

J. Tang, The Ecosystems Center, Marine Biological Laboratory, Woods Hole, MA 02543, USA.

R. Vargas, Departamento de Biología de la Conservación, Centro de Investigación Científica y de Educación Superior de Ensenada, Ensenada BC 22860, Mexico.

J. Xiao, Complex Systems Research Center, Institute for the Study of Earth, Oceans, and Space, University of New Hampshire, Durham, NH 03824, USA.

W. Yuan, College of Global Change and Earth System Science, Beijing Normal University, Beijing 100875, China.

S. Zhao, College of Urban and Environmental Sciences, Peking University, Beijing 100871, China.