

# Modeling to discern nitrogen fertilization impacts on carbon sequestration in a Pacific Northwest Douglas-fir forest in the first-postfertilization year

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## Abstract

This study investigated how nitrogen (N) fertilization with 200 kg N ha<sup>-1</sup> of urea affected ecosystem carbon (C) sequestration in the first-postfertilization year in a Pacific Northwest Douglas-fir (*Pseudotsuga menziesii*) stand on the basis of multiyear eddy-covariance (EC) and soil-chamber measurements before and after fertilization in combination with ecosystem modeling. The approach uses a data-model fusion technique which encompasses both model parameter optimization and data assimilation and minimizes the effects of interannual climatic perturbations and focuses on the biotic and abiotic factors controlling seasonal C fluxes using a prefertilization 9-year-long time series of EC data (1998–2006). A process-based ecosystem model was optimized using the half-hourly data measured during 1998–2005, and the optimized model was validated using measurements made in 2006 and further applied to predict C fluxes for 2007 assuming the stand was not fertilized. The N fertilization effects on C sequestration were then obtained as differences between modeled (unfertilized stand) and EC or soil-chamber measured (fertilized stand) C component fluxes. Results indicate that annual net ecosystem productivity in the first-post-N fertilization year increased by ~83%, from 302 ± 19 to 552 ± 36 g m<sup>-2</sup> yr<sup>-1</sup>, which resulted primarily from an increase in annual gross primary productivity of ~8%, from 1938 ± 22 to 2095 ± 29 g m<sup>-2</sup> yr<sup>-1</sup> concurrent with a decrease in annual ecosystem respiration ( $R_e$ ) of ~5.7%, from 1636 ± 17 to 1543 ± 31 g m<sup>-2</sup> yr<sup>-1</sup>. Moreover, with respect to respiration, model results showed that the fertilizer-induced reduction in  $R_e$  (~93 g m<sup>-2</sup> yr<sup>-1</sup>) principally resulted from the decrease in soil respiration  $R_s$  (~62 g m<sup>-2</sup> yr<sup>-1</sup>).

**Keywords:** Douglas-fir, ecological modeling, ecosystem respiration, net ecosystem productivity, nitrogen fertilization, photosynthesis

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## Introduction

Global inputs to the terrestrial nitrogen (N) cycle have increased two- to fivefold (Vitousek *et al.*, 1997; Galloway & Cowling, 2002; Janssens *et al.*, 2010) in the past century mainly due to human activities, particularly fertilizer use and fossil fuel burning. N addition to forest and other ecosystems has been hypothesized to have a positive or negative effect on the health and vitality of ecosystems and the terrestrial carbon (C) cycle depending on the degree of ecosystem N saturation

(Aber *et al.*, 1989, 1993, 1998). Temperate and boreal forest ecosystems are generally N-limited and the N addition has been hypothesized to result in increasing C sequestration (Aber *et al.*, 1998). A range of studies has shown that the effects of N addition are positive on forest growth and also mostly positive on soil C sequestration in the Northern Hemisphere (e.g. Vitousek & Howarth, 1991; Aber *et al.*, 1995; Bergh *et al.*, 1999; Franklin *et al.*, 2003; Reay *et al.*, 2008; De Vries *et al.*, 2009; Liu & Greaver, 2009). Earlier modeling results suggested that N addition could account for an increased C sequestration of 0.44–0.74 Pg yr<sup>-1</sup> by simply assuming that most (80%) of the deposited N would be stored in plant tissues (Townsend *et al.*, 1996; Holland *et al.*, 1997) and these estimates have been questioned to be overestimated (Nadelhoffer *et al.*, 1999). Olsson *et al.*

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(2005) found that fertilization of a boreal Norway spruce stand led to a threefold increase in aboveground net primary productivity (NPP), possibly due to decreased C allocation to roots in response to higher nutrient availability. Leggett & Kelting (2006) found that N fertilization of Loblolly pine plantations not only increased living biomass but also increased the size of soil C pools. The contribution of an average additional N deposition on C sequestration in European forests and soils in the period 1960–2000 was estimated to be  $0.0118 \text{ G t yr}^{-1}$  by De Vries *et al.* (2006), being equal to  $\sim 10\%$  of their net C sequestration in that period ( $0.117 \text{ G t yr}^{-1}$ ). Pregitzer *et al.* (2008) also reported that chronic N deposition increased C storage in northern temperate forests. Magnani *et al.* (2007) even reported N deposition to be the dominant driver of C sequestration in forest ecosystem, which generated an intense debate about the magnitude and sustainability of the N-induced C sink and its underlying mechanisms (De Vries *et al.*, 2008; Sutton *et al.*, 2008; Janssens & Luysaert, 2009; Janssens *et al.*, 2010). However, other research results have shown that N addition to ecosystems had only a slightly positive effect on C sequestration (Nadelhoffer *et al.*, 1999) or had almost no contribution to C storage (Korner, 2000), or in some cases reduced NPP and C storage at very high N inputs (hypothesized due to N saturation, e.g. Aber *et al.*, 1989) or by other pollutants (e.g. acidification, Schulze, 1989). Bauer *et al.* (2004) reported that NPP and C sequestration may be enhanced when available N does not exceed the vegetation capacity for N uptake; otherwise, nutrient imbalances can lead to a decrease in C sequestration due to N saturation (Nihlgard, 1985; Agren & Bosatta, 1988). Aber *et al.* (1989, 1998) hypothesized that forest ecosystems respond positively to N addition in the short-term and negatively in the long-term. Variable effects of N addition/fertilization to soils on soil organic C storage have been also observed as a result of enhanced, reduced or unchanged soil respiration ( $R_s$ ) as a response to litter C/N ratio and/or a reduction in belowground allocation (Bowden *et al.*, 2000, 2004; Burton *et al.*, 2004; Cleveland & Townsend, 2006; Mo *et al.*, 2006, 2008; Phillips & Fahey, 2007; Hyvönen *et al.*, 2008).

Pacific Northwest coastal forests of the United States and Canada cover approximately  $10^5 \text{ km}^2$  between Oregon and Alaska and play a significant role in the global C cycle (Paw U *et al.*, 2004; Falk *et al.*, 2008; Chen *et al.*, 2009a). In this region, there is very little N deposition from air pollution sources owing to their remote location, and the soils are generally considered deficient in N (Hanley *et al.*, 1996). As a result, N fertilization is a common management practice in British Columbia (Brix, 1991; Fisher & Binkley, 2000; Chapin *et al.*, 2002; Brooks & Coulombe, 2009) with a standard forest

fertilization application rate of  $200 \text{ kg N ha}^{-1}$  from prilled urea at midrotation (Hanley *et al.*, 1996). N fertilizer-induced decreases in  $R_s$  would increase soil C storage (Johnson & Curtis, 2001; Phillips & Fahey, 2007). N fertilization has been reported to be the only forest management activity having positive effects on the soil C pools, presumably as a result of a reduction in  $R_s$  (Johnson & Curtis, 2001). Because additional merchantable timber volumes can result from fertilization of stands of midrotation trees (i.e. of commercial thinning size, 20–40 year-old), N fertilization just before harvest of near-end-of-rotation (50–60-year-old) Douglas-fir stands provides an attractive financial return with an average increase in bole volume growth of 20% (Hanley *et al.*, 1996). This effect must result from imbalance between N-fertilization induced changes in the two ecosystem processes, gross primary productivity (GPP), and ecosystem respiration ( $R_e$ ).

The objective of this study is to investigate how N fertilization affects ecosystem C component fluxes at daily, monthly, and annual time scales in the first year following N fertilization, in a coastal Douglas-fir forest in British Columbia, Canada. While eddy-covariance (EC) allows estimation of net C sequestration, it is different from traditional experiments directed to fertilization effects on stand growth. How to distinguish fertilization and climatic effects on C fluxes on the basis of EC measurements is a challenge. It is hard to find an area with similar land surface properties to set up a control EC tower because of high spatial heterogeneity of land surface. With absence of a control EC tower, a modeling approach to predict C fluxes for the fertilized year 2007 assuming the stand was not fertilized is necessary for discerning the impact of fertilization on C sequestration. In this study, we apply a data-model synthesis approach which encompasses both model parameter optimization and data assimilation. This type of approach has recently been shown to be a powerful tool for minimizing the uncertainties in the land surface C flux estimates due to model parameter biases and measurement errors (Raupach *et al.*, 2005; Sacks *et al.*, 2006; Mo *et al.*, 2008) and allows us to integrate EC measurements, available soil-chamber measurements and a previously published process-based ecosystem model [Boreal Ecosystem Productivity Simulator (BEPS), see Liu *et al.*, 2002; Ju *et al.*, 2006; Chen *et al.*, 2007a].

## Material and methods

### Site description

This investigation occurred at a near-end-of-rotation coastal Douglas-fir (*Pseudotsuga menziesii*) stand on the eastern side of Vancouver Island, BC, Canada. This area is in the very dry

maritime subzone of the coastal western hemlock (CWH) biogeoclimatic zone (Meidinger & Pojar, 1991). The CWH covers three million hectares in coastal and interior British Columbia, as well as parts of Alaska, Oregon, and Washington, USA.

The EC tower (namely DF49, 49°52'7.8"N, 125°20'6.3"W) was established in 1997. The previous Douglas-fir stand at this site was harvested and slash-burned in 1943, followed by planting of Douglas-fir seedlings in 1949 resulting in a relatively homogeneous stand. The current second-growth stand surrounding the tower covers an area of 130 ha ranging from 300 to 400 m above sea level, with 80% Douglas-fir, 17% western red cedar (*Thuja plicata*), and 3% western hemlock (*Tsuga heterophylla*). Further details on soil and vegetation characteristics can be found in Morgenstern *et al.* (2004), Humphreys *et al.* (2006) and Chen *et al.* (2009a, b).

### Stand fertilization

About 110 ha surrounding the DF49 tower (including the EC flux footprint area of about 70 ha, which contributed >80% of the cumulative fluxes observed at the tower; see Chen *et al.*, 2009b) was aerielly fertilized with urea at 200 kg N ha<sup>-1</sup> on January 13, 2007 using a Eurocopter SA315B helicopter (Western Aerial Applications Ltd, Chilliwack, BC, Canada) with an in-house engineered hydraulic-driven spreader bucket and a GPS-assisted guidance system (Jassal *et al.*, 2008). A nonfertilized area of about 17 ha (200 m × 850 m) on the southeast side of the fertilized area (500 m from the flux tower) served as a control for comparing differences in tree growth, C stocks, and C fluxes. The location of the control area was chosen to be outside of the 95% cumulated tower footprint area (Chen *et al.*, 2009b). Some of urea was retained in the snow-laden foliage on the day of fertilizer application, which was washed down to the ground surface with the melting of intercepted snow in the following days.

### Needle mass and N concentration and growth increment measurements

To assess the response to fertilization, the increase in size of the individual needles and the needle N content were measured and a preliminary tree ring analysis was made. In the end of 2007, the foliage samples and bole cores at diameter at breast height (DBH, 1.3 m) from five representative healthy dominant and codominant trees in both the fertilized and the control areas were collected. These trees had a mean DBH of 39 cm. Samples were collected from the upper (5/6th), middle (3/6th), and lower (1/6th) sections of the live crown of each tree. Current-year needles were carefully removed. The mass of 100 needles was determined for each of the trees. Dried needle samples were ground in an electric coffee grinder, digested in concentrated sulfuric acid, and analyzed for total N content using an autoanalyzer (Autoanalyzer II, Pulse Instrumentation Ltd, Saskatoon, SK, Canada). An image analysis system (model WINDENDRO, Regent Instruments Canada Inc., Nepean, ON, USA) was used to measure the annual ring widths to the nearest 0.01 mm. Allometric equations for coastal BC Douglas-fir were used to calculate mean annual (bole) increment (MAI) (Feller, 1992; Marshall & Turnblom, 2005).

### Climate and EC measurements

Details on the climate and EC measurements and analysis for the site can be found in Morgenstern *et al.* (2004), Humphreys *et al.* (2006) and Chen *et al.* (2009a). Half-hourly net ecosystem exchange (NEE) was computed as the sum of EC-measured CO<sub>2</sub> flux ( $F_c$ , positive upward) and the rate of change in CO<sub>2</sub> storage ( $S_c$ ) in the air column from the ground to the EC measurement height, i.e.  $NEE = F_c + S_c$ . Net ecosystem productivity (NEP) was calculated as  $NEP = -NEE$ .

The Fluxnet-Canada Research Network procedure for NEE gap-filling and partitioning of NEE into  $R_e$  and GPP (Barr *et al.*, 2004; Chen *et al.*, 2009a) was followed except for using a logarithmic transformation of an exponential ( $Q_{10}$ )  $R_e$ - $T_s$  model rather than using a logistic model (see Chen *et al.*, 2009a for additional details and rationale). The nighttime relationship between  $\log R_e$  vs.  $T_s$  obtained using half hours with friction velocity >0.35 m s<sup>-1</sup> (i.e. the threshold value) was used in gap filling and estimating daytime  $R_e$ . Random sampling of NEE error populations was used to determine the uncertainties in the annual sums of NEE. Each year was divided into 24 periods (12 months, day and night). Uncertainties in gap-filled half-hours were estimated by randomly drawing from the error population defined by half-hours with valid NEE observations. The mean difference between observations and estimates ( $NEE_{\text{observed}} - NEE_{\text{estimated}}$ ) was <1 g C m<sup>-2</sup> month<sup>-1</sup> and the random error in the estimates of annual NEP was found to be within  $\pm 30$  g C m<sup>-2</sup> (see also Morgenstern *et al.*, 2004; Schwalm *et al.*, 2007; Chen *et al.*, 2009a). Two systematic biases of the analytical procedure due to variation of the threshold of friction wind speed and correction for the lack of energy balance closure were investigated (Morgenstern *et al.*, 2004), the results showed no relative biases in annual sums of C fluxes for a single method between years. Standard errors (SE) of measured annual C component fluxes were calculated to be <50 g C m<sup>-2</sup> yr<sup>-1</sup> for GPP and 30 g C m<sup>-2</sup> yr<sup>-1</sup> for NEP and  $R_e$  following the method of Schwalm *et al.* (2007).

### Soil CO<sub>2</sub> efflux data used in this study

As part of a larger, ongoing soil respiration experiment (Jassal *et al.*, 2010b), consecutive series of half-hourly soil respiration ( $R_s$ ) data (2003–2007) measured using an automated closed-type CO<sub>2</sub> efflux chamber were available and used for model calibration and validation in this study.

### Modeling approach

**Model description.** The process-based ecosystem model BEPS used in this study is an updated version by coupling with a land surface scheme (Ecosystem Atmosphere Simulation Scheme, see Chen *et al.*, 2007a). It includes modules for photosynthesis, autotrophic respiration and live biomass allocation and soil C pools dynamics, soil biogeochemical and hydrological processes modules, and a scheme for the computation of energy balance, sensible and latent heat fluxes, soil water and soil temperature status (Ju *et al.*, 2006; Chen *et al.*, 2007a, b). In

the model framework, the canopy is stratified into overstory and understory layers, each of which is separated into sunlit and shaded leaf groups. A foliage clumping index, in addition to leaf area index (LAI), is used to characterize the effects of three-dimensional canopy structure on radiation, water, and C fluxes. In the soil hydrological processes module, snow packing and melting, rainfall infiltration and runoff, and soil vertical percolation are modeled. To estimate the vertical distribution of soil moisture and temperature, the soil profile is divided into seven layers and the thickness of the layers increases exponentially from the top layer to the sixth layer (0.05, 0.1, 0.2, 0.4, 0.8, 1.6 m, respectively). The first six soil layers with a total depth of 3.15 m are designed to ensure the complete simulation of energy dissipation in the soil column. The depth of the bottom soil layer is adjusted according to water table depth. Canopy fluxes of C, water, and energy are computed through stratification of the sunlit and shaded leaf components. A brief description of the processes directly related to photosynthesis and respiration is given in Appendix S1.

The time step of the model simulations is 30 min and model input data include atmospheric variables (temperature, relative humidity, wind speed, precipitation, and solar irradiance), vegetation type and stand age, canopy clumping index, soil texture and physical properties, and initial size of C pools.

*Model experimental design.* As discussed, our approach utilizes a model-data synthesis, which encompasses both model parameter optimization and data assimilation. To undertake the simulations and validate model predictions a data-model fusion technique was combined with an 8 years of EC-measured fluxes acquired at the DF49 site. We hypothesized that the underlying processes and multiyear seasonal patterns of C fluxes can be retrieved by assimilating a long time series of EC data into a process-based ecosystem model. The BEPS model was parameterized using the EC data obtained during 1998–2005. We assume that the optimized BEPS model captures the multiyear seasonal variations of C fluxes which we then tested by predicting C fluxes in 2006 and comparing them to actual observed data. Once we had confidence in the BEPS model parameterization we simulated 2007 fluxes with differences between the observations and simulations expected to be principally the result by the N fertilization.

*Model parameter optimization algorithm.* The ensemble Kalman filter (EnKF) data-model assimilation technique, known as a stochastic-dynamic system, was used in this study. The basis of the EnKF technique is that a previous measurement can provide information about the state at the current time (Mo *et al.*, 2008). The optimum values of the model parameters, therefore, are assumed to correspond to the minima of the cost function  $J(\mathbf{x})$  (Tarantola, 1987),

$$J(\mathbf{x}) = \frac{1}{2} \left[ (\mathbf{O} - \mathbf{Y}(\mathbf{x}))^T \mathbf{C}_o^{-1} (\mathbf{O} - \mathbf{Y}(\mathbf{x})) + (\mathbf{x} - \mathbf{x}_b)^T \mathbf{P}_b^{-1} (\mathbf{x} - \mathbf{x}_b) \right], \quad (1)$$

where  $\mathbf{x}$  is the vector of unknown parameters and  $\mathbf{x}_b$  is the a priori values of  $\mathbf{x}$ ,  $\mathbf{O}$  is the vector of observations,  $\mathbf{Y}$  is the nonlinear model (BEPS),  $\mathbf{C}_o$  is the covariance matrix of observations and  $\mathbf{P}_b$  is the covariance matrix of a priori para-

eters. Following Diego *et al.* (2007), we adopted a gradient-based algorithm which converges more rapidly than standard Monte-Carlo methods to solve Eqn. (1) for optimizing model parameters, typically converging to a minimum of  $J(\mathbf{x})$  within 100 iterations.

*Parameter selection and ensemble generation.* The ensemble size (the number of parameters and the size of the moving window) is an important parameter in EnKF, which represents the number of model states predicted and analyzed concurrently. The size should be large enough to ensure the correct estimate of the error variance in the predicted model state (Williams *et al.*, 2005). However, the very large ensemble size may be a heavy computation burden. Careful selection of which parameters are to be inversely optimized is required. To identify which parameters are most sensitive to photosynthesis and respiration, we analyzed the responses of parameters to predicted C component fluxes by random sampling of parameters within their possible ranges. Seven parameters (Table 1), which are significantly sensitive to photosynthesis and respiration, were selected to be optimized.

Based on a 9-year dataset analysis, Chen *et al.* (2009a) found that the seasonal variability of C component fluxes was significantly greater than their interannual variability. In addition, most ecological model parameters have been found to vary seasonally (Mo *et al.*, 2008). We therefore binned the 8-year dataset (1998–2005) into each calendar month with the ensemble size being the number of  $8 \times \text{days in a month} \times 48$  half-hourly data points per day. The selected parameters were optimized by minimizing the difference between observations and predictions, considering model and data uncertainties, and prior information on parameters. The model was then continuously run from the beginning of 1998 through to the end of 2007 at half-hourly time steps.

### Data analysis methods

Data analysis was conducted using MATLAB (the Mathworks Company). Linear regression analysis between the measured C component fluxes and the corresponding model outputs across half-hourly to monthly time scales was chosen to test model behavior. Root mean square error (RMSE) was used to estimate the model errors. The significance levels of differences between the two data series were detected using *t*-test. We determined the probability of significance, the *P*-value, using the *F*-test or *t*-test, at the significance levels of 0.05 or 0.01. We report the *P*-value and the coefficient of determination ( $r^2$ ). If the *P*-value was  $< 0.001$ , we only show it as  $P < 0.001$ .

## Results

### Comparison of measured environmental variables between pre- and postfertilization year

The climate variables (*P*, *T<sub>a</sub>*, *θ*, *D*, and *Q*) in 2007 followed seasonal patterns similar to those observed

**Table 1** Model parameters optimized for a 58-year-old Douglas-fir stand

| Parameter symbols | Parameter description   | Units                                    | Prior value | Optimized values |      |      |
|-------------------|---|--|-------------|------------------|------|------|
|                   |   |  |             | Range            | Mean | SD   |
| $V_{cmax}^{25}$   | Maximum carboxylation rate at 25 °C   | ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) | 35          | 15–100           | 56.8 | 6    |
| $J_{max}^{25}$    | Maximum electron transport rate at 25 °C                                      | ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) | 70          | 30–180           | 89.6 | 8    |
| $m$               | Slope of stomatal conductance   | –  | 6           | 3–14             | 7.3  | 0.5  |
| $D_0$             | Sensitivity of stomatal conductance to water vapor saturation deficit         | kPa                                      | 1.6         | 1.1–2.5          | 1.9  | 0.16 |
| $f_{stress}$      | Soil water stress dependency of the sunlit/shaded leaves stomatal conductance | –  | 0.5         | 0.05–1           | 0.44 | 0.27 |
| $Q_{10,s}$        | Temperature dependency of microbial respiration                               | ( $\text{K}^{-1}$ )                      | 2           | 1–6              | 3.6  | 0.5  |
| $Q_{10,m}$        | Temperature dependency of maintenance respiration                             | ( $\text{K}^{-1}$ )                      | 2           | 1–6              | 3.2  | 0.7  |

SD, standard deviation.

during the previous nonfertilized 9 years (Fig. 1). Compared with the 9-year means, annual total  $P$  was  $\sim 100$  mm higher; annual  $Q$  was about  $\sim 7\%$  lower, and annual average  $T_a$  was  $\sim 0.5$  °C lower in 2007, which was mainly due to a higher than normal occurrence of cloudy weather in the second half of the year (Fig. 1a, e). As a result,  $\theta$  in the 0–60 cm soil layer in 2007 was much higher than the previous 9-year means (Fig. 1c). According to Morgenstern *et al.* (2004) and Chen *et al.* (2009a), the weather conditions in 2007 would suggest a possible tree growth limitation due to low  $Q$ , and enhancement or reduction of  $R_e$  and  $R_s$  due to high  $\theta$  or lower  $T_a$ , respectively.

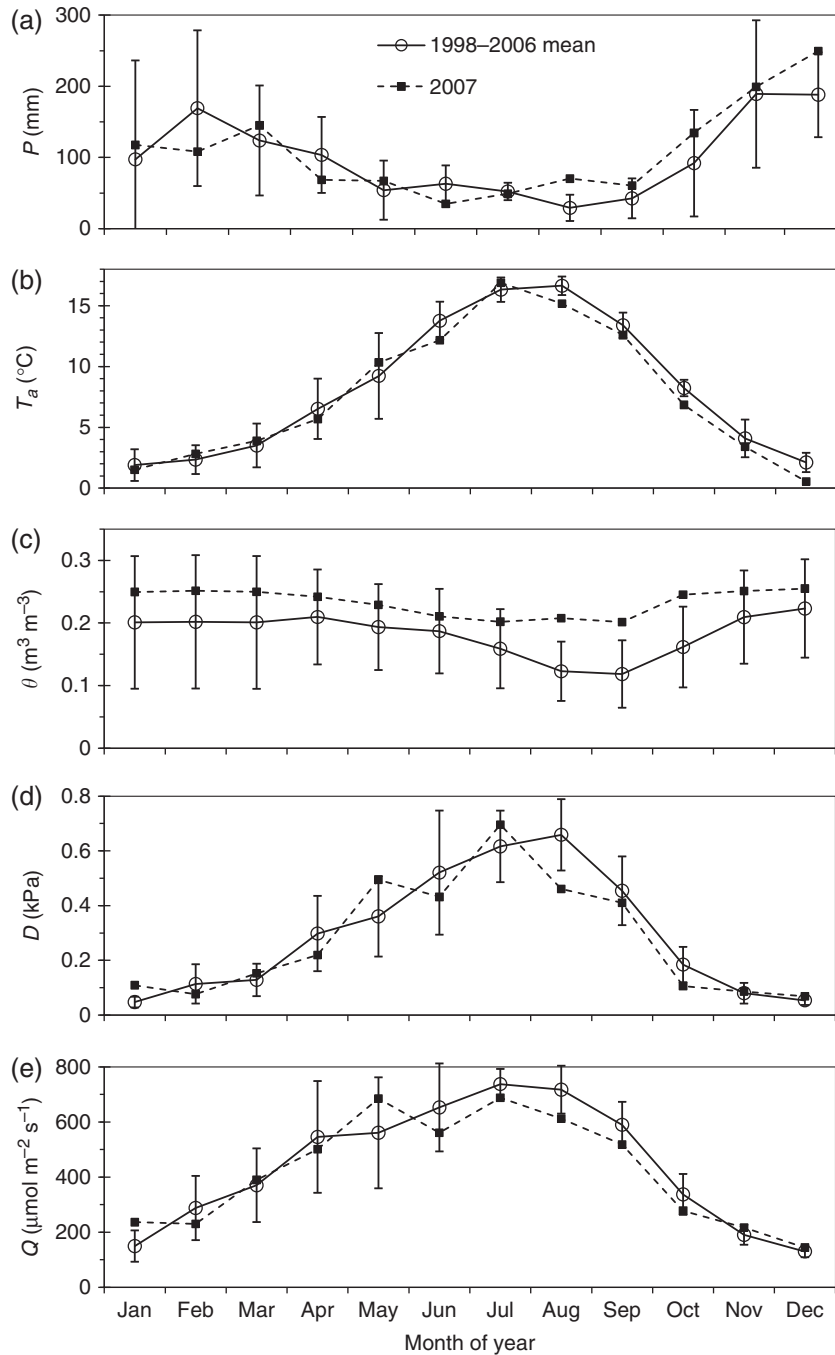
#### Comparison of measured C component fluxes between pre- and postfertilization year

Figure 2 compares the variations in the monthly values of C component fluxes in 2006 and 2007 with the mean values for 1998–2006. Overall, the monthly values of GPP in 2007 were close to the previous 9-year average values (Fig. 2a). However, the monthly  $R_e$  values in 2007 were similar to the previous 9-year averaged values before May but lower for May and the later months (Fig. 2b). The values of belowground ecosystem respiration (i.e. soil respiration,  $R_s$ ) values in 2007 were higher for January through May but lower for June, September and October compared with the 2003–2006 mean values (Fig. 2c). As a result, the monthly values of NEP in 2007 were higher than the 1998–2006 mean values during April to December (Fig. 2d). However, it is critical to recognize that besides N addition, environmental factors play an important role in C cycling processes. Climate perturbations may result in anomalies in C component fluxes.

As shown in Table 2, despite 2007 being wetter and cooler than previous years, annual NEP in 2007 was much higher than the average for the previous 9 years, while the  $R_e$ /GPP ratio for 2007 was lower than the 1998–2006 mean value because there was a much larger decrease in  $R_e$  than GPP.

#### Response of needle mass, N concentration, and growth increment to fertilization

The averaged N contents in current-year needles (averages of lower, middle, and upper sections of the live crown of each tree crown) in the unfertilized and fertilized trees were respectively 1.15% and 1.61% (dry needle basis). Foliar N analysis showed that the unfertilized trees were severely deficient in N (Ballard & Carter, 1986). As expected improved nutrition resulted in that foliar biomass increased from 445 to 559 mg per 100 dry needles on average. Tree ring analysis showed that fertilization resulted in higher annual growth increment. The annual bole diameter increments at the 1.3 m height during the first year following fertilization was 1.15 mm for the fertilized trees, which were significantly higher ( $P < 0.05$ ) than 0.78 mm for the trees in the control area, which is consistent with the modeled increases in GPP at this site. The fertilized-induced additional MAI was calculated to be 5.4 and 4.4  $\text{m}^3 \text{ha}^{-1}$ , respectively, following the method of Feller (1992) and using a growth-and-yield model of Marshall & Turnblom (2005). By assuming that Douglas-fir dry wood density is 450  $\text{kg m}^{-3}$  (Gartner *et al.*, 2002), the increase in stem wood biomass due to fertilization was further approximated to be 1980 to 2430  $\text{kg ha}^{-1}$ . We routinely measured LAI every growing season at eight plots at the research site. The measured LAI was about 7.3 ( $\pm 15\%$ ) over the past 10 years (Chen *et al.*, 2006) and

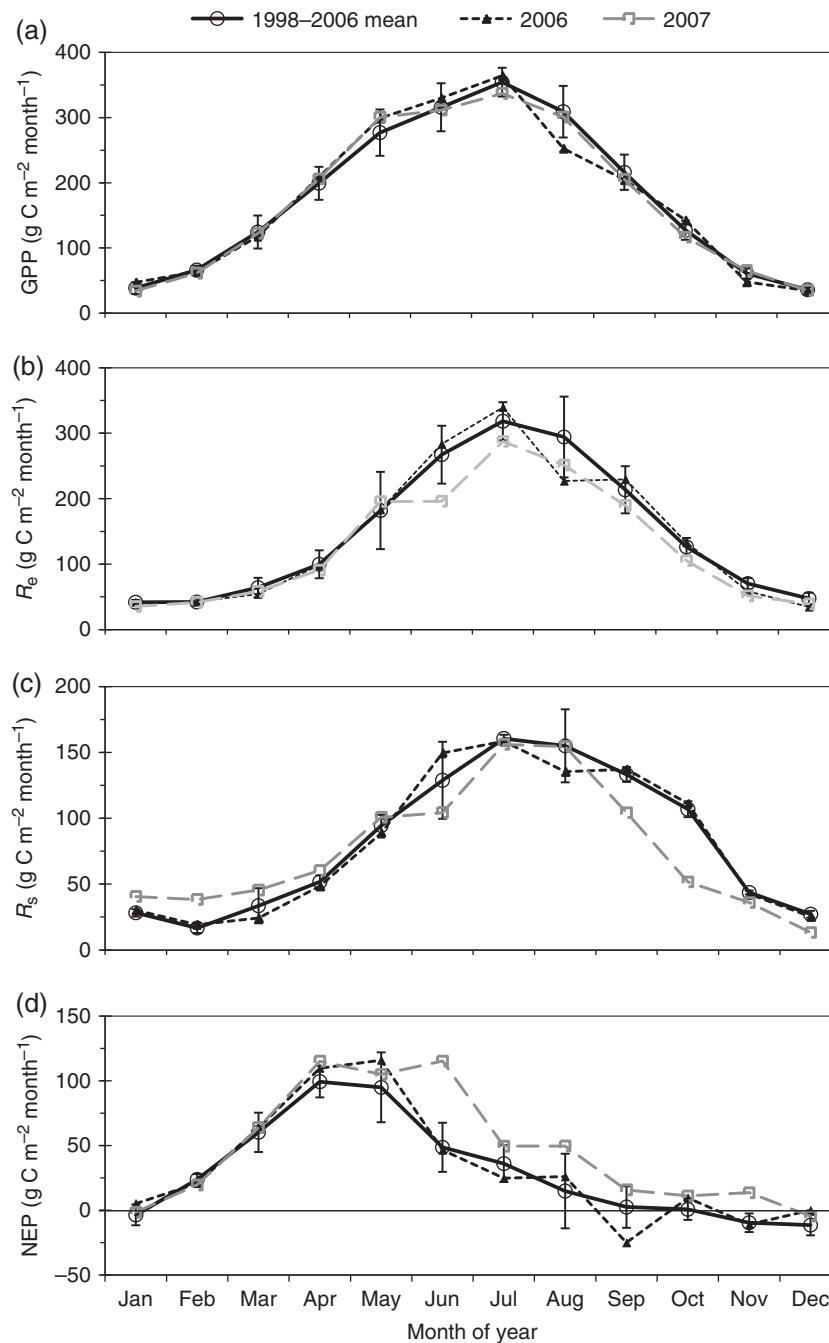


**Fig. 1** Comparison of monthly mean values of climatic and environmental variables measured at the 58-year-old West Coast Douglas-fir stand (DF49) for the fertilized year 2007 and for the 1998–2006 means. (a) Precipitation ( $P$ ), (b) air temperature above the canopy ( $T_a$ ), (c) 0–60 cm soil water content ( $\theta$ ), (d) water vapor saturation deficit above the canopy ( $D$ ), and (e) daytime total downward photosynthetically active radiation ( $Q$ ). The error bars are  $\pm 1$  SD for all the 9-year data (1998–2006).

no significant difference was found between before and after fertilization likely owing to the stage of near-end-of-rotation. We also found no significant change in fraction of absorbed photosynthetically active radiation after fertilization.

#### *Discerning N fertilization effects on C component fluxes using the optimized BEPS model*

The optimized BEPS model with inversed parameters was first calibrated using the EnKF applied 8-year data



**Fig. 2** Comparison of monthly mean values of component C fluxes measured at the 58-year-old West Coast Douglas-fir stand (DF49) for the fertilized year 2007, for the previous year 2006 and for the 1998–2006 means. (a) Gross primary productivity (GPP), (b) ecosystem respiration ( $R_e$ ), (c) belowground ecosystem (soil) respiration ( $R_s$ ), and (d) net ecosystem productivity (NEP). The error bars are  $\pm 1$  SD for all the 9-year data (1998–2006).

and further verified using the reserved nonfertilized data in 2006. Finally, the validated model was used to discern N fertilization impacts on C sequestration in 2007.

*Calibration and verification of the optimized BEPS model.* To evaluate the accuracy of the optimized BEPS model in

the prediction of the C component fluxes, the modeled results were calibrated and verified against the measurements made during 1998–2005 and during 2006, respectively. We also found the optimized parameters using 8-year-long dataset (1998–2005) and using 9-year-long dataset (1998–2006) are identical through a model

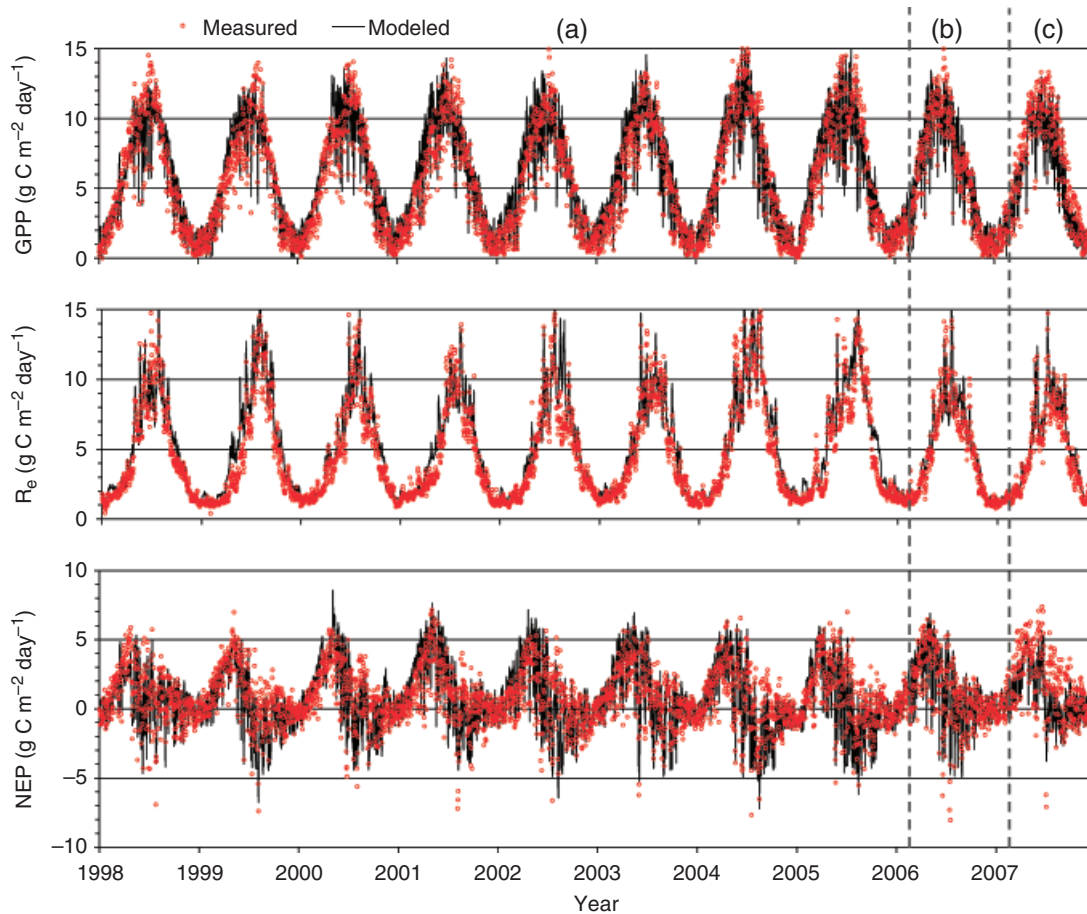
**Table 2** Comparison of measured annual C component fluxes between nonfertilization year (1998–2006) and the fertilization year (2007)\*

| NEP          |              | GPP            |               | $R_e$          |               | $R_e$ /GPP     |      |
|--------------|--------------|----------------|---------------|----------------|---------------|----------------|------|
| 1998–2006    | 2007         | 1998–2006      | 2007          | 1998–2006      | 2007          | 1998–2006      | 2007 |
| $356 \pm 51$ | $552 \pm 19$ | $2124 \pm 125$ | $2095 \pm 22$ | $1768 \pm 146$ | $1543 \pm 17$ | $0.8 \pm 0.03$ | 0.74 |

The  $\pm 1$  SD of annual values over 1998–2006 and the standard errors for the year 2007 estimated using the method of Schwalm *et al.* (2007) are also shown.

\*Urea at  $200 \text{ kg N ha}^{-1}$  applied on January 13, 2007.

GPP, gross primary productivity; NEP, net ecosystem productivity.



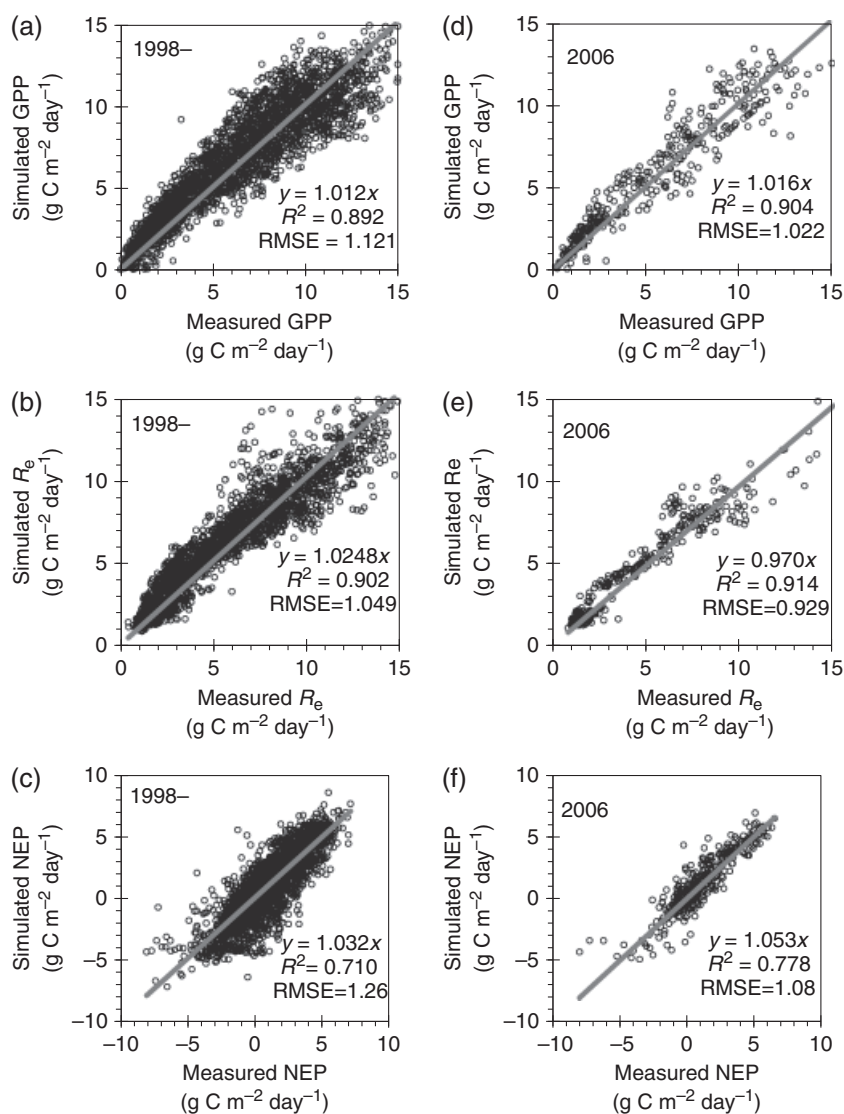
**Fig. 3** BEPS predicted and EC tower measured daily gross primary productivity (GPP), ecosystem respiration ( $R_e$ ) and net ecosystem productivity (NEP) at DF49 for 1998 to 2007, (a) for the EnKF applied years 1998–2005, (b) for the model validation year 2006, and (c) for the first-postfertilization year 2007. BEPS, Boreal Ecosystem Productivity Simulator; EC, eddy-covariance; EnKF, ensemble Kalman filter.

experiment, implying that the 8-year-long dataset is long enough to reveal the inherent seasonal relationship between the modeled C fluxes and the driving variables.

Comparisons of measured and BEPS-simulated daily GPP,  $R_e$ , and NEP for 1998–2005 are shown in Figs 3a and 4a–c. BEPS simulations explained about 89% of the variance of daily GPP, 90% of the variance of daily  $R_e$ , and 71% of the variance of daily NEP (Fig. 4a–c). Linear

regression analysis of simulated vs. measured daily values (Fig. 4a–c) indicated that the  $P$  value was  $<0.001$  for all C component fluxes; the slopes were 1.01, 1.02, and 1.03 for GPP,  $R_e$  and NEP, respectively, and RMSE values were  $1.12$ ,  $1.05$ , and  $1.26 \text{ g C m}^{-2} \text{ day}^{-1}$  for GPP,  $R_e$  and NEP, respectively. Figure 5a compares the modeled and chamber-measured values of  $R_s$ . Regression analysis for the available measured period (2003–2005) showed that  $P$  value  $<0.001$ ; slope = 0.98,





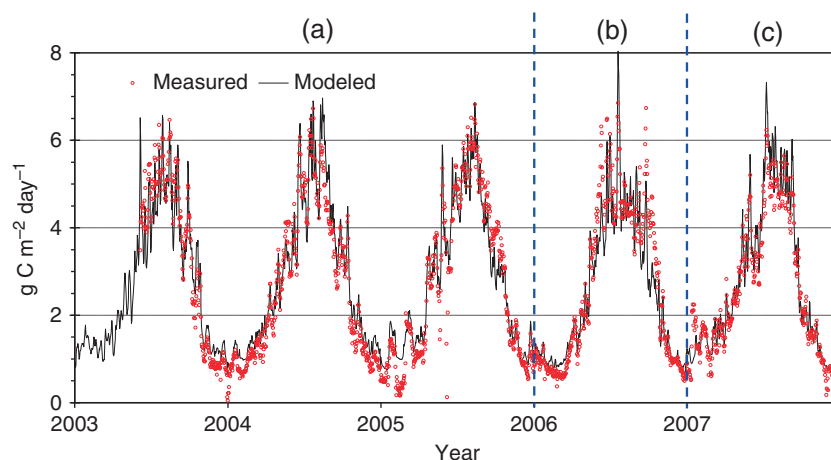
**Fig. 4** Comparison of BEPS predicted and EC tower measured daily gross primary productivity (GPP), ecosystem respiration ( $R_e$ ) and net ecosystem productivity (NEP) at DF49 for nonfertilized years, (a)–(c) for the EnKF applied years 1998–2005, and (d)–(f) for the validation year 2006. BEPS, Boreal Ecosystem Productivity Simulator; RMSE, root mean square error.

$r^2 = 0.91$ , and  $\text{RMSE} = 0.46 \text{ g C m}^{-2} \text{ day}^{-1}$ . These model results suggested that the BEPS model reasonably simulated both photosynthesis and respiration processes at a daily time step using the calibrated parameters.

Figure 6 and Table 3 compares measured and modeled annual sums of the C component fluxes. Linear regression results showed  $P < 0.001$ ;  $r^2 = 0.9$ , 0.98 and 0.95 for GPP,  $R_e$ , and NEP, respectively. Model biases (i.e. measured – modeled values) are significantly smaller ( $P < 0.01$ ) than the departures in C fluxes from their respective 1998–2006 means, suggesting BEPS reasonably captured interannual variations of observed C component fluxes.

Figure 7 compares modeled and measured half-hourly NEP for 3 separate weeks in 2006, which were

selected to show the model's performance in different phases of the growing season (early, middle, and late) and under different weather conditions (clear, cloudy, and rainy). Modeled half-hourly NEP followed the observations reasonably except the spikes in observations during some nights. Linear regression analysis for half-hourly NEP showed that  $P < 0.001$ ;  $r^2 = 0.76$  and  $\text{RMSE} = 4.56 \mu\text{mol m}^{-2} \text{ s}^{-1}$ . Data-model plots of daily C fluxes and linear regression results are shown in Fig. 4d–f, which are similar to data-model comparisons for the model calibration period 1998–2005 (Fig. 4). Relative annual model biases for 2006 were  $-0.9\%$ ,  $-1.7\%$  and  $2.9\%$  for GPP,  $R_e$ , and NEP are similar to the respective values for 1998–2005 (Table 3). After verification against measurements at half-hourly to



**Fig. 5** BEPS predicted and measured daily soil respiration ( $R_e$ ) using an auto-chamber at DF49 (a) for the EnKF applied years 2003–2005, (b) for the model validation year 2006, and (c) for the first-postfertilization year 2007. BEPS, Boreal Ecosystem Productivity Simulator; EnKF, ensemble Kalman filter.

annual time scales, we have confidence that the BEPS model with the optimized parameters performed well in predicting C component fluxes.

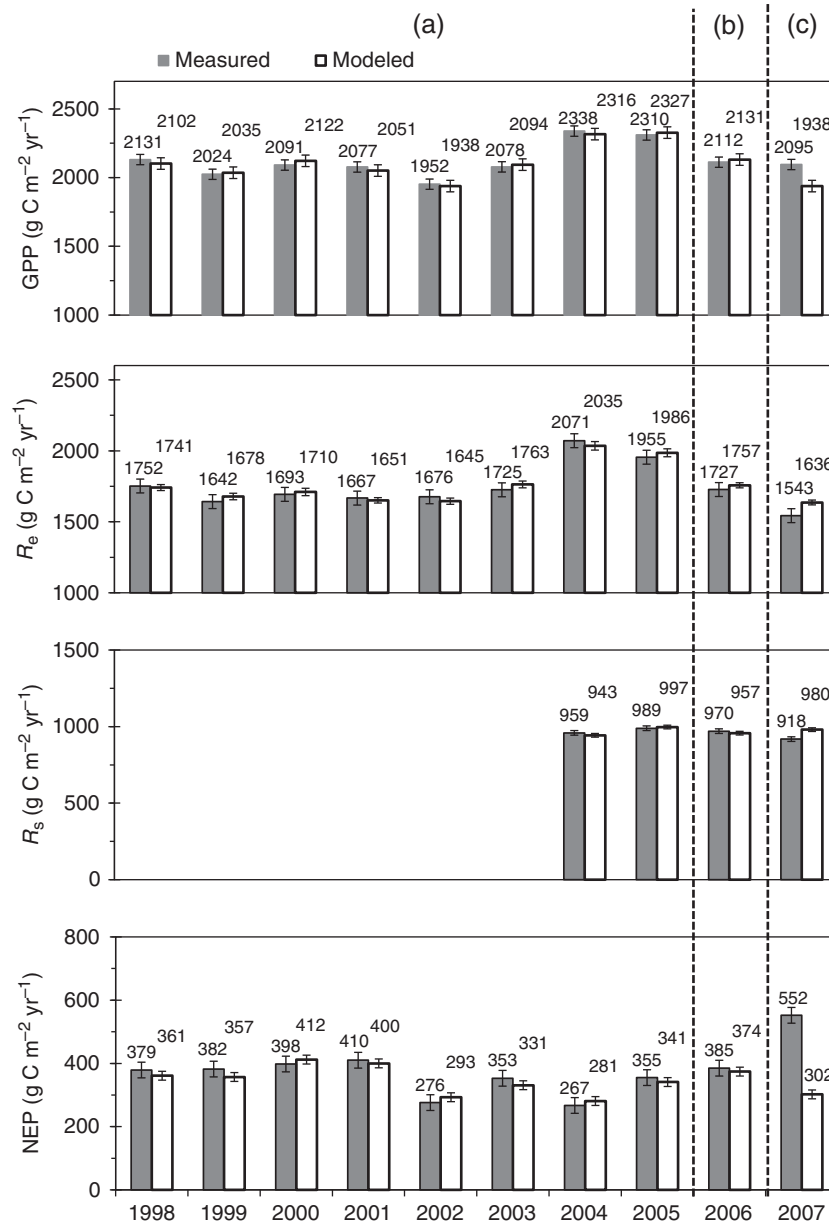
*Discerning N fertilization impacts.* After optimization, BEPS was applied to predict C fluxes for 2007 assuming the stand was not fertilized. The N fertilization impacts in 2007 were then obtained as differences in C component fluxes between measured (fertilized) and the predicted values (unfertilized). As shown in Figs 3–6 and 8, the differences between modeled and measured C component fluxes at different time scales in 2007 were significantly larger than that in other unfertilized years (student *t*-test showed the regression slopes for 2007 were significantly different from all other years with  $P < 0.01$ ). BEPS modeled daily values were lower than measurements for GPP (Fig. 8a, slope of predicted vs. observed = 0.88) and higher for  $R_e$  (Fig. 8b, slope of predicted vs. observed = 1.06), and as a result, it simulated daily NEP values were lower than measured values (Fig. 8c, slope of predicted vs. observed = 0.69). BEPS predicted daily  $R_s$  values were also higher than measured values (Fig. 5c, slope of predicted vs. observed = 1.07, not shown). Figure 9 shows 7-day running averages of measured and modeled C fluxes, and N fertilization effects on C component fluxes, which were quantified by the differences between measured and modeled values. For most days in 2007, N fertilization had negative effects on  $R_e$  and  $R_s$ , while having positive effects on GPP and NEP. Large N effects were found in summer and fall. Figure 10 shows the cumulative plot for each of the C component fluxes for 2007 with error bars, which were calculated using  $\pm 1$ SD of the optimized parameters. The overall N effects on C fluxes in the

first-postfertilization year are shown in Table 3 and Fig. 6 and summarized as follows: (i) annual GPP increased by  $\sim 8.1\%$  from  $1938 \pm 22$  to  $2095 \pm 29 \text{ g m}^{-2} \text{ yr}^{-1}$ , (ii) annual  $R_e$  decreased by  $5.7\%$  from  $1636 \pm 17$  to  $1543 \pm 31 \text{ g m}^{-2} \text{ yr}^{-1}$ , and (iii) as a result, NEP increased by  $82.8\%$  from  $302 \pm 19$  to  $552 \pm 36 \text{ g m}^{-2} \text{ yr}^{-1}$ . Moreover, in terms of respiration, the model results showed that fertilizer-induced reduction in total  $R_e$  ( $\sim 93 \text{ g m}^{-2} \text{ yr}^{-1}$ ) mostly resulting from the decrease in belowground  $R_e$  (i.e.  $R_s$ ,  $\sim 62 \text{ g m}^{-2} \text{ yr}^{-1}$ ).

## Discussion

### *Forest fertilization effects on photosynthesis*

Fertilization application in such N-limited stands likely stimulates aboveground NPP (Fisher & Binkley, 2000; Chapin *et al.*, 2002). After fertilization, needle mass at the end of the first year increased by  $\sim 26\%$ . Our model results also showed fertilization increased GPP by  $\sim 8.1\%$  ( $= 157 \text{ g m}^{-2} \text{ yr}^{-1}$ ) in this stand. These results are consistent with, but lower than, the results for this same site obtained by Jassal *et al.* (2010a) that N-fertilization increased GPP by  $11\%$  ( $= 203 \text{ g m}^{-2} \text{ yr}^{-1}$ ). However, in their study, NEE was partitioned by calculating daytime respiration using the relationship between daytime NEP and photosynthetically active radiation and the monthly values of unfertilized GPP for 2007 were calculated using a simple linear regression analysis based on monthly values in the nonfertilized years 1998–2006. These findings are also consistent with other studies: Brix (1991) reported an increase in net photosynthesis rate in response to improved nutrition in Douglas-fir; Canary *et al.* (2000) report that N fertiliza-



**Fig. 6** Comparisons of measured and modeled annual gross primary productivity (GPP), ecosystem respiration ( $R_e$ ), soil respiration ( $R_s$ ), and net ecosystem production (NEP). The error bars show the standard errors (SE). The SE values for the eddy-covariance measured annual C fluxes were estimated using the method of Schwalm *et al.* (2007), while the SE values for modeled annual values were estimated using the  $\pm 1$  SD of optimized model parameters. (a) For the EnKF applied years, (b) for the model validation year 2006, and (c) for the first-postfertilization year 2007. EnKF, ensemble Kalman filter.

tion of Douglas-fir plantations in western Washington State added an average of  $26.7 \text{ Mg ha}^{-1}$  to the live tree component over a 16-year-period comparing with adjacent unfertilized control sites; Adams *et al.* (2005) reported a similar result for the same forest as Canary *et al.* (2000) reported that the N-fertilized sites ( $161 \text{ Mg C ha}^{-1}$ ) had an average of 20% more C in the tree biomass compared with unfertilized sites ( $135 \text{ Mg C ha}^{-1}$ ) over an 8-year-period, suggesting

enhancement of tree growth due to N fertilization; Footen *et al.* (2009) found that N fertilization increased site productivity of young Douglas-fir stands on low quality sites in the Pacific Northwest 15–22 years after application by a carryover effect; Hyvönen *et al.* (2008) found the positive effects of fertilizer N on C stocks in trees (stems, stumps, branches, needles, and coarse roots) and these effects were quantified by analyzing data from 15 long-term (14–30 years) experiments in

**Table 3** Comparisons of measured and modeled annual gross primary productivity (GPP), net ecosystem productivity (NEP), ecosystem respiration ( $R_e$ ), and soil respiration ( $R_s$ )\*

|          | GPP        |            |            | $R_e$       |            |             | $R_s$      |             | NEP        |            |             |
|----------|------------|------------|------------|-------------|------------|-------------|------------|-------------|------------|------------|-------------|
|          | dep        | bias       | bias%      | dep         | bias       | bias%       | bias       | bias%       | dep        | bias       | bias%       |
| 1998     | 7          | 29         | 1.4        | -16         | 11         | 0.6         |            |             | 23         | 18         | 5.0         |
| 1999     | -100       | -11        | -0.5       | -126        | -36        | -2.1        |            |             | 26         | 25         | 7.0         |
| 2000     | -33        | -31        | -1.5       | -75         | -17        | -1.0        |            |             | 42         | -14        | -3.4        |
| 2001     | -47        | 26         | 1.3        | -101        | 16         | 1.0         |            |             | 54         | 10         | 2.5         |
| 2002     | -172       | 14         | 0.7        | -92         | 31         | 1.9         |            |             | -80        | -17        | -5.8        |
| 2003     | -46        | -16        | -0.8       | -43         | -38        | -2.2        |            |             | -3         | 22         | 6.6         |
| 2004     | 214        | 22         | 0.9        | 303         | 36         | 1.8         | 16         | 1.7         | -89        | -14        | -5.0        |
| 2005     | 186        | -17        | -0.7       | 187         | -31        | -1.6        | -8         | -0.8        | -1         | 14         | 4.1         |
| $\Sigma$ | 101        | 21         | 1.0        | 120         | 27         | 1.5         | 12         | 1.2         | 41         | 15         | 4.6         |
| $\sigma$ | 134        | 23         | 1.1        | 155         | 31         | 1.7         | 17         | 1.8         | 54         | 18         | 5.3         |
| 2006     | -12        | -19        | -0.9       | -41         | -30        | -1.7        | 13         | 1.4         | 29         | 11         | 2.9         |
| 2007     | <b>-29</b> | <b>157</b> | <b>8.1</b> | <b>-225</b> | <b>-93</b> | <b>-5.7</b> | <b>-62</b> | <b>-6.3</b> | <b>196</b> | <b>250</b> | <b>82.8</b> |

\*Urea at 200 kg N ha<sup>-1</sup> applied on January 13, 2007. The unit for GPP, NEP,  $R_e$  and  $R_s$  is g m<sup>-2</sup> yr<sup>-1</sup>. The bias and bias% for 2007 are approximated as absolute and relative N fertilization effects on respective C fluxes, respectively, and positive values indicate positive effects, *visa versa*. The values for the fertilized year 2007 are highlighted in bold.

dep, departures in C fluxes from their respective 1998–2006 mean; bias, measured–modeled; percentage of bias (bias%) = (measured–modeled)/model × 100%;  $\Sigma$ , the average of the absolute values of the deviations of data points from their mean for 1998–2005;  $\sigma$ , standard deviation of annual values over 1998–2005.

*Picea abies* and *Pinus sylvestris* stands in Sweden and Finland; Olsson *et al.* (2005) reported a threefold increase in aboveground productivity in response to fertilization of a boreal Norway spruce stand; Magill *et al.* (2004) found that long-term fertilization at Harvard Forest resulted in an increase in aboveground NPP of the high N hardwood stand relative to the control plot, and Leggett & Kelting (2006) found N fertilization increased both aboveground and belowground biomass of Loblolly pine plantations.

Brooks & Coulombe (2009) found that latewood  $\Delta^{13}\text{C}$  sharply decreased by 1.4‰ after fertilization and was significantly lower than controls for 4 years, but no differences existed between fertilization levels, and the effect disappeared after 4 years in an 85-year-old Douglas-fir stand based on tree ring and isotope analyses. They further concluded that these findings indicate intrinsic water use efficiency increased in response to fertilization (Brooks & Coulombe, 2009). Jassal *et al.* (2010a), on contrast, showed that there was no first-year response of evapotranspiration and water use efficiency to N fertilization in a 58-year-old Douglas-fir stand. These findings may imply the N-fertilization had little first-year response on leaf stomatal conductance. The fertilizer-induced increases in photosynthesis may be related to the effect of leaf N on  $V_{\text{cmax}}$ . The net photosynthetic rate  $A_{\text{net}}$  at the leaf level is a function of two tightly correlated parameters  $V_{\text{cmax}}$  and  $J_{\text{cmax}}$  [see Eqns. (A1)–(A2)]. In nutrient-limited forests, such as West

Coast Douglas-fir stands,  $A_{\text{net}}$  is generally limited by  $A_c$ , while  $A_c$  is dominantly controlled by  $V_{\text{cmax}}$  (e.g. Arain *et al.*, 2006; see also Eqn. A1a). As many research results (e.g. Arain *et al.*, 2006) have shown  $V_{\text{cmax}}$  is a nonlinear function of leaf N status,

$$V_{\text{cmax}}(N) = \alpha[1 - \exp(-1.8N_r)], \quad (2)$$

where  $\alpha$  is the maximum value of  $V_{\text{cmax}}$  and  $N_r$  is leaf Rubisco-N content (in g N m<sup>-2</sup> leaf area) of the canopy. Substituting the above values of foliar N of unfertilized trees (1.15%) and fertilized trees (1.61%) into Eqn. (2) indicates that the fertilizer-induced increase in  $V_{\text{cmax}}$  is 8%, which is similar to modeled increase in GPP (7.9%) due to N fertilization (Table 3 and Fig. 10).

#### Forest fertilization effects on respiration

The results of our model simulation indicate that  $R_e$  decreased in the first year after fertilization by  $\sim 93 \text{ g m}^{-2} \text{ yr}^{-1}$  ( $\sim 5.7\%$ ), in which, the aboveground  $R_e$  declined by  $\sim 31 \text{ g m}^{-2} \text{ yr}^{-1}$  ( $\sim 4.4\%$ ) and belowground  $R_e$  (i.e.  $R_s$ ) declined  $\sim 62 \text{ g m}^{-2} \text{ yr}^{-1}$  ( $\sim 6.3\%$ , Figs 5c and 6 and Table 3). This contrasts to an increase of  $35 \text{ g m}^{-2} \text{ yr}^{-1}$  calculated by Jassal *et al.* (2010b) following a different type of NEE partitioning and empirical modeling as explained above, though, however, the disagreement can partly be due to a reported uncertainty of  $\sim 30 \text{ g m}^{-2} \text{ yr}^{-1}$  in the EC-measured  $R_e$  values (e.g. Schwalm *et al.*, 2007).

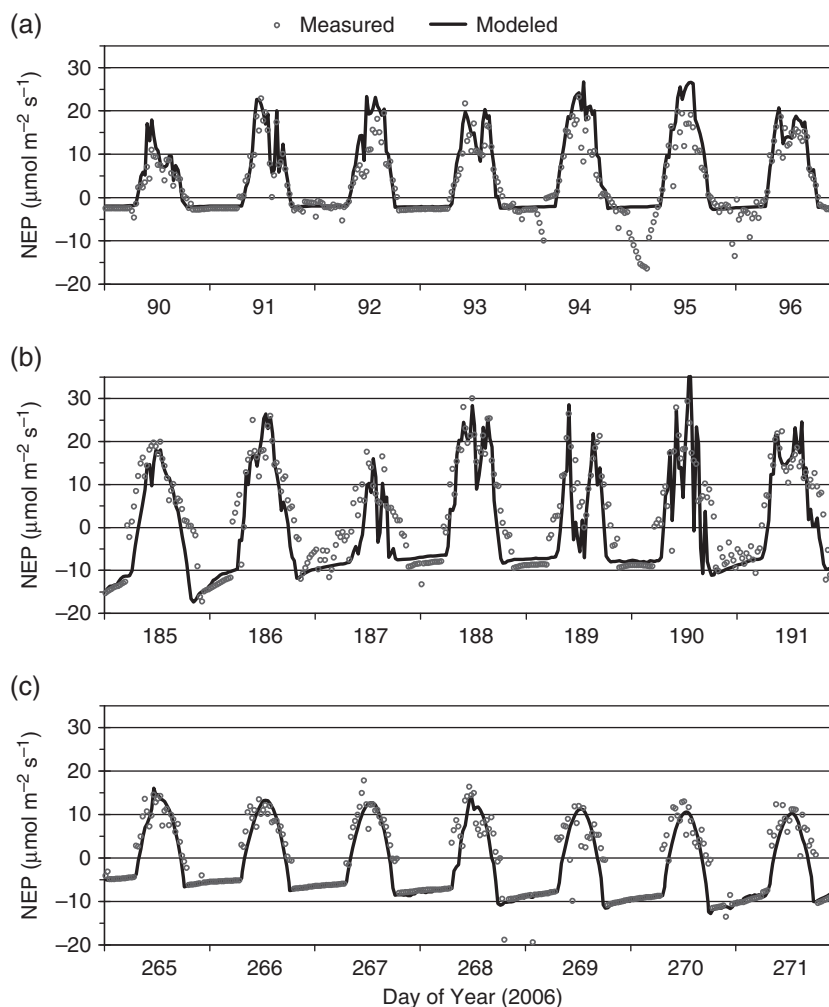
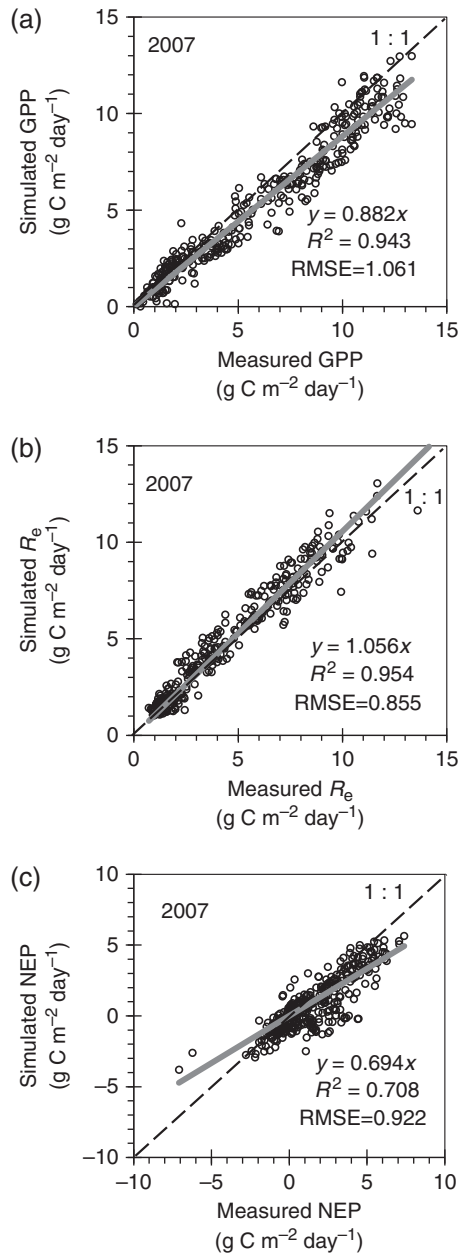


Fig. 7 BEPS predicted and EC tower measured net ecosystem productivity (NEP) in the early (a), middle (b), and late (c) stages of the growing season in 2006 at DF49. BEPS, Boreal Ecosystem Productivity Simulator; EC, eddy-covariance.

Given a significant increase in GPP (by  $\sim 157 \text{ g m}^{-2} \text{ yr}^{-1}$ ) and an increase in aboveground NPP (by  $\sim 126 \text{ g m}^{-2} \text{ yr}^{-1}$ ), it is an unexpectedly weak response of aboveground  $R_e$  to fertilization (reduction of only  $\sim 31 \text{ g m}^{-2} \text{ yr}^{-1}$ ). Fertilizer-induced increases in aboveground productivity (Olsson *et al.*, 2005), increases in both aboveground and belowground biomass (Leggett & Kelting, 2006), and increases in aboveground biomass with decreases in belowground biomass (Teskey *et al.*, 1995) have also been reported for other forests. Reich *et al.* (1998) reported that mass-based leaf dark respiration rate was positively related to leaf N content for 69 species from four functional groups (forbs, broad-leafed trees and shrubs, and needle-leafed conifers) in six biomes traversing the Americas (alpine tundra/subalpine forest, Colorado; cold temperate forest/grassland, Wisconsin; cool temperate forest, North Carolina; desert/shrubland, New Mexico; subtropical forest, South Carolina; and tropical rain forest, Amazonas,

Venezuela). Based on their findings, we may deduce that a reduction in above ground  $R_e$  found in this study might result mainly from stem respiration. Comparatively weak effects of fertilization on aboveground  $R_e$  with considerable increases in aboveground biomass may be related to the following mechanisms: N fertilization may (i) depress the sensitivity of aboveground  $R_e$  (i.e. both growth and maintenance respiration) to temperature (i.e. a decline in  $Q_{10}$ ), (ii) alter the relationship between GPP and growth respiration, and (iii) change patterns of photosynthate allocation which is related to  $R_e$ , i.e. as summarized by Janssens & Luysaert (2009) that C allocation tends to shift from fine roots and mycorrhizal symbionts, with a relatively low C:N ratio, to woody biomass with a high ratio. For instance, Koehler *et al.* (2009) found a shift in C partitioning from below- to aboveground in the N-addition plots in a tropical montane forest in which stem diameter growth was promoted.



**Fig. 8** Comparison of BEPS predicted (no fertilization) and EC tower measured daily gross primary productivity (GPP), ecosystem respiration ( $R_e$ ) and net ecosystem productivity (NEP) at DF49 for the fertilized year 2007. BEPS, Boreal Ecosystem Productivity Simulator; EC, eddy-covariance; RMSE, root mean square error.

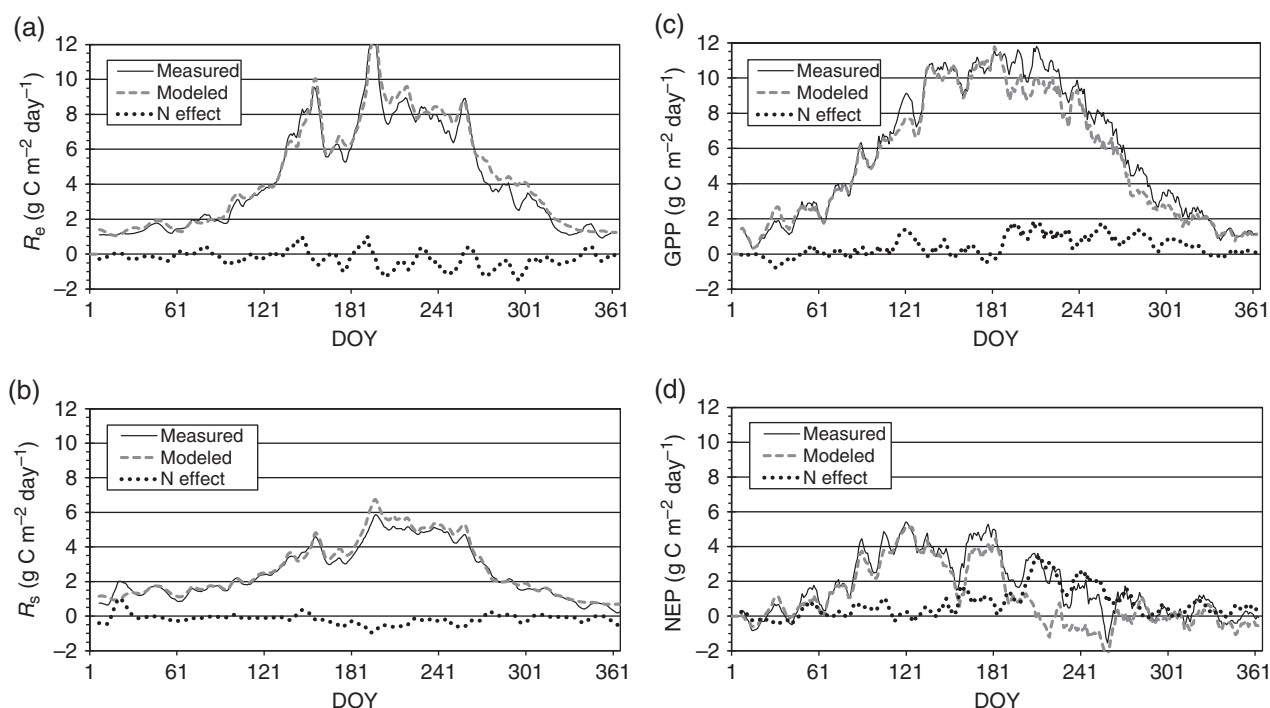
Our findings that N fertilization decreased annual  $R_s$  are consistent with those studies for temperate forests (e.g. Haynes & Gower, 1995; Fahey *et al.*, 1998; Bowden *et al.*, 2000, 2004; Maier & Kress, 2000; Butnor *et al.*, 2003; Burton *et al.*, 2004; Phillips & Fahey, 2007); however, the magnitude of the impact of N fertilization on  $R_s$  in this study (a 6.3% decrease in  $R_s$ ) is at the low end of the

range (5–40%) of the previous findings. The mechanisms behind N-fertilizer-induced  $R_s$  reduction have not been clearly identified because it is usually difficult to separate the contributions of root respiration ( $R_r$ ) and microbial decomposition to  $R_s$  (Hanson *et al.*, 2000; Baggs, 2006; Phillips & Fahey, 2007). We simply assumed that a reduction in  $R_s$  attributed to both  $R_a$  and  $R_h$ . N-fertilizer-induced decreases in  $R_a$  are most likely associated with reduction in fine-root biomass after fertilization as fine-root biomass is significantly correlated with  $R_s$  (e.g. Davidson *et al.*, 2004; Mo *et al.*, 2008). Decreases in fine-root biomass in fertilized forest soils have been reported in numerous studies (Aber & Melillo, 1991; Haynes & Gower, 1995; Boxman *et al.*, 1998; Bowden *et al.*, 2004), and are consistent with plant C allocation theory which states that trees decrease C allocation to roots when nutrient availability is high (Bloom *et al.*, 1985). Janssens *et al.* (2010) revealed that the average response of  $R_h$  to N addition is much more pronounced than that of leaf-litter decomposition alone on the basis a statistical meta-analysis. Averaged over 36 N-manipulation studies in forest ecosystems, N addition decreased  $R_h$  by 15%, with responses ranging from a reduction of 57% to a stimulation of 63% (Janssens *et al.*, 2010). N-fertilizer-induced  $R_h$  reduction is thought to be related to the soil C:N ratio, it has been found to be associated with a decrease in soil microbial biomass (Arnebrandt *et al.*, 1990; Wallenstein, 2003; Bowden *et al.*, 2004; Compton *et al.*, 2004; Frey *et al.*, 2004) or with an increase in microbial C use efficiency if an increased proportion of C is assimilated into new biomass (Phillips & Fahey, 2007).

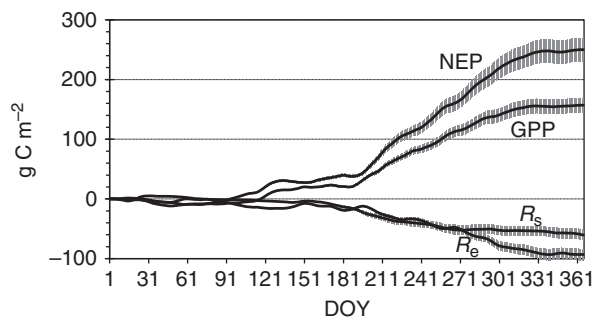
The findings in this study which show that N fertilization decreased  $R_s$ , however, differ from the field observations at Harvard Forest reported by Micks *et al.* (2004), and manual and automated chamber measurements made at this site by Jassal *et al.* (2010b). Using manual soil  $\text{CO}_2$  efflux measurements, made at 2–4-weekly intervals in 16 plots [eight root-exclusion plots ( $R_h$ ) and eight adjacent control plots ( $R_s$ )], Jassal *et al.* (2010b) showed that fertilization resulted in a significant (20%) increase in  $R_s$  during the first 3–4 months due mainly to an increase in autotrophic (or rhizospheric) soil respiration ( $R_a$ ). In the following 3 months, they found little effect on  $R_s$  but a small (~6%) decrease in  $R_h$ . They attributed the increase in  $R_a$  to fertilization causing an increased production of fast-turnover fine roots (Cleveland & Townsend, 2006; Pan *et al.*, 2009), which would stimulate higher C allocation belowground to balance high N concentration in these tissues (Chapin *et al.*, 1990; Field *et al.*, 1992).

Thus, a definitive answer on the short-term responses of  $R_s$  and its components to N addition is not readily apparent, however regardless of sign, changes in  $R_s$





**Fig. 9** Seven-day moving averages of BEPS predicted and measured C component fluxes for the fertilization year 2007 at DF49. The C component fluxes are (a) ecosystem respiration ( $R_e$ ), (b) soil respiration ( $R_s$ ), (c) gross primary productivity, and (d) net ecosystem respiration. The N fertilization effects on the C component fluxes were estimated as the differences between the measured C fluxes and their corresponding modeled values. BEPS, Boreal Ecosystem Productivity Simulator.



**Fig. 10** Cumulative N fertilization effects on C component fluxes with  $\pm 1$  SE in 2007 at DF49, which were estimated as the differences between the measured C fluxes and the corresponding modeled values. Standard errors were estimated using the  $\pm 1$  SD of optimized model parameters. The C component fluxes are gross primary productivity (GPP), ecosystem respiration ( $R_e$ ), soil respiration ( $R_s$ ), and net ecosystem respiration (NEP).

induced by N were small and within uncertainties or biases in both modeling and/or measurement approaches. Future research is therefore required to help resolve the question of N-fertilization effects on  $R_s$  and its components.

#### *N-use efficiency for C sequestration*

As Janssens & Luyssaert (2009) summarized, three main mechanisms for a N–C link in forests are: (i) accelerated photosynthesis, (ii) a change in tree C allocation from roots and root symbionts to woody biomass, and (iii) slowing of the microbial degradation of soil C (these were discussed at a recent workshop ‘The Impact of N on the Forest Carbon Cycle’ held in Stockholm, Sweden, in February, 2009). The response of C sequestration to N addition, in term of N-use efficiency [ $\text{kg C (sequestered) kg}^{-1}(\text{N added})$ ] relates to the spatial variations in each of the three mechanisms, in other words, it depends on geographical situation, soil status, tree species, stand age, fertilizer composition, and dose (Hyvönen *et al.*, 2008). Magnani *et al.* (2007) reported a strong positive relation between mean lifetime C sequestration (in terms of net ecosystem production,  $\text{NEP}_{\text{av}}$ ) and N deposition for midlatitude forests based on an analysis of 20 European forest stands using an Arrhenius function. Such a finding differs markedly from other estimates (De Vries *et al.*, 2008; Sutton *et al.*, 2008), and induces a major debate on the relationship between atmospheric N deposition and forest C sequestration (De Schrijver *et al.*, 2008; De Vries *et al.*, 2008;

Sutton *et al.*, 2008). Sutton *et al.* (2008) found that the response of net C sequestration to total N was about 50–75:1, by reanalysis of 22 European forest stands and accounting for the effects of intersite climatological differences. A most common range of C sequestration per kg N addition in aboveground biomass and in soil organic matter for forests was estimated to be about 20–40 kg C kg<sup>-1</sup> N using multiple approaches (De Vries *et al.*, 2009). By analyzing data from 15 long-term (14–30 years) experiments in *P. abies* and *P. sylvestris* stands in Sweden and Finland, Hyvönen *et al.* (2008) found low application rates (30–50 kg N ha<sup>-1</sup> yr<sup>-1</sup>) were always more efficient per unit of N than high application rates (50–200 kg N ha<sup>-1</sup> yr<sup>-1</sup>), suggesting the size of dose will affect the N-use efficiency. N fertilization with the amount of 200 kg N ha<sup>-1</sup> in one single dose is different from N deposition with characteristics of long-term and low-dose N addition. N-use efficiency in the near-end-of-rotation Douglas-fir stand (58-year-old in 2007) in this study was 12.5 kg C (sequestered) kg<sup>-1</sup>(N added) in the first year following fertilization, which is expected to be lower than the common range of N-use efficiency (20–40 kg C kg<sup>-1</sup> N) for forests due to atmospheric N deposition (De Vries *et al.*, 2009). N fertilization with the amount of 200 kg N ha<sup>-1</sup> in one single dose is a common forest management activity in N-limited forests, e.g. Pacific Northwest coastal forests of the United States and Canada covering approximately 10<sup>5</sup> km<sup>2</sup> between Oregon and Alaska. Therefore, to assess the effects of this common N fertilization activity on net C sequestration is also important. N-use efficiency in the 58-year-old Douglas-fir stand is lower than that in the stand at middle rotation stage (19-year old) with value of 18 kg C (kg N)<sup>-1</sup> (Jassal *et al.*, 2010a), implying the stand age effect on N-use efficiency.

#### *Uncertainty and limitation of this modeling approach*

The 9-year EC data (1998–2006) at DF49 before fertilization shows the apparent interannual variability of NEP, GPP, and  $R_e$  were ( $\pm$ SD) 357  $\pm$  51, 2124  $\pm$  125, and 1767  $\pm$  146 g C m<sup>-2</sup> yr<sup>-1</sup>, with ranges of 267–410, 1592–2338, and 1642–2071 g C m<sup>-2</sup> yr<sup>-1</sup>, respectively (see Chen *et al.*, 2009a). The major drivers of interannual variability in annual C fluxes were interannual climatic perturbations (especially annual and spring mean air temperatures and water deficiency during late summer and autumn; Chen *et al.*, 2009a). How to distinguish fertilization and climatic effects on C fluxes is a challenge. One may either design measurement or modeling experiments. Given the high spatial heterogeneity of land surface in nature, it is hard to find an EC flux area with similar land surface properties (e.g. tree age, density, LAI and soil properties, etc.) to set up a control

EC tower as in this case. The EC sensor location bias (a measure of uncertainties of EC tower data owing to the land surface heterogeneity) for DF49 based on footprint climatology and remote sensing analyses was about 15% for GPP estimation (Chen *et al.*, 2009b), which is larger than the magnitude of N fertilization effects on GPP and  $R_e$  but lower than of the effects on NEP. The measuring experiment with control tower, therefore, is not a pragmatic and reliable approach. For example, Hollinger *et al.* (2004) had shown the considerable difference in C fluxes between the paired measurements from two flux towers (e.g. Richardson *et al.*, 2006). Soil chamber measuring experiments face a similar spatial representativeness challenge. The responses of forest ecosystems to N addition are likely different among years after fertilization (Aber *et al.*, 1989, 1998). The modeling approach is necessary to explore the N fertilization effects on C sequestration in first-postyear in this research. A desirable process-based ecosystem model with high accuracy (model uncertainty must be less than the N fertilization effect on C sequestration, i.e. 5–10%) is required in a modeling approach. This type of model, one with high accuracy, may not exist. In this study, we designed a modeling experiment by taking advantage of the data-model fusion technique to eliminate the effects of interannual variations on C fluxes based on an 9-year-long series of EC data (1998–2006) before fertilization (see “Climate and EC measurements”). A set of key model parameters was optimized based on the binned month dataset with the ensemble size of  $\sim 8 \times 30 \times 48$  in order to account for the effects of interannual climatic perturbations but reveal seasonal controlling factors of C fluxes including both biotic and abiotic factors. The objective of model runs is to distinguish the N fertilization effects on C exchanges rather than to obtain good agreement between model outputs and measurements for each modeling year. One may argue about the uncertainty of the N fertilization effects on net and component C fluxes derived from the data-model approach as it is not easy to assess. Alternative methods are worthwhile to explore for future studies for assessing the effects of fertilization, e.g. using a process-based model with a full description of N dynamics.

#### **Conclusions**

Fertilization of a 58-year-old Pacific Northwest Douglas-fir forest with 200 kg N ha<sup>-1</sup> was found to increase annual NEP by  $\sim 83\%$ , from 302  $\pm$  19 to 552  $\pm$  36 g m<sup>-2</sup> yr<sup>-1</sup> in the first year. On the basis of a data-model fusion approach, this N fertilizer-induced increased in NEP was found to have resulted primarily from increases in annual GPP by  $\sim 8\%$ , from 1938  $\pm$  22



to  $2095 \pm 29 \text{ g m}^{-2} \text{ yr}^{-1}$  and secondly from decreases in annual  $R_e$  by  $\sim 5.7\%$ , from  $1636 \pm 17$  to  $1543 \pm 31 \text{ g m}^{-2} \text{ yr}^{-1}$ .

Modeling results indicated that fertilizer-induced decreases in belowground  $R_e$  (i.e.  $R_s$ ) mainly contributed to the reduction in total  $R_e$  while aboveground  $R_e$  had less response to N fertilization. The fertilizer-induced enhancement of photosynthesis ( $\sim 157 \text{ g m}^{-2} \text{ yr}^{-1}$ ) was more pronounced than the depression of soil respiration ( $\sim 62 \text{ g m}^{-2} \text{ yr}^{-1}$ ). The former is likely related to the functional relationship of the maximum carboxylation rate to leaf N content. The uncertainties or biases in estimated N effects, stemming from errors of both measurements and modeling results are still considerable but  $<10\%$  of their quantities. These results suggest that N fertilization as a forest management activity in such N-limited forests and soils, may significantly increase C sequestration and may have potential consequences for feedbacks to global change.

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## References

Aber JD, Magill A, Boone R, Melillo JM, Steudler PA, Bowden R (1993) Plant and soil responses to three years of chronic nitrogen additions at the Harvard Forest, Petersham, MA. *Ecological Applications*, **3**, 156–166.

Aber JD, Magill A, McNulty SG, Boone R, Nadelhoffer KJ, Downs M, Hallett RA (1995) Forest biogeochemistry and primary production altered by nitrogen saturation. *Water, Air, and Soil Pollution*, **85**, 1665–1670.

Aber JD, McDowell W, Nadelhoffer K *et al.* (1998) Nitrogen saturation in temperate forest ecosystems. *BioScience*, **48**, 921–934.

Aber JD, Melillo JM (1991) *Terrestrial Ecosystems*. Saunders College Publishing, Philadelphia, PA, USA.

Aber JD, Nadelhoffer KJ, Steudler P, Melillo JM (1989) Nitrogen saturation in northern forest ecosystems. *BioScience*, **39**, 378–386.

Adams AB, Harrison RB, Sletten RS, Strahm BD, Turnblom EC, Jensen CM (2005) Nitrogen-fertilization impacts on carbon sequestration and flux in managed coastal Douglas-fir stands of the Pacific Northwest. *Forest Ecology and Management*, **220**, 313–325.

Agren GI, Bosatta E (1988) Nitrogen saturation of terrestrial ecosystems. *Environmental Pollution*, **54**, 185–197.

Arain MA, Yuan F, Black TA (2006) Soil-plant nitrogen cycling modulated carbon exchanges in a western temperate conifer forest in Canada. *Agricultural and Forest Meteorology*, **140**, 171–192.

Arnebrant K, Baath E, Soderstrom B (1990) Changes in microfungal community structure after fertilization of scots pine forest soils with ammonium nitrate or urea. *Soil Biology and Biochemistry*, **22**, 309–312.

Baggs EM (2006) Partitioning the components of soil respiration: a research challenge. *Plant and Soil*, **284**, 1–5.

Ballard TM, Carter RE (1986) *Evaluating forest stand nutrient status*. Land Management Report 20, BC Ministry of Forests, Vic., BC, Canada.

Barr AG, Black TA, Hogg EH, Kljun N, Morgenstern M, Nestic Z (2004) Inter-annual variability in the leaf area index of a boreal aspen-hazelnut forest in relation to net ecosystem production. *Agricultural Forest Meteorology*, **126**, 237–255.

Bauer GA, Bazzaz FA, Minocha R, Long S, Magill A, Aber J, Berntson GM (2004) Effects of chronic N additions on tissue chemistry, photosynthetic capacity, and carbon sequestration potential of a red pine (*Pinus resinosa* Ait.) stand in the NE United States. *Forest Ecology and Management*, **196**, 173–186.

Bergh J, Linder S, Lundmark T, Elfving B (1999) The effect of water and nutrient availability on the productivity of Norway spruce in northern and southern Sweden. *Forest Ecology and Management*, **119**, 51–62.

Bloom AJ, Chapin FS, Mooney HA (1985) Resource limitation in plants – an economic analogy. *Annual Review of Ecology and Systematics*, **16**, 363–392.

Bowden RD, Davidson E, Savage K, Arabia C, Steudler 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.

Bowden RD, Rullo G, Sevens GR, Steudler PA (2000) Soil fluxes of carbon dioxide, nitrous oxide, and methane at a productive temperate deciduous forest. *Journal of Environmental Quality*, **29**, 268–276.

Boxman AW, Blanck K, Brandrud TE *et al.* (1998) Vegetation and soil biota response to experimentally-changed nitrogen inputs in coniferous forest ecosystems of the NITREX project. *Forest Ecology and Management*, **101**, 65–79.

Brix H (1991) Mechanisms of response to fertilization. II. Utilization by trees and stands. In: *Improving Forest Fertilization Decision-Making in British Columbia* (eds Lousier JD, Brix H, Brockely R, Carter R, Marshall VG) pp. 76–93. BCMoF, Victoria.

Brooks JR, Coulombe R (2009) Physiological responses to fertilization recorded in tree rings: isotopic lessons from a long-term fertilization trial. *Ecological Applications*, **19**, 1044–1060.

Burton AJ, Pregitzer K, Crawford JN, Zogg GP, Zak DR (2004) Simulated chronic  $\text{NO}_3^-$  deposition reduces soil respiration in northern hardwood forests. *Global Change Biology*, **10**, 1080–1091.

Butnor JR, Johnsen KH, Oren R, Katul GG (2003) Reduction of forest floor respiration by fertilization on both carbon dioxide-enriched and reference 17-year-old loblolly pine stands. *Global Change Biology*, **9**, 849–861.

Canary JD, Harrison RB, Compton JE, Chappell HN (2000) Additional carbon sequestration following repeated urea fertilization of second-growth Douglas-fir stands in western Washington. *Forest Ecology and Management*, **138**, 225–232.

Chapin FS, Matson PA, Mooney HA (2002) *Principles of Terrestrial Ecosystem Ecology*. Springer, New York.

Chapin FS, Schulze ED, Mooney HA (1990) The ecology and economics of storage in plants. *Annual Review of Ecology and Systematics*, **21**, 423–448.

Chen B, Black A, Coops NC, Jassal R, Nestic Z (2009a) Seasonal controls on interannual variability in carbon dioxide exchange of a Pacific Northwest Douglas-fir forest, 1997–2006. *Global Change Biology*, **15**, 1962–1981.

Chen B, Black A, Coops NC, Hilker T, Trofymow T, Nestic Z, Morgenstern K (2009b) Assessing tower flux footprint climatology and scaling between remotely sensed and eddy covariance measurements. *Boundary-Layer Meteorology*, **130**, 137–167.

Chen B, Chen JM, Ju W (2007a) Remote sensing based ecosystem-atmosphere simulation Scheme (EASS) – model formulation and test with multiple-year data. *Ecological Modelling*, **209**, 277–300.

Chen B, Chen JM, Mo G, Yuen C-W, Margolis H, Higuchi K, Chan D (2007b) Modeling and scaling coupled energy, water, and carbon fluxes based on eddy sensing: an application to Canada's landmass. *Journal of Hydrometeorology*, **8**, 123–143.

Chen JM, Govind A, Sonnentag O (2006) Leaf area index measurements at Fluxnet-Canada forest sites. *Agricultural and Forest Meteorology*, **140**, 257–268.

Cleveland CC, Townsend AR (2006) Nutrient additions to a tropical rain forest drive substantial soil carbon dioxide losses to the atmosphere. *Proceedings of National Academy of Sciences*, **103**, 10316–10321.

- Compton JE, Watruda LS, Porteous L, DeGroot S (2004) Response of soil microbial biomass and community composition to chronic nitrogen additions at Harvard forest. *Forest Ecology and Management*, **196**, 143–158.
- Davidson EA, Ishida FY, Nepstad DC (2004) Effects of an experimental drought on soil emissions of carbon dioxide, methane, nitrous oxide, and nitric oxide in a moist tropical forest. *Global Biogeochemical Cycles*, **10**, 718–730.
- De Schrijver A, Verheyen K, Mertens J, Staelens J, Wuyts K, Muys B (2008) Nitrogen saturation and net ecosystem production. *Nature*, **451**, E26.
- De Vries W, Reinds GJ, Gundersen P, Sterba H (2006) The impact of nitrogen deposition on carbon sequestration in European forests and forest soils. *Global Change Biology*, **12**, 1151–1173.
- De Vries W, Solberg S, Dobbertin M *et al.* (2008) Ecologically implausible carbon response? *Nature*, **451**, E26–E28.
- De Vries W, Solberg S, Dobbertin M *et al.* (2009) The impact of nitrogen deposition on carbon sequestration by European forests and heathlands. *Forest Ecology and Management*, **258**, 1814–1823.
- Diego S, Peylin P, Viovy N, Ciais P (2007) Optimizing a process-based model with eddy-covariance flux measurements: a pine forest in southern France. *Global Biogeochemical Cycles*, **21**, GB2013, doi: 10.1029/2006GB002834.
- Fahey TJ, Battles JJ, Wilson GF (1998) Responses of early successional northern hardwood forests to changes in nutrient availability. *Ecological Monographs*, **68**, 183–212.
- Falk M, Wharton S, Schroeder M, Ustin S, Paw UKT (2008) Flux partitioning in an old-growth forest: seasonal and interannual dynamics. *Tree Physiology*, **28**, 509–520.
- Feller MC (1992) Generalized versus site-specific biomass regression equations for *Pseudotsuga menziesii* var. *menziesii* and *Thuja plicata* in coastal British Columbia. *Bioresource Technology*, **39**, 9–16.
- Field CB, Chapin FS III, Matson PA, Mooney HA (1992) Responses of terrestrial ecosystems to the changing atmosphere: a resource-based approach. *Annual Review of Ecology and Systematics*, **23**, 201–235.
- Fisher RF, Binkley D (2000) *Ecology and Management of Forest Soils*. John Wiley, New York.
- Footen PW, Harrison RB, Strahm BD (2009) Long-term effects of nitrogen fertilization on the productivity of subsequent stands of Douglas-fir in the Pacific Northwest. *Forest Ecology and Management*, **258**, 2194–2198.
- Franklin O, Högberg P, Ekblad A, Ågren GI (2003) Pine forest floor carbon accumulation in response to N and PK additions – bomb 14C modelling and respiration studies. *Ecosystems*, **6**, 644–658.
- Frey SD, Knorr M, Parrent JL, Rodney ST (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, Cowling EB (2002) Reactive nitrogen and the world: 200 years of change. *Ambio*, **31**, 64–71.
- Gartner BL, North EM, Johnson GR, Singleton R (2002) Effects of live crown on vertical patterns of wood density and growth in Douglas-fir. *Canadian Journal of Forest Research*, **32**, 439–447.
- Hanley DP, Chappell HN, Nadelhoffer EH (1996) *Fertilizing coastal Douglas-fir forests*. Washington State University Extension Bulletin 1800.
- Hanson PJ, Edwards NT, Garten CT, Andrews JA (2000) Separating root and soil microbial contributions to soil respiration: a review of methods and observations. *Biogeochemistry*, **48**, 115–146.
- Haynes BE, Gower ST (1995) Belowground carbon allocation in unfertilized and fertilized red pine plantations in northern Wisconsin. *Tree Physiology*, **15**, 317–325.
- Holland EA, Braswell BH, Lamarque JF *et al.* (1997) Variations in the predicted spatial distribution of atmospheric nitrogen deposition and their impact on carbon uptake by terrestrial ecosystems. *Journal of Geophysical Research*, **102**, 15849–15866.
- Hollinger DY, Aber J, Dail B *et al.* (2004) Spatial and temporal variability in forest-atmosphere CO<sub>2</sub> exchange. *Global Change Biology*, **10**, 1689–1706.
- Humphreys ER, Black TA, Morgenstern K, Caia T, Drewitt GB, Nesica Z, Trofymow JA (2006) Carbon dioxide fluxes in three coastal Douglas-fir stands at different stages of development after harvesting. *Agricultural and Forest Meteorology*, **140**, 6–22.
- Hyvönen R, Persson T, Andersson S, Olsson B, Ågren GI, Linder S (2008) Impact of long-term nitrogen addition on carbon stocks in trees and soils in northern Europe. *Biogeochemistry*, **89**, 121–137.
- Janssens IA, Dieleman W, Luysaert S (2010) Reduction of forest soil respiration in response to nitrogen deposition. *Nature Geoscience*, **3**, 315–322.
- Janssens IA, Luysaert S (2009) Nitrogen's carbon bonus. *Nature Geoscience*, **2**, 318–319.
- Jassal RS, Black TA, Cai T *et al.* (2010a) Impact of nitrogen fertilization on carbon and water balances in a chronosequence of three Douglas-fir stands in the Pacific Northwest. *Agricultural and Forest Meteorology*, **150**, 208–218.
- Jassal RS, Black TA, Chen B, Roy R, Nesic Z, Spittlehouse DL, Trofymow JA (2008) N<sub>2</sub>O emissions and carbon sequestration in a nitrogen-fertilized Douglas fir stand. *Journal of Geophysical Research*, **113**, G04013, doi: 10.1029/2008JG000764.
- Jassal RS, Black TA, Trofymow JA, Roy R, Nesic Z (2010b) Soil CO<sub>2</sub> and N<sub>2</sub>O flux dynamics in a nitrogen-fertilized Pacific Northwest Douglas-fir stand. *Geoderma*, **157**, 118–125.
- Johnson DW, Curtis PS (2001) Effects of forest management on soil C and N storage: meta analysis. *Forest Ecology and Management*, **140**, 227–238.
- Ju W, Chen JM, Black TA, Barr AG, Liu J, Chen B (2006) Modelling multi-year coupled carbon and water fluxes in a boreal aspen forest. *Agricultural Forest Meteorology*, **140**, 136–151.
- Koehler B, Corre MD, Veldkamp E, Sueta JP (2009) Chronic nitrogen addition causes a reduction in soil carbon dioxide efflux during the high stem-growth period in a tropical montane forest but no response from a tropical lowland forest on a decadal time scale. *Biogeosciences*, **6**, 2973–2983.
- Korner C (2000) Biosphere responses to CO<sub>2</sub> enrichment. *Ecological Applications*, **10**, 1590–1619.
- Leggett ZH, Kelting DL (2006) Fertilization effects on carbon pools in loblolly pine plantations on two upland sites. *Soil Science Society of America Journal*, **70**, 279–286.
- Liu J, Chen JM, Cihlar J, Chen W (2002) Net primary productivity mapped for Canada at 1-km resolution. *Global Ecology Biogeography*, **11**, 115–129.
- Liu L, Greaver TL (2009) Nitrogen addition stimulates emissions of biogenic greenhouse gases in terrestrial and wetland ecosystems. *Ecology Letters*, **12**, 1103–1117.
- Magill AH, Aber JD, Currie WS, Nadelhoffer KJ, Martin ME, McDowell WH, J Melillo JM, Steudler P (2004) Steudler. Ecosystem response to 15 years of chronic nitrogen additions at the Harvard Forest LTER, Massachusetts, USA. *Forest Ecology and Management*, **196**, 7–28.
- Magnani F, Mencuccini M, Borghetti M *et al.* (2007) The human footprint in the carbon cycle of temperate and boreal forests. *Nature*, **447**, 848–850.
- Maier CA, Kress LW (2000) Soil CO<sub>2</sub> evolution and root respiration in 11 year-old loblolly pine (*Pinus taeda*) plantations as affected by moisture and nutrient availability. *Canadian Journal of Forest Research*, **30**, 347–359.
- Marshall DD, Turnblom EC (2005) Wood productivity of Pacific Northwest Douglas-fir: estimates from growth-and-yield models. *Journal of Forestry*, **103**, 71–72.
- Meidinger D, Pojar J (compilers and editors) (1991) *Ecosystems of British Columbia*. BC Ministry For Special Report Series No. 6., 330 pp.
- Micks P, Aber JD, Boone RD, Davidson EA (2004) Short-term soil respiration and nitrogen immobilization response to nitrogen applications in control and nitrogen-enriched temperate forests. *Forest Ecology and Management*, **196**, 57–70.
- Mo JM, Brown S, Xue JH, Fang Y, Li Z (2006) Response of litter decomposition to simulated N deposition in disturbed, rehabilitated and mature forests in subtropical China. *Plant and Soil*, **282**, 135–151.
- Mo JM, Zhang W, Zhu W, Per G, Fang Y, Li D, Wang H (2008) Nitrogen addition reduces soil respiration in a mature tropical forest in southern China. *Global Change Biology*, **14**, 403–412.
- Mo X, Chen JM, Ju W (2008) Optimization of ecosystem model parameters through assimilating eddy covariance flux data with an ensemble Kalman filter. *Ecological Modelling*, **217**, 157–173.
- Morgenstern K, Black TA, Humphreys ER *et al.* (2004) Sensitivity and uncertainty of the carbon balance of a Pacific Northwest Douglas-fir forest during an El Niño/La Niña cycle. *Agricultural Forest Meteorology*, **123**, 201–219.
- Nadelhoffer KJ, Emmett BA, Gundersen P *et al.* (1999) Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests. *Nature*, **398**, 145–148.
- Nihlgard B (1985) The ammonium hypothesis – an additional explanation to the forest dieback. *European Ambio*, **14**, 2–8.
- Olsson P, Linder S, Giesler R, Högberg P (2005) Fertilization of boreal forest reduces both autotrophic and heterotrophic soil respiration. *Global Change Biology*, **11**, 1745–1753.
- Pan Y, Birdsey R, Hom J, McCullough K (2009) Separating effects of changes in atmospheric composition, climate and land-use on carbon sequestration of U.S. Mid-Atlantic temperate forests. *Forest Ecology and Management*, **259**, 151–164.
- Paw UKT, Falk M, Suchanek TH *et al.* (2004) Carbon dioxide exchange between an old-growth forest and the atmosphere. *Ecosystems*, **7**, 513–524.
- Phillips RP, Fahey TJ (2007) Fertilization effects on fineroot biomass, rhizosphere microbes and respiratory fluxes in hardwood forest soils. *New Phytologist*, **176**, 655–664.
- Pregitzer KS, Burton JA, Zak DR (2008) Simulated chronic nitrogen deposition increases carbon storage in Northern Temperate forests. *Global Change Biology*, **14**, 142–153.
- Raupach MR, Rayner PJ, Barrett DJ *et al.* (2005) Model-data synthesis in terrestrial carbon observation: methods, data requirements and data uncertainty specifications. *Global Change Biology*, **11**, 378–397.

- Reay DS, Dentener F, Smith P *et al.* (2008) Global nitrogen deposition and carbon sinks. *Nature Geoscience*, **1**, 430–437.
- Reich PB, Walters MB, Ellsworth DS, Vose JM, Volin JC, Gresham C, Bowman WD (1998) Relationships of leaf dark respiration to leaf nitrogen, specific leaf area and leaf life-span: a test across biomes and functional groups. *Oecologia*, **114**, 471–482.
- Richardson AD, Hollinger DY, Burba GG *et al.* (2006) A multi-site analysis of random error in tower-based measurements of carbon and energy fluxes. *Agriculture and Forest Meteorology*, **136**, 1–18.
- Sacks W, Schimel DS, Monson RK, Braswell BH (2006) Model-data synthesis of diurnal and seasonal CO<sub>2</sub> fluxes at Niwot Ridge, Colorado. *Global Change Biology*, **12**, 240–259.
- Schulze ED (1989) Air pollution and forest decline in a spruce (*Picea abies*) forest. *Science*, **244**, 776–783.
- Schwalm CR, Black TA, Morgenstern K, Humphreys ER (2007) A method for deriving net primary productivity and component respiratory fluxes from tower-based eddy covariance data: a case study using a 17-year data record from a Douglas-fir chronosequence. *Global Change Biology*, **13**, 370–385.
- Sutton MA, Simpson D, Levy PE, Smith RJ, Reis S, Van Oijen M, De Vries W (2008) Uncertainties in the relationship between atmospheric nitrogen deposition and forest carbon sequestration. *Global Change Biology*, **14**, 2057–2063.
- Tarantola A (1987) *Inverse Problem: Theory Methods for Data Fitting and Parameter Estimation*. Elsevier, New York.
- Teskey RO, Gholz HL, Cropper WP (1995) Influence of climate and fertilization on net photosynthesis of mature slash pine. *Tree Physiology*, **14**, 1215–1227.
- Townsend AR, Braswell BH, Holland EA, Penner JE (1996) Spatial and temporal patterns in terrestrial carbon storage due to deposition of fossil fuel nitrogen. *Ecological Applications*, **6**, 806–814.
- Vitousek PM, Aber JD, Howarth RW *et al.* (1997) Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Applications*, **7**, 737–750.
- Vitousek PM, Howarth RW (1991) Nitrogen limitation on land and in the sea: how can it occur? *Biogeochemistry*, **13**, 87–115.
- Wallenstein MD (2003) Effects of nitrogen fertilization on soil microbial communities, geophysical research abstracts. *European Geophysical Society*, **5**, 13087.
- Williams M, Schwarz PA, Law BE, Irvine J, Kurpius MR (2005) An improved analysis of forest carbon dynamics using data assimilation. *Global Change Biology*, **11**, 89–105.

### Supporting Information

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

**Appendix S1.** Photosynthesis and respiration calculations in the BEPS model.

**Appendix S2.** Sensitivity of stomatal conductance to soil water variability.

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