Global Change Biology

Global Change Biology (2013) **19**, 2389–2400, doi: 10.1111/gcb.12224

Long-term changes in forest carbon under temperature and nitrogen amendments in a temperate northern hardwood forest

KATHLEEN E. SAVAGE*, WILLIAM J. PARTON†, ERIC A. DAVIDSON*,
SUSAN E. TRUMBORE‡ and SERITA D. FREY§

The Woods Hole Research Center, 149 Woods Hole Rd, Falmouth, MA 02540, USA, †Colorado State University, Fort Collins, CO 80523, USA, ‡Max Planck Institute for Biogeochemistry, 07745 Jena, Germany, §University of New Hampshire, Durham, NH 03824, USA

Abstract

Currently, forests in the northeastern United States are net sinks of atmospheric carbon. Under future climate change scenarios, the combined effects of climate change and nitrogen deposition on soil decomposition, aboveground processes, and the forest carbon balance remain unclear. We applied carbon stock, flux, and isotope data from field studies at the Harvard forest, Massachusetts, to the ForCent model, which integrates above- and belowground processes. The model was able to represent decadal-scale measurements in soil C stocks, mean residence times, fluxes, and responses to a warming and N addition experiment. The calibrated model then simulated the longer term impacts of warming and N deposition on the distribution of forest carbon stocks. For simulation to 2030, soil warming resulted in a loss of soil organic matter (SOM), decreased allocation to belowground biomass, and gain of aboveground carbon, primarily in large wood, with an overall small gain in total system carbon. Simulated nitrogen addition resulted in a small increase in belowground carbon pools, but a large increase in aboveground large wood pools, resulting in a substantial increase in total system carbon. Combined warming and nitrogen addition simulations showed a net gain in total system carbon, predominately in the aboveground carbon pools, but offset somewhat by losses in SOM. Hence, the impact of continuation of anthropogenic N deposition on the hardwood forests of the northeastern United States may exceed the impact of warming in terms of total ecosystem carbon stocks. However, it should be cautioned that these simulations do not include some climate-related processes, different responses from changing tree species composition. Despite uncertainties, this effort is among the first to use decadal-scale observations of soil carbon dynamics and results of multifactor manipulations to calibrate a model that can project integrated aboveground and belowground responses to nitrogen and climate changes for subsequent decades.

Keywords: ForCent, nitrogen, radiocarbon isotopes, soil warming, soil organic matter

Received 9 January 2013 and accepted 12 March 2013

Introduction

Temperate forests in the northeastern United States are currently a sink for atmospheric carbon due to forest regrowth after logging, however, under future climate change scenarios there is uncertainty in how this balance may change (Goodale *et al*., 2002). The enormous quantity of soil carbon that is susceptible to increased rates of decomposition with climate change has probably been underestimated (Tarnocai *et al*., 2009). Although estimates of global soil C stocks vary widely, it is clear that soils store several times more C than is present in the atmosphere as CO_2, and a significant fraction of soil C stocks are potentially subject to faster rates of decomposition in a warmer world. In addition to increasing global temperatures, it is expected that the deposition of reactive nitrogen, from fossil fuel combustion and agricultural fertilizer application, will continue over the next century (Galloway *et al*., 2004). From soil warming experiments, it has been clear that increased temperatures are linked to increases in soil decomposition (Czimczik & Trumbore, 2007; Contosta *et al*., 2011) and hence the release of soil carbon to the atmosphere through soil respiration. Observed increased aboveground vegetation carbon from soil warming studies indicates that there is an important change in the balance between release of carbon via soil decomposition and sequestration of carbon into aboveground biomass (Melillo *et al*., 2011). Results from nitrogen addition experiments have been mixed, showing increases, decreases, or no effect on soil organic matter (Waldrop & Firestone, 2004; Knorr *et al*., 2005; Cusack *et al*., 2010; Lavoie *et al*., 2011). Soil warming and nitrogen amendment studies focused on their individual effects on soil

Correspondence: Kathleen E. Savage, The Woods Hole Research Center, 149 Woods Hole Rd, Falmouth, Ma 02540. tel. 508-444-1542, fax 508-444-1742, e-mail: savage@whrc.org

and aboveground forest carbon; however, under future climate change scenarios, these factors are expected to interact (Pinder *et al.*, 2012), and hence the combined effects of temperature and nitrogen change on soil decomposition processes and the forest carbon balance remain unclear.

Soil organic matter is comprised of many substrates, which vary in degree of lability and in degree of physical and chemical protection from decomposition processes (Davidson *et al.*, 2006; Conant *et al.*, 2011). This variation results in a large range of mean residence times of soil organic matter (SOM) substrates, from years to millennia. Increases in temperature are linked to increased decomposition rates of SOM, but SOM response to temperature may differ depending on the temperature sensitivity of decomposition of each SOM pool and whether the substrates in each pool are accessible to, or physically and chemically protected from microbial enzymatic activity (Davidson *et al.*, 2006; Conant *et al.*, 2011). Soil respired C is a combination of belowground decomposition of organic matter (heterotrophic respiration) and root and rhizosphere respiration (autotrophic respiration). Often there is an initial spike in soil CO_2 efflux in the years following initiation of a soil warming treatment; however, over prolonged warming, CO_2 efflux declines (Melillo *et al.*, 2002, 2011). Faster decomposition of soil carbon can also increase net nitrogen mineralization, resulting in short-term increased net primary productivity (NPP), (Janssens *et al.*, 2010; Melillo *et al.*, 2011).

The response to nitrogen additions includes changes in microbial community composition, which corresponds to short-lived increased decomposition rates for SOM pools with turnover times on decadal scales, whereas decreasing decomposition of complex SOM substrates with longer turnover times (Neff *et al.*, 2002; Frey *et al.*, 2004; Waldrop & Firestone, 2004). Over prolonged periods of amendments, nitrogen additions have also decreased rates of soil CO_2 efflux (Bowden *et al.*, 2004; Janssens *et al.*, 2010), likely the result of changes in microbial community composition, changes in microbial enzyme production, and decreased allocation of carbon to roots and the rhizosphere (Frey *et al.*, 2004; Pillips & Fahey, 2007). An increase in aboveground biomass over prolonged nitrogen amendments was reported for a temperate hardwood forest in New England (Magill *et al.*, 2004).

Radiocarbon (^{14}C) measurements of both respired carbon and in SOM fractions are an effective tool for identifying soil carbon sources for soil respiration (autotrophic and heterotrophic) and for determining the mean residence times (MRTs) of multiple SOM pools. Gaudinski *et al.* (2000) used this methodology to develop a six-pool, steady-state, belowground carbon budget for the Harvard forest based on annual estimates of litterfall, soil respiration, fine root biomass, soil C fractionation, ^{14}C of soil C pools, and soil $^{14}CO_2$ efflux. This multiple SOM pool model is based on the concepts of the original CENTURY model (Parton, 1987). Gaudinski estimated that <10% of the soil C stock has a MRT of <10 years, and most of this rapidly cycling C is in the litter layer. Often called the 'fast' pool, this soil C cycles on annual timescales and dominates the heterotrophic component of soil respiration. It can respond rapidly when inputs or decomposition rates change, but because it represents a small fraction of C stored in soil, changes in this pool have only modest effects on total soil C stocks. At the other extreme, nearly half of the soil C is associated with mineral surfaces and has depleted ^{14}C signatures, indicating that it has a MRT of several hundred years or more. This so-called 'passive' pool turns over so slowly that it is mostly irrelevant for modern carbon budgets. Between these two extremes is the decadal-cycling pool, often called the 'slow' pool because it turns over slowly, but at timescales (decades) that are relevant to human lifetimes and to current climate change mitigation. Gaudinski *et al.* (2000) estimated that the fraction of decadal-cycling soil C makes up about half of the soil C stock at the Harvard forest and has a MRT of 30–80 years. Responses of this decadal soil C pool to decadal-scale changes in climate, nutrient inputs, and management could result in important feedbacks to the global carbon cycle.

The decadal predictions of changing radiocarbon signatures of SOM and CO_2 efflux of Gaudinski *et al.* (2000) based on sampling and modeling of soil carbon pools in 1996 were validated by Sierra *et al.* (2012) using soil and gas samples collected again from the same site in 2007. Sierra *et al.* (2012) also challenged Gaudinski's model with data from a nearby field manipulation experiment of soil warming and nitrogen addition. The model was able to represent belowground C pool cycling at decadal timescales for control plots and for warming and nitrogen addition treatments in the organic soil pools. Although the model was unable to capture some of the short-term response of SOM in mineral soil horizons to temperature and nitrogen treatments, it was able to represent most of the observations from the field manipulation experiment with respect to fluxes and radiocarbon signatures.

The DayCent model (Del Grosso *et al.*, 2001) is a daily time-step version of the original CENTURY model (Parton, 1987). The ForCent model (Parton *et al.*, 2010) is a modification of the DayCent model for use in forests. Although it shares with the Gaudinski model the same CENTURY heritage of a multipool soil C cycling model, the ForCent model also links above- and belowground processes, allows for changes in inputs to soil carbon pools, and is not constrained by the assumption of steady-state conditions.

Estimated SOM pools from the Gaudinski model, along with long–term, eddy covariance measurements at the Harvard forest, were used to parameterize and improve the ForCent model. Once the model was parameterized for Harvard forest, field observations and model-based activities were conducted to examine how manipulations of soil temperature and nitrogen supply affect above- and belowground responses, the relative age of soil C substrates that are respired, and the overall changes to the forest carbon balance. The ForCent model results were compared with those of Sierra *et al.* (2012), which utilized the same set of radiocarbon data from the Harvard forest, to examine the model output between a simple mixing model to a more complex integrative model structure like ForCent.

Materials and methods

Site description

At the Harvard forest, near Petersham, Massachusetts USA (42°32′N, 72°11′W), we have been studying a well-drained mixed hardwood forest since 1995. This forest is approximately 70 years old and the dominant tree species is red oak. Soils are classified as Canton fine sandy loam, Typic Distrochrepts. Most of this area was cleared for grazing in the late 19th century then abandoned in the early 20th century. In 1938 a hurricane leveled most of the regrown forest. The mean annual temperature is +8.5 °C, and the mean annual precipitation is 1050 mm. See Compton & Boone (2000) and Savage & Davidson (2001) for further descriptions. This site is located within the foot print of an eddy covariance tower which has been running since 1991.

Long-term soil carbon efflux monitoring site field data

The methodologies and carbon isotope data presented in this manuscript have been published previously. The methods will be briefly described here, with references to the original studies for further details.

Soil temperature and moisture. At the Harvard forest, soil pits (<50 m from the eddy covariance tower) were excavated to a depth of 60 cm and Campbell Scientific Water Content Reflectometry probes (CS615) were installed at 5, 9, 26, and 55 cm. Within this same pit, soil temperature was measured (type T-thermocouple) at the same depths as the moisture probes. Since 1996, soil temperature and water content have been measured at half-hourly intervals and data were stored on a Campbell Scientific CR10X datalogger (Campbell Scientific, Logan, UT, USA).

During the excavation of these pits in 1996, soil samples were collected and analyzed for radiocarbon in organic matter fractions (Gaudinski *et al.*, 2000; Gaudinski, 2001). Methods for radiocarbon analysis are presented below.

Annual leaf litter. Aboveground litter inputs (<50 m from eddy covariance tower) were measured in six 0.41 × 0.41 m baskets. Samples were collected biannually, dried and weight. Annual litterfall was the average sum of these biannual collections – i.e., the late fall collection of 2007 was added to the spring collection of 2008 to estimate the annual litterfall for 2007. Annual litterfall has been collected from 1996 through 2009, with one missing year of 2005.

Soil respiration. Manual measurements of soil respiration, using a vented, flow-through, non–steady-state system (Hutchinson & Livingston, 2001), were made weekly in the spring–summer–fall, and monthly during the winter. Respiration measurements were made <50 m from the eddy covariance tower. Soil respiration was measured using a Licor 6252 portable Infrared Gas Analyzer (IRGA, Lincoln, NE, USA) mounted on a backpack frame. For a more complete description of these measurements see Savage & Davidson (2001). To calculate annual C respiration, fluxes were linearly interpolated between sampling day and then summed over the entire year. Soil respiration has been continually collected at this site from 1995 through 2010.

Soil respired ^{14}C. Samples for isotopic measurements in soil CO_2 efflux were collected from soil respiration chambers (described above) that enclosed air headspace in contact with the soil surface using a closed dynamic chamber system to collect accumulated CO_2 in stainless steel traps. Details about the method are presented in Gaudinski *et al.* (2000) and Sierra *et al.* (2012). All measurements of respired ^{14}C are also presented in the Sierra *et al.* (2012) manuscript.

Radiocarbon in organic matter fractions. Soil samples were collected in 1996 from the soil pits described above and analyzed for radiocarbon. In 2007, three new soils pits were dug at locations within 1–5 m of the original soil pits sampled in 1996 by J. Gaudinski for analysis of radiocarbon organic matter fraction (Sierra *et al.*, 2012). Soils were sieved (to <2 mm), and large roots removed. Treatment of soil samples and isolation of fractions were the same as reported in Gaudinski *et al.* (2000) and Sierra *et al.* (2012). Data are reported as the average of the three replicates, the error bar represents the standard deviation. Radiocarbon measurements are reported as $\Delta^{14}C$ values (Stuiver & Polach, 1977), the deviation of the $^{14}C/^{12}C$ ratio in the sample (SN) from the $^{14}C/^{12}C$ ratio value of oxalic acid decay corrected (ABS). These same measurements of organic matter fractions used in this manuscript are also presented in Sierra *et al.* (2012).

Forest–atmosphere carbon and water exchange. Net ecosystem exchange (NEE), gross primary productivity (GPP), total ecosystem respiration (TER), and actual evapotranspiration (AET) data for Harvard forest 1992 through 2010 were obtained from the Ameriflux web site http://ameriflux.ornl.

gov/. AET was calculated from the available latent heat flux using a conversion algorithm (Senay, 2008).

Soil warming and nitrogen addition treatments. A soil warming and nitrogen addition experiment, located 250 m SW of the eddy covariance tower, was initiated at the Harvard forest in 2006 (Contosta *et al*., 2011). The experiment consists of six replicates of four treatments; control (C), heated (+H), nitrogen (+N), and heat + nitrogen (+HN). Heating began in August 2006. Soil temperatures in the heated plots are continuously elevated 5 °C above ambient and for the fertilized plots an aqueous solution of NH_4NO_3 is applied at a rate of 50 kg N ha^{-1} yr^{-1}. Soil respiration from these plots was measured ($n = 24$, 6 per treatment) biweekly throughout the year, whereas $^{14}CO_2$ was measured (3 samples per treatment) several times during the summer months from 2006 to 2010. For a more complete description of this study see Contosta *et al.* (2011). Annual estimates of soil efflux from these treatments (2007–2009) were calculated by linearly interpolating between sampling dates and summing over the year. Radiocarbon measurements in this experiment followed the same protocol as in Sierra *et al*. (2012).

The soil respiration measurement method at the long-term site (which was used to parameterize the ForCent model) utilized a dynamic flow-through system, whereas the method used at the soil warming and nitrogen addition site used a static chamber method (see Contosta *et al*., 2011). It has been shown that the static chamber method underestimates soil respiration (Heinemeyer & McNamara, 2011). To standardize between these two methods, soil respiration at the warming and nitrogen addition sites was measured on the same sampling date (July 22, 2008) using both methods. A linear regression of soil respiration between the two methods showed that the static chamber method underpredicted soil C efflux relative to the dynamic chamber method ($y = 0.64 \times -32.1$, $R^2 = 0.86$, where y = soil respiration using static chamber and x = soil respiration using dynamic chamber). To standardize between methods we adjusted all measured soil respiration from the static chamber method using this linear relationship.

ForCent model description

The DayCent model (Del Grosso *et al*., 2001) is a daily time-step version of the original CENTURY model (Parton, 1987). The ForCent model (Fig. 1) is a modification of the DayCent model for use in forests and includes the SIPNET photosynthesis model (Braswell *et al*., 2005; Sacks *et al*., 2006, 2007) which is a simplified Farquhar plant photosynthesis and respiration submodel, a forest plant growth model where carbon allocation is a function of plant phenology, and water and nutrient stress (Parton *et al*., 2010), the DayCent soil carbon and nutrient dynamics submodels (Parton *et al*., 2001), nitrogen and CH_4 trace gas flux submodels, (Del Grosso *et al*., 2000a,b), and detailed daily time-step soil water and temperature submodels (Parton *et al*., 1998; Eitzinger *et al*., 2000). Two of the major improvements included in the ForCent model include: (i) the addition of a detailed fine root growth submodel, and (ii) a detailed description of the surface organic matter dynamics which include the Oe/Oa organic layer (Parton *et al*., 2010). The detailed description of the surface organic matter dynamics is important for the Harvard forest as more than 60% of the fine root growth occur in the organic surface litter layer.

Initial inputs to the ForCent model included long-term precipitation and air temperature maximum and minimum

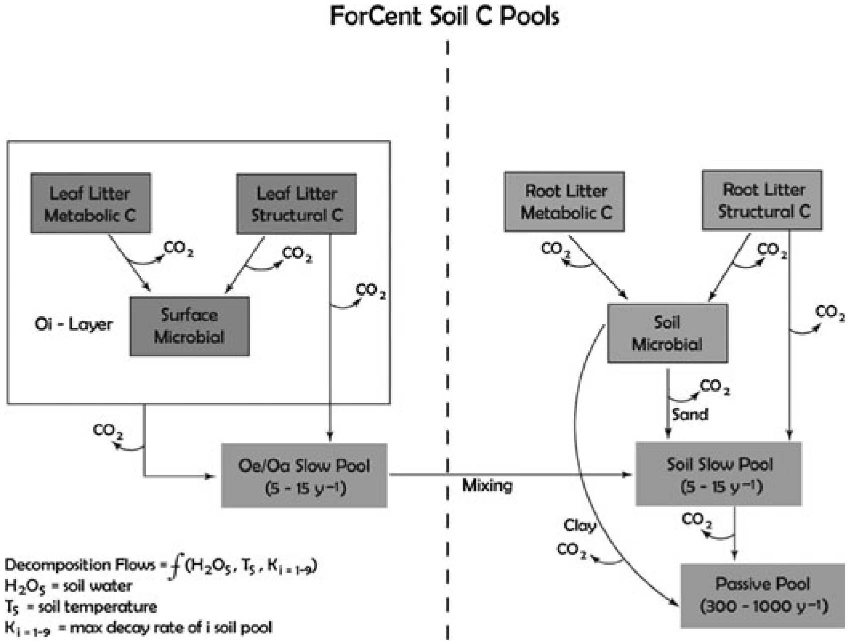

Fig. 1 Flow diagram for the surface organic and soil mineral soil layers in the ForCent model.

(Harvard forest met station), soil texture – including bulk density, sand, silt and clay, pH and soil depth (Davidson *et al.*, 1998) – estimated N deposition (5 kg N ha^{-1} yr^{-1}), and site latitude and longitude. Deciduous forest tree parameters values (Parton *et al.*, 2010) for the Harvard forest were used in model runs. Using these base site parameters, the model was spun up from time 0 through 2010 using the known land-use history of this area to produce a reasonable tree canopy and soil organic matter profile. See supplementary documentation (S1) for websites providing the ForCent model, model parameter files, and validation data used for this analysis.

Table 1 Soil temperature and moisture profile comparison of ForCent model vs. observed values

Variables	Observed	ForCent	R^2
Volumetric soil moisture*			
5 cm	0.32 (0.17–0.56)	0.35 (0.16–0.66)	0.06
10 cm	0.21 (0.06–0.38)	0.20 (0.10–0.32)	0.10
30 cm	0.18 (0.06–0.35)	0.15 (0.08–0.17)	0.18
Soil temperature†			
5 cm	9.2 (0.1–21.3)	9.4 (−0.3–23.7)	0.93
10 cm	9.2 (0.9–20.6)	9.4 (0.01–22.2)	0.94
60 cm	8.6 (3.5–16.5)	9.0 (3.9–14.7)	0.82

Mean (min. to max.) $n = 719$.
*Mean volumetric soil moisture comparisons only during the snow- and ice-free months 1996–2007.
†Mean soil temperature for 2008.
Note: only the top two measurements, which represent the most important depth for soil C activity and a lower depth soil temperature, are represented in this table for simplicity. R^2 is between observed and ForCent model results, $P = 0.48$ for VSM at 5 cm and $P < 0.001$ for all other comparisons.

Results

ForCent model calibration and validation

Observed soil temperature and moisture data were used to refine the belowground moisture and temperature distribution for a forest soil. Observed GPP and NEE data from the eddy covariance site were used to estimate photosynthesis and maintenance respiration parameters for the SIPNET submodel. ForCent model estimates of soil temperature and moisture distribution throughout the soil profile agreed well with observations (Table 1, $P < 0.001$) for all depths with the exception of 5-cm soil water content.

Gaudinski *et al.* (2000) estimates of soil organic matter pools were utilized to parameterize the belowground carbon pool submodel. As the ForCent and Gaudinski model carbon pools are not identical, SOM pools from the Gaudinski model were grouped to better reflect SOM pools in the ForCent model (Table 2). Although the ForCent model estimated a mineral active pool size 93% larger than the Gaudinski model, all other ForCent estimates of pool sizes were within 25% of the Gaudinski estimate. Figure 2 shows the belowground soil carbon pools, fluxes to the atmosphere, and transfers of carbon between carbon pools from the ForCent model run for an example year 1991.

In conjunction with the belowground carbon pools, observed respired ^{14}C measurements and ^{14}C of organic matter fractions were used to further constrain the belowground carbon pool submodel (Fig. 3). ForCent model respired ^{14}C agreed well for observed measurements (Fig 3a). Similarly for modeled Oi fraction ^{14}C.

Table 2 Soil organic matter carbon pool equivalents (g C m^{-2}) from the Gaudinski and the ForCent model simulation. Measured and model soil profile to 60 cm depth

SOM pool	Gaudinski *et al.* (2000) SOM Pools	ForCent SOM Pools	Gaudinski model estimate	ForCent
Organic layer	Oi, Oe + Oa (L_R), Oe + Oa (H)	Leaf litter structural C Leaf litter metabolic C Surface microbial Oe/Oa slow pool	2020	1493
Mineral active	A(L_R)	Root litter metabolic C Soil microbial	60	116
Mineral slow	A(H), Ap(H) Bw1(H), Bw2(H)	Root litter Structural C Soil slow pool	2615	2808
Passive	A(M), Ap(M), Bw1(M), Bw2(M)	Passive pool	4020	2979
Fine root biomass			255	194
Leaf litter			184	181

Pool sizes calculated from Table 2 in Gaudinski 2000 study.
ForCent SOM Pool descriptions see Fig. 1.

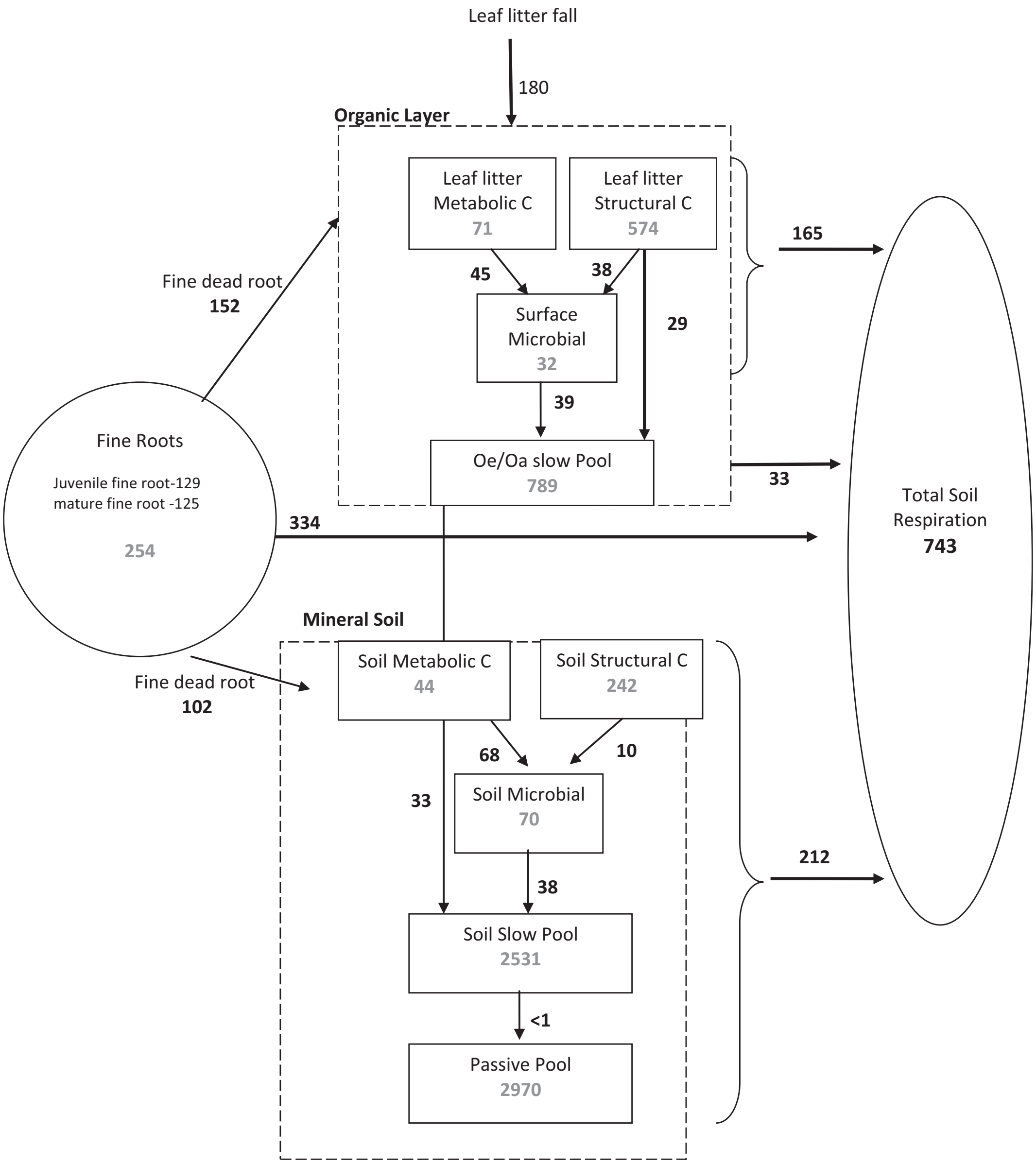

Fig. 2 Soil carbon pools, fluxes to the atmosphere, and transfers of carbon between belowground carbon pools for an example year 1991. Black – fluxes between pools; Gray – carbon pools.

However, there was a much larger discrepancy with the Oe fraction of observed vs. modeled ^{14}C. Some of the discrepancy between modeled and observed values may come from the difficulty in clearly separating out Oi and Oe soil fractions for analysis.

Once these submodels were constrained, annual estimates of NEE, GPP, and TER were analyzed and agreed reasonably well with observed estimates (Fig. 4). The overall R^2 between observed NEE and ForCent modeled NEE for 1992–2010 was $R^2 = 0.40$, with a range of R^2 values between 0.23 and 0.61 on a yearly comparison basis.

The final parameterized model was then run from 2006 through 2030 under control and treatment (+H, +N, and +HN) conditions as described in the soil warming and nitrogen addition experiment section, to assess how these treatments may affect the sources and age of respired belowground carbon and how they affect the overall distribution of carbon in the forest system.

Treatment effects on age of respired carbon

Although there was an overall increase in simulated respired carbon under +H treatments, the largest

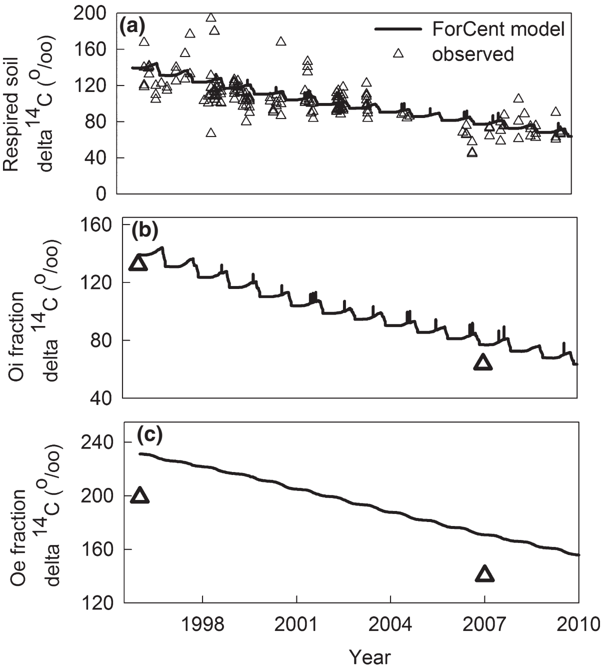

Fig. 3 Modeled and observed (a) respired ^{14}C, (b) Oi fraction, and (c) Oe fraction. Observed measurements also presented in Sierra *et al.* (2012). Small spikes in modeled ^{14}C is the result of short 'pulses' of soil decomposition related to precipitation events.

response being in the first 2 years following treatment application, this increase primarily came from increased simulated heterotrophic respiration and subsequent decline in simulated autotrophic respiration (Fig. 5a). Initially, in the first year there is an approximate 10% increase in simulated respired C, which declined in subsequent years and levels off after 4 years to a consistent 5% above the control. There is little consistent change in simulated annual soil carbon efflux from the +N treatment (Fig. 5b). The +HN treatment (Fig. 5c) showed the greatest increase in simulated soil respired carbon compared with control, most evident in the first year following initiation of treatment, with the bulk of this response coming from simulated heterotrophic respiration. With continuation of the treatments, differences between simulated control and the +HN treatment decline and stabilize. Overall there is an initial increase in respired C of about 20% due to the +HN treatment, but that declines by 2010 and the net change is <10% (Fig. 5c). The net change in simulated soil R for each treatment shown in Fig. 5 equates to increases of 28–92 g C m^{-2} yr^{-1} for +H and 10–163 g C m^{-2} yr^{-1} for +HN. For the +N treatment there is an initial increase in soil respired carbon of 3–67 g C m^{-2} yr^{-1}, but from 2011 onwards there are inconsistent changes (Fig. 5b). The observed annual estimates of respired total soil carbon showed a large initial increase for +H and +HN treatments with a small increase initially in the +N treatment (Fig. 5).

Sierra *et al.* (2012) reported that there were no statistically significant differences in respired $^{14}CO_2$ among the control, warming, and nitrogen treatments. They concluded from this result that the initial increase in CO_2 efflux with warming could not be due only to a change in decomposition of the labile fraction that later becomes exhausted, but rather that decomposition of all SOM fractions must have responded to the warming. The ForCent model results are consistent with this result (Table 3). A small but not significant increase in the simulated radiocarbon values for the +H and +HN treatments is due to less simulated allocation of modern carbon to root respiration.

Treatment effects on total forest system carbon – ForCent model results

ForCent model simulation of +H, +N, and +HN treatments began in midsummer of 2006 and were applied continually from 2006 through 2030 to examine the potential long-term impacts on the above- and belowground forest carbon pools. Following the initiation of treatments, there was an increase in NPP for all three treatments (Fig. 6), with the greatest increase in the +HN treatment. NPP values stabilized quickly at consistently higher values than control even with continued application of treatments (Fig. 6a). Over the model run (2006–2030), the average increase in NPP (treatment – control) for +H was 0.63 Mg C ha^{-1} yr^{-1}, for +N was 2.2 Mg C ha^{-1} yr^{-1}, and for +HN was 2.2 Mg C ha^{-1} yr^{-1}.

There were continual small increases in aboveground litter production throughout the treatment period (Fig. 6b), although increases begin to stabilize after 15 years. Following initial increases in root biomass from fine roots (Fig. 6c) for the first 3 years following treatment initiation, root mass either declined below or near control levels. Large initial increases were simulated in both large wood and fine branch (Fig. 6d), but over prolonged continual treatment application the branch and wood biomass reached a new equilibrium. The addition of nitrogen was the key player in increasing NPP, primarily from increases in wood production.

Aboveground live carbon showed the greatest increase relative to the total system carbon (Fig. 7a and d) with the largest increase under +N and +HN amendments. Although there is a decrease in SOM with these treatments, with the largest decrease in the +H treatment, neither SOM nor changes in dead wood have large impacts (Fig. 7b and c; Table 4) on total system

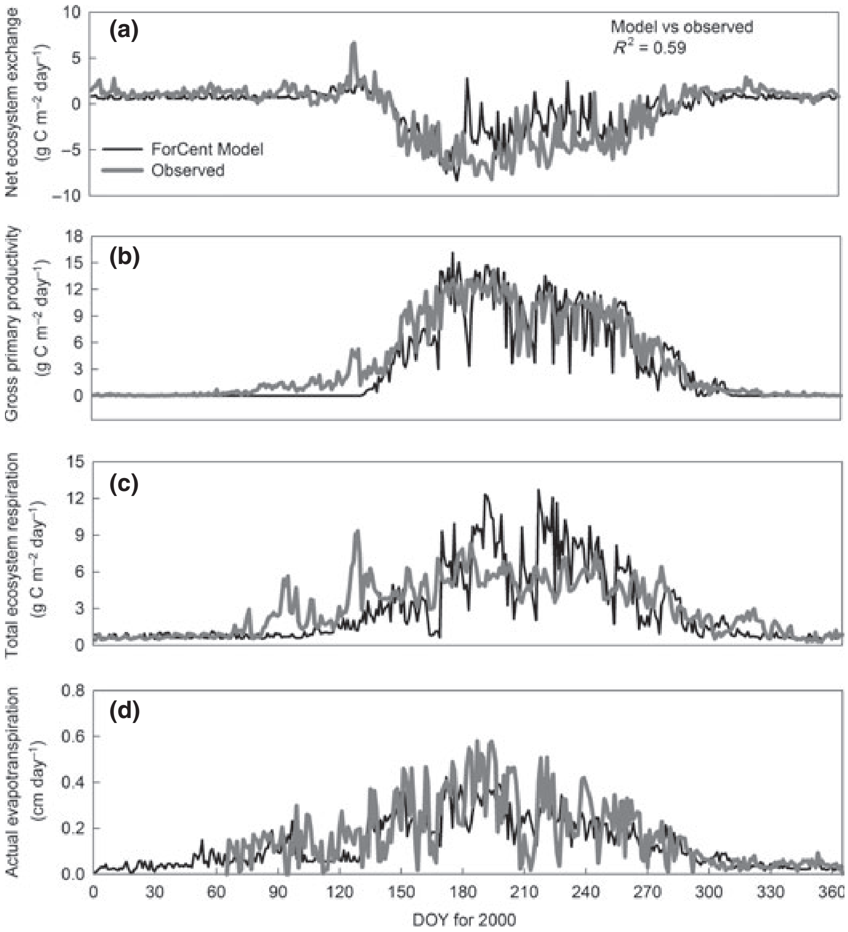

Fig. 4 Seasonal output for modeled and observed values for the year 2000. (a) Net ecosystem exchange, (b) gross primary productivity, (c) total ecosystem respiration, and (d) actual evapotranspiration.

carbon. The largest change in the total forest system carbon comes from increased nitrogen input and that change occurs in the wood and fine branch allocation within the aboveground live carbon (Table 4).

Discussion

The six-pool, steady-state Gaudinski *et al.* (2000) model provides a good representation of dynamics in belowground carbon cycling over decadal timescales in the SOM pools based on measured SOM fractions and their ^{14}C content (Sierra *et al.*, 2012). However, it is confined to soil processes and does not account for changes in C inputs to the soil due to changes in aboveground processes. We utilized the same data from Harvard forest as Sierra *et al.* (2012), but applied it to the ForCent model, which integrates both above- and belowground processes and allows changes in carbon stocks over time. The ForCent model was able to represent decadal-scale measurements in soil C stocks, mean residence times, and fluxes and responses to a warming and N addition experiment. The calibrated model was then used to simulate the longer term impacts of warming and N deposition on the distribution of forest carbon stocks.

For the ForCent model simulation from 2006 to 2030, the +H manipulation showed a loss of SOM, decreased allocation to belowground biomass, and gain of aboveground carbon, primarily in large wood and branch. Overall, the net change in the forest carbon structure was a small gain in total system carbon. This is consistent with other soil warming studies that have found a loss of SOM, corresponding increase in heterotrophic respiration greatest in the initial years after treatment, and a small increase in aboveground biomass (Melillo *et al.*, 2011). Melillo *et al.* (2011) determined the cumulative change (7 years) in vegetation carbon storage in heat plots was 7.0 Mg C ha^{-1}, equating to a yearly change of approximately 1.0 Mg C ha^{-1} yr^{-1}. The cumulative change in ForCent-simulated vegetation

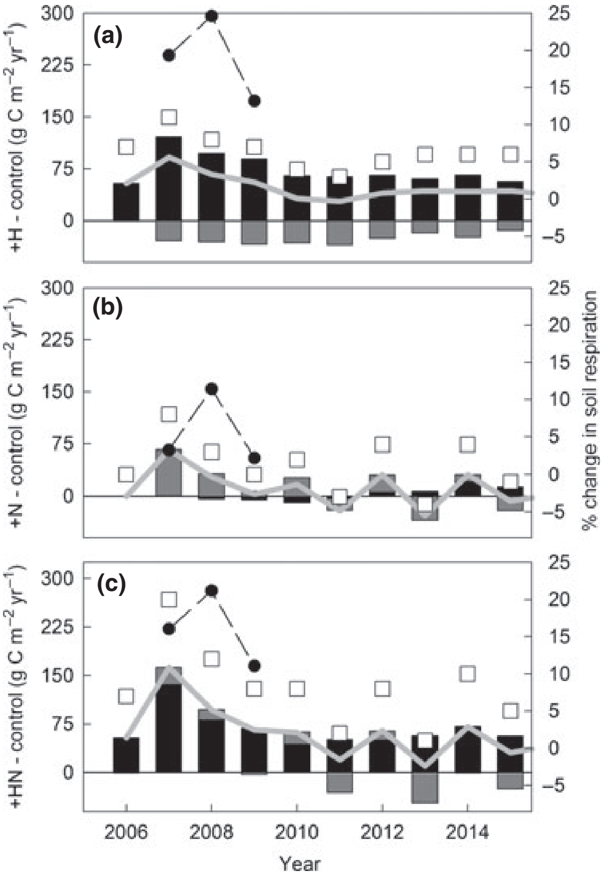

Fig. 5 Modeled treatment – control annual respired carbon for heterotrophic (black) and autotrophic (dark gray) components. Observed treatment – observed control annual respired total soil carbon (solid circles with dashed lines). Light gray line is the sum of heterotrophic and autotrophic components. Left-hand side *y*-axis for bars and lines. The white squares are the percentage (%) change between control and treatment and read on the right-hand side *y*-axis.

Table 3 Average change in respired delta ^{14}C for the entire sampling period (2006–2010) from observed data and ForCent-simulated results

Treatment	Observed Avg ^{14}C	Stdev	ForCent Modeled Avg ^{14}C	Stdev
C	74	13	83	11
+H	84	26	86	11
+N	72	10	84	9
+HN	78	11	86	11

Averages for observed average ^{14}C ($^{o}{}_{/00}$) values for all collars sampled across the entire summer sampling period (2006–2010). There are no statistically significant differences in measured control ^{14}C values and any of the treatment. To calculate the ForCent model average across the sampling period we used the monthly ^{14}C which corresponded to the same month for which observed ^{14}C was measured. The average ForCent was then calculated as the average of those same sampling dates from 2006 to 2010. The Stdev for both observed and modeled is across sample years.

carbon storage was 2.6 Mg C ha^{-1} for the first 7 years, corresponding to a rate of change of approximately 0.4 Mg C ha^{-1} yr^{-1}, a value smaller than that measured by Melillo *et al.* (2011). Melillo *et al.* (2011) based their estimate of belowground root growth on a percentage of aboveground biomass growth for determination of vegetation carbon storage. ForCent models above- and belowground processes separately and simulated a loss of belowground vegetation carbon due to warming (Table 4). This difference in methods may be one reason why ForCent estimated a lower vegetation carbon storage rate due to warming than observed by Melillo *et al.* (2011).

The +N manipulation showed a small simulated increase in belowground carbon pools, but large increase in aboveground pools, particularly evident in the large wood C allocation. The net effect being a substantial simulated increase, on a yearly basis, in total system carbon, dominated by increased aboveground biomass. Increased nitrogen additions to soils are linked to changes in microbial community structure, and a reduction in lignin-degrading enzymes (Frey *et al.*, 2004; Janssens *et al.*, 2010), corresponding to decreased decomposition, particularly of older more recalcitrant SOM. In a nearby chronic nitrogen addition experiment at the Harvard forest, where a hardwood stand has been receiving 50 kg N ha^{-1} yr^{-1}, (S. D. Frey, personal communication) found after 20 years with +N additions, there were observed increases in the organic soil pools of 0.24 Mg C ha^{-1} yr^{-1} and total aboveground vegetation increased to 0.34 Mg C ha^{-1} yr^{-1}. The ForCent +N model simulated a smaller increase in SOM pools of 0.05 Mg C ha^{-1} yr^{-1} and a much faster rate of aboveground vegetation storage of 1.53 Mg C ha^{-1} yr^{-1} compared to observations (Table 4). Although observed and modeled results agree on direction of change in vegetation carbon and SOM pools, the rates of change differ substantially. This is similar to our findings from ^{14}C comparison between observed and ForCent simulation, in which model and observed findings show directionally the same response, however, magnitudes differed, indicating that current sampling methodologies and modeling structures still need improvement. ForCent model includes, within its soil carbon submodel, estimated stable isotope of carbon from respired soils. Newly developed and deployed instrumentation for measuring stable isotopes from soil respired carbon *in situ* may provide the necessary information to improve ForCent model outcomes.

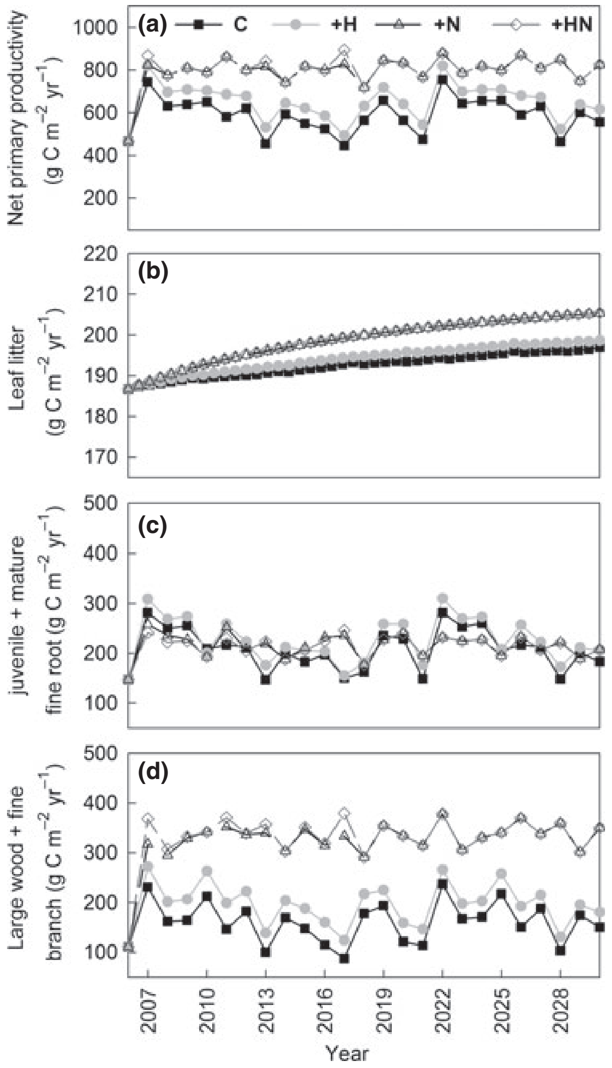

Fig. 6 Modeled annual accumulations of carbon for (a) net primary productivity, (b) leaf litter, (c) fine root biomass, (d) large wood ,and fine branch.

Table 4 Change in modeled system carbon (Mg C ha^{-1} yr^{-1}) with nitrogen and temperature manipulations. Change per year from 2006 through 2030

Carbon Pool	Heated	Nitrogen	Heat + Nitrogen
AG-Live	0.33	1.53	1.58
AG-Dead	−0.02	0.11	0.07
BG-Root	−0.04	0.02	−0.02
VLC (AG + BG)	0.29	1.55	1.56
SOM	−0.24	0.05	−0.24
Total system carbon	0.03	1.70	1.39

Changes determined by differencing treatment – control per year from 2006 through 2030 then taking the slope.

AG, aboveground; BG, belowground; VLC, vegetation live carbon; SOM, soil organic matter.

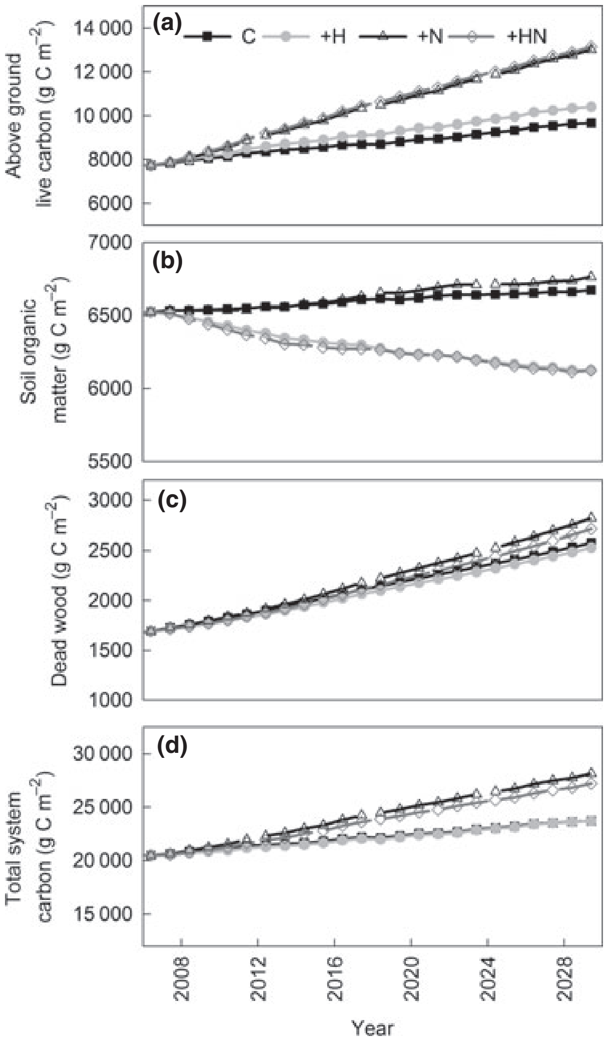

Fig. 7 Total system carbon: data are the average carbon from June of each year. (a) Aboveground live carbon, (b) soil organic matter (c) dead wood carbon, (d) total system carbon (all live, dead, and SOM pools).

Upon continuation of the +N treatment simulation, decreased allocation to root biomass corresponded to decreased autotrophic respiration. Decreased belowground biomass under +N may also be linked to decreased rhizosphere microbial activity; as with decreased roots, there would be less root-derived carbon exudates (Pillips & Fahey, 2007). Although studies have indicated that the addition of nitrogen to soils inhibits heterotrophic respiration (Janssens *et al*., 2010), ForCent model predictions showed almost no response of heterotrophic respiration to nitrogen additions over the long term.

It appears temperature has the larger influence on belowground carbon dynamics, nitrogen alone has only a relatively small effect on belowground SOM pools, but nitrogen additions stimulate aboveground biomass growth in this nitrogen-limited deciduous forest. The +HN simulation showed a net gain in total system carbon, predominately in the aboveground carbon pools, but offset somewhat by losses in SOM. Hence, the impact of continuation of anthropogenic N deposition on the hardwood forests of the northeastern United States is likely to exceed the impact of warming in terms of total ecosystem carbon stocks. However, it should be cautioned that there is uncertainty in the magnitude of the positive response of the aboveground biomass of hardwoods and that this response may not apply to the region's coniferous forests. S. D. Frey (personal communication) and Magill *et al.* (2004) found that the addition of nitrogen to a pine stand at the Harvard forest resulted in stand mortality, suggesting that nitrogen additions may stimulate growth in midsuccessional deciduous forests but not in all coniferous forests of this region.

In addition, it should be cautioned that these simulations do not include some climate-related processes, such as more frequent extreme droughts, precipitation events, frost and winter thaw events, different responses from changing tree species composition, and susceptibility to insects and diseases. Currently, forests in the northeastern United States are net sinks of atmospheric carbon, and it appears that the simulated effects of continued nitrogen deposition could increase carbon sequestration from the atmosphere to a larger extent than expected losses of soil carbon due to anticipated warming, provided that other climate responses not included in the model structure are not important.

Acknowledgements

We would like to thank Cindy Keough for her support with the ForCent model. This research was funded by the National Institute for Climate Change Research (NICCR) through the US Department of Energy (Cooperative Agreement Nos. DE-FC02-06ER64157 and DE-SC0007053). Partial funding for this study was supported by funds from the Oak Ridge National Lab. EBIS Ameriflux research project (No. DOE 5-339610). Any opinion, findings, and conclusions or recommendations expressed in this publication are those of the authors and do not necessarily reflect the views of the DOE.

References

Bowden RD, Davidson EA, Savage K, Arabia C, Stuedler P (2004) Chronic nitrogen additions reduce total soil respiration and microbial respiration in temperate forest soils at the Harvard Forest. *Forest Ecology and Management*, **196**, 43–56.

Braswell BH, Sacks WJ, Linder E, Schimel DS (2005) Estimating diurnal to annual ecosystem parameters by synthesis of a carbon flux model with eddy covariance net ecosystem exchange observations. *Global Change Biology*, **11**, 335–355.

Compton JE, Boone RD (2000) Long-term impacts of agriculture on organic matter pools and nitrogen transformation in central New England forests. *Ecology*, **81**, 2314–2330.

Conant RT, Ryan MG, Agren GI *et al.* (2011) Temperature and soil organic matter decomposition rates- synthesis of courrent knowledge and a way forward. *Global Change Biology*, **17**, 3392–3404.

Contosta AR, Frey SD, Cooper AB (2011) Seasonal dynamics of soil respiration and N mineralization in chronically warmed and fertilized soils. *Ecosphere*, **2**, 1–21.

Cusack DF, Torn MS, McDowell WH, Silver WL (2010) The response of heterotrophic activity and carbon cycling to nitrogen additions and warming in two tropical soils. *Global Change Biology*, **16**, 2555–2572.

Czimczik CI, Trumbore SE (2007) Short-term controls on the age of microbial carbon sources in boreal forest soils. *Journal of Geophysical Research-Biogeoscience*, **112**, 8–18. doi:10.1029/2006JG000389.

Davidson EA, Belk E, Boone RD (1998) Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. *Global Change Biology*, **4**, 217–227.

Davidson EA, Janssens IA, Luo YQ (2006) On the variability of respiration in terrestrial ecosystems: moving beyond Q(10). *Global Change Biology*, **12**, 154–164.

Del Grosso SJ, Parton WJ, Mosier AR, Ojima DS, Kulmala AE, Phongpan S (2000a) General model for N_2O and N_2 gas emissions from soils due to denitrification. *Global Biogeochemical Cycles*, **14**, 1045–1060.

Del Grosso SJ, Parton WJ, Mosier AR *et al.* (2000b) General CH_4 oxidation model and comparisons of CH_4 oxidation in natural and managed systems. *Global Biogeochemical Cycles*, **14**, 999–1019.

Del Grosso SJ, Parton WJ, Mosier AR (2001) Simulated interaction of carbon dynamics and nitrogen trace gas fluxes using the DAYCENT model. In: *Modeling Carbon and Nitrogen Dynamics for Soil Management*, (eds Schaffer M, Hansen ML), pp. 303–332. CRC Press, Boca Raton, FL.

Eitzinger J, Parton WJ, Hartman M (2000) Improvement and validation of a daily soil temperature submodel for freezing/thawing periods. *Soil Science*, **165**, 525–534.

Frey SD, Knorr M, Parrent JL, Simpson RT (2004) Chronic nitrogen enrichment affects the structure and function of the soil microbial community in temperate hardwood and pine forests. *Forest Ecology and Management*, **196**, 159–171.

Galloway JN, Dentener FJ, Capone DG *et al.* (2004) Nitrogen cycles: past, present and future. *Biogeochemistry*, **70**, 153–226.

Gaudinski JB (2001) *Belowground Carbon Cycling in Three Temperate Forests of the Eastern United States*. Ph.D.University of California at Irvine, Irvine.

Gaudinski JB, Trumbore SE, Davidson EA, Zheng S (2000) Soil carbon cycling in a temperate forest: radiocarbon-based estimates of residence times, sequestration rates and partitioning fluxes. *Biogeochemistry*, **51**, 33–69.

Goodale CL, Apps MJ, Birdsey RA *et al.* (2002) Forest carbon sinks in the northern hemisphere. *Ecological Applications*, **12**, 891–899.

Heinemeyer A, McNamara NP (2011) Comparing the closed static versus the closed dynamic chamber flux methodology: implications for soil respiration studies. *Plant and Soil*, **346**, 145–151.

Hutchinson G, Livingston G (2001) Vents and seals in non-steady state chambers used for measuring gas exchange between soil and atmosphere. *Eurasian Journal of Soil Science*, **52**, 675–682.

Janssens IA, Dieleman W, Luyssaert S *et al.* (2010) Reduction of forest soil respiration in response to nitrogen deposition. *Nature Geoscience*, **3**, 315–322.

Knorr M, Frey SD, Curtis PS (2005) Nitrogen additions and litter decomposition: a meta-analysis. *Ecology*, **86**, 3252–3257.

Lavoie M, Mack MC, Schurr EAG (2011) Effects of elevated nitrogen and temperature on carbon and nitrogen dynamics in Alaskan arctic and boreal soils. *Journal of Geophysical Research-Biogeosciences*, **116**, G03013. doi:10.1029/2010JG001629.

Magill AH, Aber JD, Currie WS *et al.* (2004) Ecosystem response to 15 years of chronic nitrogen additions at the Harvard Forest LTER, Massachusetts, USA. *Forest Ecology and Management*, **196**, 7–28.

Melillo JM, Steudler P, Aber JD *et al.* (2002) Soil warming and carbon-cycle feedbacks to the climate system. *Science*, **298**, 2173–2176.

Melillo JM, Butler S, Johnson J *et al.* (2011) Soil warming, carbon-nitrogen interactions, and forest carbon budgets. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 9508–9512.

Neff JC, Townsend AR, Gleixner G, Lehman SJ, Turnbull J, Bowman WD (2002) Variable effects of nitrogen additions on the stability and turnover of soil carbon. *Nature*, **419**, 915–917.

Parton WJ (1987) Analysis of factors controlling SOM levels in Great Plains grasslands. *Soil Science Society of America Journal*, **51**, 1173–1179.

Parton WJ, Hartman M, Ojima D, Schimel D (1998) DAYCENT and its land surface submodel: description and testing. *Global and Planetary Change*, **19**, 35–48.

Parton WJ, Holland EA, Del Grosso SJ *et al.* (2001) Generalized model for NOx and N2O emissions from soils. *Journal of geophysical Research*, **106**, 17403–17420.

Parton WJ, Hanson PJ, Swanston C, Torn M, Trumbore SE, Riley W, Kelly R (2010) ForCent model development and testing using the Enriched Background Isotope Study experiment. *Journal of Geophysical Research-Biogeosciences*, **115**, G04001. doi:10.1029/2009JG001193.

Pillips RP, Fahey TJ (2007) Fertilization effects on fineroot biomass, rhizosphere microbes and respiratory fluxes in hardwood forest soils. *New Phytologist*, **176**, 655–664.

Pinder RW, Bettez ND, Bonan GB, Greaver TL, Wieder WR, Schlesinger WH, Davidson EA (2012) Impacts of human alteration of the nitrogen cycle in the US on radiative forcing. *Biogeochemistry*, **115**, G04001. doi: 10.1007/s10533-012-9787-z

Sacks WJ, Schimel DS, Monson RK, Brawell BH (2006) Model-data synthesis of diurnal and seasonal CO_2 fluxes at Niwot Ridge, Colorado. *Global Change Biology*, **12**, 240–259.

Sacks WJ, Schimel DS, Monson RK (2007) Coupling between carbon cycling and climate in a high-elevation, subapline forest: a model-data fusion analysis. *Oecologica*, **151**, 54–68.

Savage KE, Davidson EA (2001) Interannual variation of soil respiration in two New England forests. Global Biogeochemical Cycles. *Global Biogeochemical Cycles*, **15**, 337–350.

Senay GB (2008) Modeling landscape evaportranspiration by integrating land surface phenology and a water balance algorithm. *Algorithms*, **1**, 52–68.

Sierra CA, Trumbore SE, Davidson EA, Frey SD, Savage KE, Hopkins FM (2012) Predicting decadal trends and transient responses of radiocarbon storage and fluxes in a temperate forest soil. *Biogeosciences*, **9**, 3013–3028.

Stuiver M, Polach HA (1977) Reporting of C-14 data–discussion. *Radiocarbon*, **19**, 355–363.

Tarnocai C, Canadell JG, Schuur EAG, Kuhry P, Mazhitova G, Zimov S (2009) Soil organic carbon pools in the northern circumpolar permafrost region. *Global Biogeochemical Cycles*, **23**, GB2023. doi:10.1029/2008GB003327.

Waldrop MP, Firestone MK (2004) Altered utilization patterns of young and old soil C by microorganisms caused by temperature shifts and N additions. *Biogeochemistry*, **67**, 235–248.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. Model file and validation data.