



Estimated carbon residence times in three forest ecosystems of eastern China: Applications of probabilistic inversion

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[1] Carbon residence time is one critical parameter for predicting future land carbon sink dynamics but has not been well quantified for many plant and soil pools. This study applied a probabilistic inverse analysis of multiple observations to estimate mean residence times of carbon among three forest ecosystems in eastern China. Three assimilation experiments were conducted with either net ecosystem exchange data from eddy-flux measurements or six biometric and soil data (i.e., foliage biomass, fine root biomass, woody biomass, litterfall, soil organic carbon, and soil respiration) or all data to evaluate their relative effectiveness on estimation of carbon residence times of different pools in a terrestrial ecosystem model. Estimated mean residence times of carbon ranged from 2 to 10 months for metabolic litter and microbial biomass pools, from 1 to 3 years for foliage, fine root biomass, and structural litter pools, and from 17 to 1361 years for woody biomass, slow and passive soil organic matter pools at three forest sites. The residence times of carbon were longer for leaf, litter and microbes pools but shorter for fine root and wood pools in the young evergreen coniferous plantation at Qianyanzhou site than the two mature mixed forests at Changbaishan and Dinghushan sites. Carbon residence times were well constrained for three plant pools and slow soil organic matter by biometric and soil data, whereas residence times for metabolic and structural litter, and microbial biomass pools were constrained by daily net ecosystem exchange data. Overall, our study demonstrated that biometric, soil and net ecosystem exchange data are complementary in constraining mean residence times of an ecosystem model.

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1. Introduction

[2] Understanding mechanisms underlying terrestrial carbon sequestration is critical for improving model predictions of future climate change [Friedlingstein *et al.*, 2003]. Carbon influx and residence time are two key factors for determining carbon sequestration capacity of a terrestrial ecosystem [Luo *et al.*, 2003]. Ecosystems usually store more carbon with an enhanced carbon influx via canopy photosynthesis or longer carbon residence times or both. At the ecosystem scale, while canopy photosynthesis can be relatively well estimated with modeling approaches [Farquhar *et al.*, 1980], our understanding of carbon residence times is greatly limited [Trumbore, 2000; Luo *et al.*, 2003].

[3] Residence times of carbon in plant and soil organic matter (SOM) are often inferred by isotope techniques in individual pools [Trumbore *et al.*, 1996; Gaudinski *et al.*, 2000; Ehleringer *et al.*, 2000]. Isotopic techniques have improved our understanding of environmental controls of carbon transfer processes. However, soil radiocarbon measurements often overestimate the residence time of short-term SOM because of failure to account for the heterogeneity of soil organic matter [Trumbore, 2000], and stable isotope techniques are not suited to quantify carbon residences for ecosystems without different isotope signatures of source components [Bernoux *et al.*, 1998; Ehleringer *et al.*, 2000; Richards *et al.*, 2007]. On the other hand, carbon residence times are the key parameters of carbon cycling and land surface models, such as Rothamsted SOC model [Jenkinson and Rayner, 1977], CENTURY model [Parton *et al.*, 1987], and CLASS [Wang *et al.*, 2002]. These models consist of several conceptual carbon pools with different residence times, which range from weeks to hundreds or thousands of years. Carbon residence times in models are usually temperature- and moisture-corrected, and then modified by quantity and quality of substrate, and sometimes further by characteristics of the microbial community, to determine decomposition of litter and soil organic matter [Swift *et al.*,

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Table 1. Site Characteristics of Three Forest Ecosystems

	Changbaishan	Qianyanzhou	Dinghushan
Latitude (°N)	42.45	26.73	23.17
Longitude (°E)	128.10	115.06	112.53
Elevation (m)	736	102	300
Mean annual temperature ^a (°C)	3.6	17.9	21.0
Annual precipitation ^a (mm)	695	1485	1956
Predominant species	<i>Pinus koraiensis</i> , <i>Quercus mongolica</i> , <i>Acer mono</i> , <i>Tilia amurensis</i> , <i>Fraxinus mandshurica</i>	<i>Pinus massoniana</i> Lamb, <i>Pinus elliotii</i> Engelm, <i>Cunninghamia lanceolata</i> Hook	<i>Schima superba</i> , <i>Castanopsis chinensis</i> , <i>Pinus massoniana</i>
Canopy height (m)	26	12	20
Forest age (year)	200	23	100
Soil type	dark brown forest soil	red soil	latosolic red soil
pH value of soil	5.8	4.8	4.5

^aValues are the averages from 1985 to 2005.

1979]. Residence times of carbon in conceptual pools cannot easily be estimated from isotope data or obtained directly from field observations [Christensen, 1996; Wang and Hsieh, 2002]. Therefore, it is imperative to estimate carbon residence times so as to improve modeling studies and measurements.

[4] Data assimilation is an approach to estimate model parameters and state variables, and associated uncertainties, by minimizing deviations between models and observations. The approach has frequently been used in terrestrial carbon and water cycles research [Raupach et al., 2005; O'Neill and Melnikov, 2008; Luo et al., 2009; Wang et al., 2009; Williams et al., 2009]. Recently, data assimilation techniques have been used to estimate carbon residence times of terrestrial ecosystems as affected by CO₂ treatments [Luo et al., 2003; Xu et al., 2006], among five terrestrial ecosystems in southeast Sweden [Karlberg et al., 2006], and among biomes in Australia [Barrett, 2002] and United States [Zhou and Luo, 2008]. The probabilistic inversion at Duke Forest indicated that carbon residence times of plant biomass and structural litter pools can be well constrained by six biometric and soil data sets over five years but the best estimates of residence times for metabolic litter, microbes, and passive SOM pools cannot be identified [Xu et al., 2006].

[5] Eddy flux networks record net ecosystem exchange (NEE) of CO₂ between the atmosphere and ecosystems and offer another important data source to estimate parameters of carbon cycle models [Wang et al., 2001; Braswell et al., 2005] and to reduce parameter and prediction uncertainties [Knorr and Kattge, 2005; Williams et al., 2005]. A recent study suggested that parameters associated with dynamics of wood and fine roots were poorly characterized by eddy covariance data alone [Fox et al., 2009]. Clearly, multiple data sets obtained from measurements of different carbon processes potentially contribute information to constrain parameters at different timescales. Combinations of biometric, soil data and NEE measurements would be beneficial to constrain carbon residence times. In particular, biometric and soil data are useful to constrain residence times in slow turnover pools while NEE measurements provide additional information to quantify residence times in fast turnover pools.

[6] This study was designed to evaluate the effectiveness of daily NEE, biometric and soil data sets from 2003 to

2005 for estimating mean residence times in eight carbon pools (i.e., foliage, fine root, wood, metabolic litter, structural litter, microbes, slow and passive soil organic matter) with a terrestrial ecosystem (TECO) model. Biometric and soil measurements consisted of 6 data sets, which are foliage biomass, fine root biomass, woody biomass, litter-fall, soil organic carbon (SOC), and soil respiration. We conducted Bayesian probabilistic inversions to estimate mean residence times of carbon by using biometric and soil measurements, daily NEE measurements alone, and all data sets in three respective simulation experiments. A Markov Chain Monte Carlo (MCMC) sampling method was used to construct the posterior probability density functions of residence times for eight carbon pools. All three simulation experiments were performed at three different forest ecosystems in eastern China.

2. Methods

2.1. Data

[7] The data used in this study were obtained at three ChinaFLUX sites, Changbaishan temperate broad-leaved Korean pine mixed forest, Qianyanzhou subtropical coniferous plantation and Dinghushan subtropical evergreen coniferous and broad-leaved mixed forest. The three sites had distinct climate conditions and vegetation types from north to south in eastern China. The mean annual temperatures were 4.1°C, 18.3°C and 20.0°C, and the average of annual precipitations were 604 mm, 1240 mm and 1337 mm over 2003–2005 for Changbaishan, Qianyanzhou and Dinghushan, respectively. Detailed descriptions of sites characteristics were made by L. M. Zhang et al. [2006] and Yu et al. [2008] and summarized in Table 1.

[8] Two types of data sets were used in this data assimilation study for estimating carbon residence times, NEE, biometric and soil measurements. All data were collected from 2003 to 2005 at each of the three forest sites. NEE were aggregated to a daily time step from half-hourly CO₂ flux data measured by eddy covariance technique [Baldocchi et al., 1988] at 40 m, 39 m, and 27 m heights above the canopies at Changbaishan, Qianyanzhou and Dinghushan, respectively. Outlier data with extremely large CO₂ flux ($|F_c| > 3 \text{ mg CO}_2 \text{ m}^2 \text{ s}^{-1}$) were rejected and unreasonable nighttime values were excluded according to friction velocity ($u^* < 0.15 \text{ m s}^{-1}$). We used gap-filled flux data in this

analysis because the percentage of daily intervals with no gap-filled data after quality control was less than 10%. Gaps in half-hourly CO₂ flux data were filled using nonlinear regression algorithm [Falge *et al.*, 2001]. Detailed steps in data processing of NEE at the three sites were described by L. M. Zhang *et al.* [2006]. To reduce the impact of gap-filled data on estimating parameters, we only aggregated NEE data for days with at least 50% observed half-hourly fluxes in this analysis. We obtained 728 daily NEE values at Changbaishan, 455 at Qianyanzhou and 524 at Dinghushan site during 2003–2005.

[9] Biomass of foliage, fine root and wood were estimated from measured diameters at breast height (DBH) and tree heights using an allometric method. DBH and heights of all trees were recorded in main plots at Changbaishan (0.16 ha), Qianyanzhou (1 ha), and Dinghushan (0.25 ha) near eddy flux towers. All allometric equations (correlation coefficients ranged from 0.90 to 0.99) from the literature were derived from destructive harvest of trees for dominated species at Changbaishan [Xu *et al.*, 1985], Qianyanzhou [Li *et al.*, 2006; Shen *et al.*, 2006], and Dinghushan [Peng *et al.*, 1989; Peng, 1996; Fang *et al.*, 2003]. During 2003–2005, DBH and tree height measurements were sampled twice (December 2003 and August 2005) at Changbaishan, twice (August 2003 and July 2005) at Qianyanzhou, and once at Dinghushan in October 2004.

[10] Aboveground litterfall biomass was measured by 10 replicates of 100 cm × 100 cm baskets monthly at Qianyanzhou and Dinghushan but monthly during the growing season (from May to October) and only once in the nongrowing season at Changbaishan from 2003 to 2005. All collected litter was dried at 70°C for 24 h and weighed. We used annual litterfall biomass data for the inverse analysis to avoid the effect of wind on litterfall biomass measurement within an individual month. The carbon contents of litter were assumed to be 0.50 g C g⁻¹ at Changbaishan and Dinghushan [Zhou *et al.*, 2006], and 0.55 g C g⁻¹ at Qianyanzhou [Shen *et al.*, 2006].

[11] Soil carbon content was calculated from SOM measured by potassium dichromate oxidation titrimetric method at each forest site. At least three soil samples were collected from five soil layers (0–10, 10–20, 20–40, 40–60 and 60–100 cm) at Changbaishan in September 2005 and Dinghushan in October 2004 and October 2005, from all soil horizons at Qianyanzhou in December 2003 and August 2005. We converted SOM to SOC by multiplying 0.58 [Post *et al.*, 1985].

[12] Soil respiration was measured using static chamber-gas chromatograph techniques at each forest site. Six repeats were collected with weekly sampling time at 9:00 to 11:30 A.M. from January 2003 to October 2005, except in winter with only once or twice measurements. All samples were taken back to the lab and analyzed using HP4890D Gas Chromatographer in sample days. The method of soil respiration measurement was described in detail by D. Q. Zhang *et al.* [2006]. We estimated daily soil respiration on the basis of a constant rate in each sample day.

2.2. Modified TECO Model and Parameters

[13] We used a modified version of the terrestrial ecosystem (TECO) model [Luo *et al.*, 2003; Xu *et al.*, 2006] with

eight carbon pools. The nonwoody biomass pool in the original version was divided into foliage and fine root biomass pools for data assimilation in this study. Carbon entered the ecosystem through canopy photosynthesis and was allocated into foliage (X_1), fine root (X_2) and wood biomass (X_3) (Figure S1, available as auxiliary material).¹ Dead plant material went to metabolic (X_4) and structure litter (X_5) pools and was decomposed by microbes (X_6). Part of structure litter carbon was respired and the rest was incorporated into slow (X_7) and passive SOM (X_8). In this model, carbon cycling processes are expressed by a first-order ordinary differential equation as:

$$\begin{aligned} \frac{dX(t)}{dt} &= \xi(t)ACX(t) + BU(t) \\ X(0) &= X_0 \end{aligned} \quad (1)$$

where $X(t) = (X_1(t), X_2(t), \dots, X_8(t))$ is a vector of carbon pool sizes at a daily time step ($t = 1$ day), A is an 8×8 matrix and represents partitioning of carbon among the eight pools, C is a diagonal matrix with element vector $c = (c_1, c_2, \dots, c_8)'$, representing the exit rate of carbon left in its own pool at each time step, $U(t)$ is canopy carbon influx to the ecosystem and the input to drive the TECO model, B is a vector of allocation coefficients that distribute carbon influx to different plant pools, X_0 is initial values of carbon pool sizes, and $\xi(t)$ is an environmental scalar.

[14] In this study, carbon transfer coefficients (i.e., exit rate c) were the main target parameters to be estimated (see Table 2 for more description), the inverse of which is equal to carbon residence times in individual pools ($1/c$). Canopy carbon influx $U(t)$ was estimated by a canopy photosynthesis model from Ji [1995]. Canopy photosynthesis is a function of LAI, photosynthetically active radiation, air temperature, and soil moisture (see supplementary Text S1). Modeled carbon influx was compared with estimated daily gross primary productivity (GPP) from eddy covariance NEE measurements (Text S2). The prediction of GPP was generally consistent with estimated GPP from NEE measurements at Changbaishan, Qianyanzhou, and Dinghushan (Table 3). Estimated average annual GPP over 2003–2005 are 1207, 1610, and 1251 g C m⁻² for Changbaishan, Qianyanzhou, and Dinghushan, respectively.

[15] Allocation coefficients of canopy photosynthesis to plant pools were defined by $B = (0.13 \ 0.12 \ 0.30 \ 0 \ 0 \ 0 \ 0 \ 0)$, which indicates that 13%, 12%, and 30% of carbon influx were allocated to foliage, fine root and woody biomass pools, respectively. The remaining 45% of canopy input was consumed by plant respiration. The allocation percentages of net primary production to plant tissues and respiration were estimated from our prior knowledge for forest ecosystems [Shan *et al.*, 1993; Wen *et al.*, 1999; Luo *et al.*, 2003].

[16] An environmental scalar $\xi(t)$ was defined to represent the effects of soil temperature and moisture on carbon decomposition [Luo *et al.*, 2001]. Thus, our estimated mean residence times by probabilistic inversion were temperature

¹Auxiliary materials are available in the HTML. doi:10.1029/2009JG001004.

Table 2. Target Parameters of the TECO Model to Be Optimized and Their Prior Ranges at Three Forest Sites

Parameters	Description	Units	Changbaishan	Qianyanzhou	Dinghushan
$X_0(1)$	initial value of foliage pool	gC m ⁻²	100~400	100~400	200~400
$X_0(2)$	initial value of fine root pool	gC m ⁻²	100~400	10~200	300~400
$X_0(3)$	initial value of woody pool	gC m ⁻²	15,000~20,000	3,000~5,000	8,000~9,000
$X_0(4)$	initial value of metabolic pool	gC m ⁻²	40~100	150~300	10~100
$X_0(5)$	initial value of structural pool	gC m ⁻²	200~400	300~500	100~300
$X_0(6)$	initial value of fast SOM pool	gC m ⁻²	100~200	10~200	100~250
$X_0(7)$	initial value of slow SOM pool	gC m ⁻²	2,000~3,000	3,000~4,000	2,200~3,200
$X_0(8)$	initial value of passive pool	gC m ⁻²	4,000~6,000	1,500~4,000	4,000~5,500
c_1	exit rate of C from foliage pool	gC d ⁻¹ gC ⁻¹	1.76E-04~6.55E-03	1.76E-04~2.95E-03	1.76E-04~2.95E-03
c_2	exit rate of carbon from fine root pool	gC d ⁻¹ gC ⁻¹	1.76E-04~2.95E-03	1.76E-04~2.95E-03	1.76E-04~2.95E-03
c_3	exit rate of carbon from wood pool	gC d ⁻¹ gC ⁻¹	2.48E-05~2.74E-04	2.48E-05~2.74E-04	2.48E-05~2.74E-04
c_4	exit rate of carbon from metabolic litter pool	gC d ⁻¹ gC ⁻¹	5.48E-03~2.74E-02	5.48E-03~2.74E-02	5.48E-03~2.74E-02
c_5	exit rate of carbon from structural litter pool	gC d ⁻¹ gC ⁻¹	5.48E-04~2.74E-02	5.48E-04~2.74E-03	5.48E-04~2.74E-02
c_6	exit rate of carbon from fast soil pool	gC d ⁻¹ gC ⁻¹	2.74E-03~6.85E-02	2.74E-03~6.85E-03	2.74E-03~6.85E-03
c_7	exit rate of carbon from slow soil pool	gC d ⁻¹ gC ⁻¹	2.28E-05~4.26E-04	2.28E-05~2.84E-04	2.28E-05~2.84E-04
c_8	exit rate of carbon from passive soil pool	gC d ⁻¹ gC ⁻¹	1.37E-06~9.13E-06	1.37E-06~9.13E-06	1.37E-06~9.13E-06
a_1	fraction of carbon in foliage pool transferring to metabolic litter	-	0.7~0.8	0.7~0.8	0.7~0.8
a_2	fraction of carbon in fine root biomass transferring to metabolic litter	-	0.7~0.8	0.7~0.8	0.7~0.8
a_3	fraction of carbon in woody transferring to metabolic litter	-	0.2~0.3	0.2~0.3	0.2~0.3
a_4	fraction of carbon in metabolic litter transferring to fast SOM	-	0.3~0.7	0.3~0.7	0.3~0.7
a_5	fraction of carbon in structural litter transferring to fast SOM	-	0.1~0.3	0.1~0.3	0.1~0.3
a_6	fraction of carbon in structural litter transferring to slow SOM	-	0.1~0.3	0.1~0.3	0.1~0.3
a_7	fraction of carbon in fast SOM transferring to slow SOM	-	0.1~0.4	0.1~0.4	0.1~0.4
a_8	fraction of carbon in fast SOM transferring to slow SOM	-	0.001~0.008	0.001~0.008	0.001~0.008
a_9	fraction of carbon in slow SOM transferring to fast SOM	-	0.2~0.6	0.2~0.6	0.2~0.6
a_{10}	fraction of carbon in slow SOM transferring to passive SOM	-	0.01~0.04	0.01~0.04	0.01~0.04
a_{11}	fraction of carbon in passive SOM transferring to fast SOM	-	0.3~0.7	0.3~0.7	0.3~0.7

and moisture independent residence times. Values of off-diagonal, nonzero elements in the A matrix were given as:

$$A = \begin{pmatrix} -1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & -1 & 0 & 0 & 0 & 0 & 0 & 0 \\ a_1 & a_2 & a_3 & -1 & 0 & 0 & 0 & 0 & 0 \\ 1 - a_1 & 1 - a_2 & 1 - a_3 & 0 & -1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & a_4 & a_5 & -1 & a_9 & a_{11} & 0 \\ 0 & 0 & 0 & 0 & a_6 & a_7 & -1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & a_8 & a_{10} & -1 & 0 \end{pmatrix} \quad (2)$$

Besides carbon exit rates, the initial carbon pools and all parameters in the A matrix were also estimated simultaneously. There were a total of 19 parameters and 8 initial conditions were allowed to be estimated (Table 2). The ranges of a_i ($i = 1, 2, \dots, 11$) were estimated according to lignin and N content [Parton *et al.*, 1987; Luo and Reynolds, 1999; Luo *et al.*, 2001, 2003]. Initial values of pool sizes, X_0 , were inverted within the ranges according to measurements in relevant studies at Changbaishan [Yang and Li, 2003; Jiang *et al.*, 2005], Qianyanzhou [Li *et al.*, 2006] and Dinghushan [Fang *et al.*, 2003]. Lower and

upper limits of parameter c were set based on the model output and values reported by Luo *et al.* [2003] and Xu *et al.* [2006].

2.3. Parameter Estimation

[17] We used a Bayesian probabilistic inversion approach to estimate carbon transfer coefficients. According to Bayesian theorem, the posterior probability density function (PDF) of parameter c was expressed by

$$p(c|Z) = \frac{p(Z|c)p(c)}{p(Z)} \quad (3)$$

Table 3. Fitness Between Modeled and Observed Daily GPP at Three Forest Sites^a

Site	Sample Size	Regression Equation	R ²	RMSE (g C m ⁻² d ⁻¹)
Changbaishan	59	$y = 0.99x + 0.05$	0.86 ^b	1.72
Qianyanzhou	11	$y = 1.01x - 0.27$	0.90 ^b	0.63
Dinghushan	23	$y = 1.27x - 1.54$	0.52 ^b	1.61

^aThe observed daily GPP was derived from NEE measurements for days without missing values. Fitness was indicated by root mean square error (RMSE) and coefficient of determination (R^2).

^bSignificance $p < 0.001$.

Table 4. Standard Deviation, σ , of Observation Data Sets at Three Forest Sites

	Symbol	Changbaishan	Qianyanzhou	Dinghushan
Foliage biomass (g C m ⁻² d ⁻¹)	σ_1	1.43	0.76	0.95
Fine root biomass (g C m ⁻² d ⁻¹)	σ_2	989.2	442.6	323.1
Woody biomass (g C m ⁻² d ⁻¹)	σ_3	17.0	31.1	44.6
Litterfall (g C m ⁻² yr ⁻¹)	σ_4	17.7	11.3	12.7
Soil respiration (g C m ⁻² d ⁻¹)	σ_5	36.2	14.6	50.5
Soil organic C (g C m ⁻²)	σ_6	100.4	247.5	169.7
NEE (g C m ⁻² d ⁻¹)	σ_7	1.83	1.31	1.15

Where $p(c)$ represent prior probability density distributions, $p(Z)$ is the probability of observed data, and $p(Z|c)$ is the conditional probability density of observed data with prior knowledge, also called likelihood function for parameter c . Given the errors $e_i(t)$ follow a Gaussian distribution with a zero mean, the likelihood function can be expressed by

$$P(Z|c) \propto \exp \left\{ - \sum_i \frac{1}{2\sigma_i^2} \sum_{t \in \text{obs}(Z_i)} (e_i(t))^2 \right\} \quad (4)$$

Where $e_i(t)$ is the error for each modeled value $Y_i(t)$ compared with the observed value $Z_i(t)$ at time t , expressed by

$$e_i(t) = Z_i(t) - Y_i(t) \quad (5)$$

σ_i^2 is the measurement error variance of each data set. We assumed that each of elements $e_i(t)$ was independent over the observation times and the covariance is zero, so σ_i^2 was expressed by the variance for each observation data (Table 4).

[18] To calculate modeled variables $Y_i(t)$ from modeled pool sizes $X_i(t)$, we defined observation operators φ_i for each measurement [Luo *et al.*, 2003; Xu *et al.*, 2006; White *et al.*, 2006] as

Foliage biomass	$\varphi_1 = (1 \ 0 \ 0 \ 0 \ 0 \ 0 \ 0 \ 0 \ 0)$
Fine root biomass	$\varphi_2 = (0 \ 1 \ 0 \ 0 \ 0 \ 0 \ 0 \ 0 \ 0)$
Woody biomass	$\varphi_3 = (0 \ 0 \ 1 \ 0 \ 0 \ 0 \ 0 \ 0 \ 0)$
Litterfall	$\varphi_4 = (0.75c_1 \ 0.75c_2 \ 0.75c_3 \ 0 \ 0 \ 0 \ 0 \ 0)$
Soil organic C	$\varphi_5 = (0 \ 0 \ 0 \ 0 \ 0 \ 1 \ 1 \ 1)$
Soil respiration	$\varphi_6 = (0.25c_1 \ 0.25c_2 \ 0.25c_3 \ 0.55c_4 \ 0.45c_5 \ 0.7c_6 \ 0.55c_7 \ 0.55c_8)$
NEE	$\varphi_7 = (1 \ 1 \ 1 \ 1 \ 1 \ 1 \ 1 \ 1)$

For each biometric and soil variable, the modeled value was expressed as

$$Y_i(t) = \varphi_i X(t), \quad i = 1, 2, \dots, 6 \quad (6)$$

Daily NEE was the sum of carbon change in all pools per step time [White *et al.*, 2006], which was expressed as

$$Y_7(t) = \frac{d}{dt} \varphi_7 X(t) \quad (7)$$

The posterior PDFs for model parameters were generated from prior PDFs $p(c)$ with observations Z by a Markov chain Monte Carlo (MCMC) sampling technique. This study used the Metropolis-Hastings (M-H) algorithm [Metropolis *et al.*, 1953; Hastings, 1970] as the MCMC sampler. Whether a new point c^{new} was accepted or not according to the value of ratio $R = \frac{p(c^{new}|Z)}{p(c^{k-1}|Z)}$ compared with a uniform random number U from 0 to 1. Only if $R \geq U$, then the new point was accepted; otherwise $c^k = c^{k-1}$ (see Xu *et al.* [2006] for detailed description on MCMC sampling procedure).

[19] Five parallel runs of the M-H algorithm were performed with 20,000 simulations for each run. We assumed a Gaussian distribution for prior probability function $p(c)$ in the parameter space, and then new proposal points were generated by $c^{new} = c^{k-1} + N(0, \text{cov}^0(c))$. To find an effective proposal distribution, a test run of the M-H algorithm with 20,000 simulations was made using a uniform proposal posterior distribution. Constant variance of parameters $\text{cov}^0(c)$ was then calculated from the test run. Specific steps of the algorithm were described by Xu *et al.* [2006]. All five parallel runs started from random initial conditions in parameter spaces to eliminate the effect of initial condition on stochastic sampling. The acceptance rates for the five runs in three experiments ranged from 22 to 47% at three sites.

[20] We chose the Gelman-Rubin (G-R) diagnostic method [Gelman and Rubin, 1992] to examine whether Markov chains converged. The value of scale reduction factor for each parameter in all experiments approached to 1.0 after the first 10,000 samples (data not shown). Furthermore, means and standard deviations of posterior parameter sets were approximately stabilized after the first 10,000 samples. Thus, we regarded the first 10,000 times as the burn-in period for each MCMC run. All accepted samples from five runs after burn-in periods (about 50,000 samples) were used to compute posterior parameter statistics of modes, correlations, and 90% confidence intervals. The 90% confidence intervals were estimated from the cumulative distributions to quantify the uncertainty of estimated parameters.

2.4. Simulation Experiments and Sensitivity Analysis

[21] We designed three simulation experiments to estimate mean residence times of carbon at the three sites. The first experiment (experiment 1) used all biometric, soil and NEE data in probabilistic inversion. Biometric and soil data in this study included observed values of foliage biomass, fine root biomass, woody biomass, litterfall, soil organic carbon, and soil respiration. The second experiment (experiment 2) used

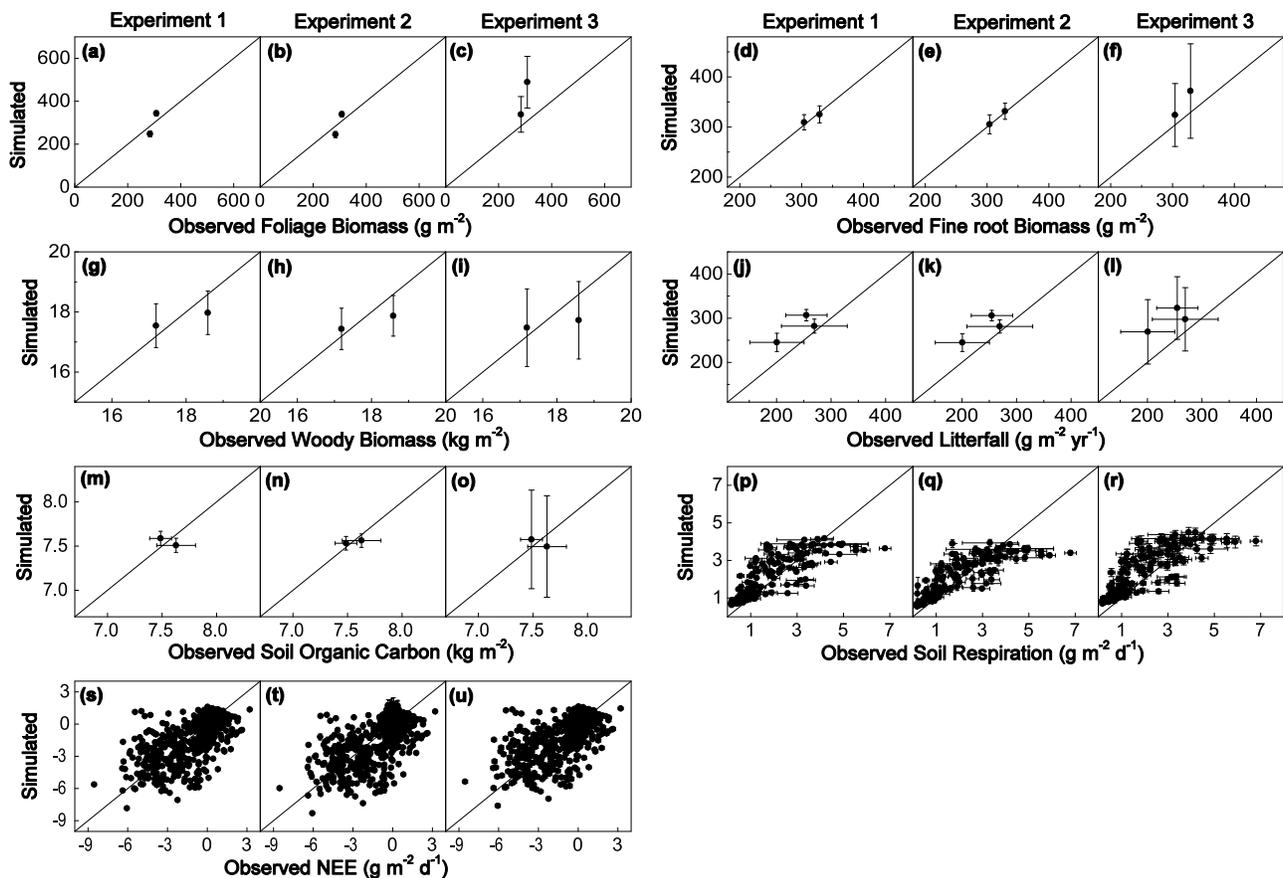


Figure 1. Comparisons between observed and modeled (a–c) foliage biomass, (d–f) fine root biomass, (g–i) woody biomass, (j–l) litterfall, (m–o) soil organic matter, (p–r) soil respiration, and (s–u) NEE at the Changbaishan site after the target parameters listed in Table 2 were optimized. For each set of plots, data-model comparisons are presented for experiment 1 (using all biometric, soil, and NEE data to constrain parameter estimation), experiment 2 (using biometric and soil data only), and experiment 3 (using NEE data only).

biometric and soil data only. The third experiment (experiment 3) only used NEE data in the inverse analysis.

[22] In this study, the inverse model, TECO (i.e., the model used for inverse analysis), uses daily GPP as input, which was estimated from another independent canopy photosynthesis model [Ji, 1995]. Ideally, we need to estimate all the parameters simultaneously in an integrated photosynthesis-carbon cycle model. In this study, we only optimized parameters in the carbon cycle model and did sensitivity analysis to explore the influence of GPP on posterior estimates of carbon transfer coefficients. Specifically, we increased or decreased values of parameters in the GPP model (Table S1) by 10% and 20%. The sensitivity analysis was conducted by a one-parameter-at-a-time method.

[23] Observation errors can substantially influence estimates of parameters. We increased the standard deviations of foliage, fine root, and woody biomass by 10% and 20%. To evaluate influences of allometric equations, we performed two Monte-Carlo simulations (1000 times) by randomly adding Gaussian noises to the allometric conversions. The standard deviations of Gaussian noises were assigned as 0.1 kg for foliage and root, 5 kg for stem and branch in Monte-Carlo simulation 1 and 0.2 kg for foliage

and root, 10 kg for stem and branch in Monte-Carlo simulation 2.

3. Results

3.1. Performance of MCMC Simulations

[24] We evaluated the performance of MCMC simulations by comparing observed and modeled values of six biometric and soil variables and NEE. Figure 1 presented comparisons among three assimilation experiments at the Changbaishan site. Overall, the model fitted biometric and soil data better than NEE when biometric and soil data were used in experiments 1 and 2 but fitted NEE better than biometric and soil variables when only NEE data were used in experiment 3 (Figure 1). If carbon residence times were inferred from NEE data together with biometric and soil data (experiment 1), the modeled NEE using the optimized residence times were improved compared with that from biometric and soil data only (experiment 2). Root mean square errors (RMSE) between modeled and observed NEE values were 1.55, 1.27 and 1.33 $\text{g C m}^{-2} \text{d}^{-1}$ in experiment 1, less than RMSE of 1.63, 1.56 and 1.62 g C m^{-2} in experiment 2 at the Changbaishan, Qianyanzhou and Dinghushan sites, respectively (Table S2). However, this

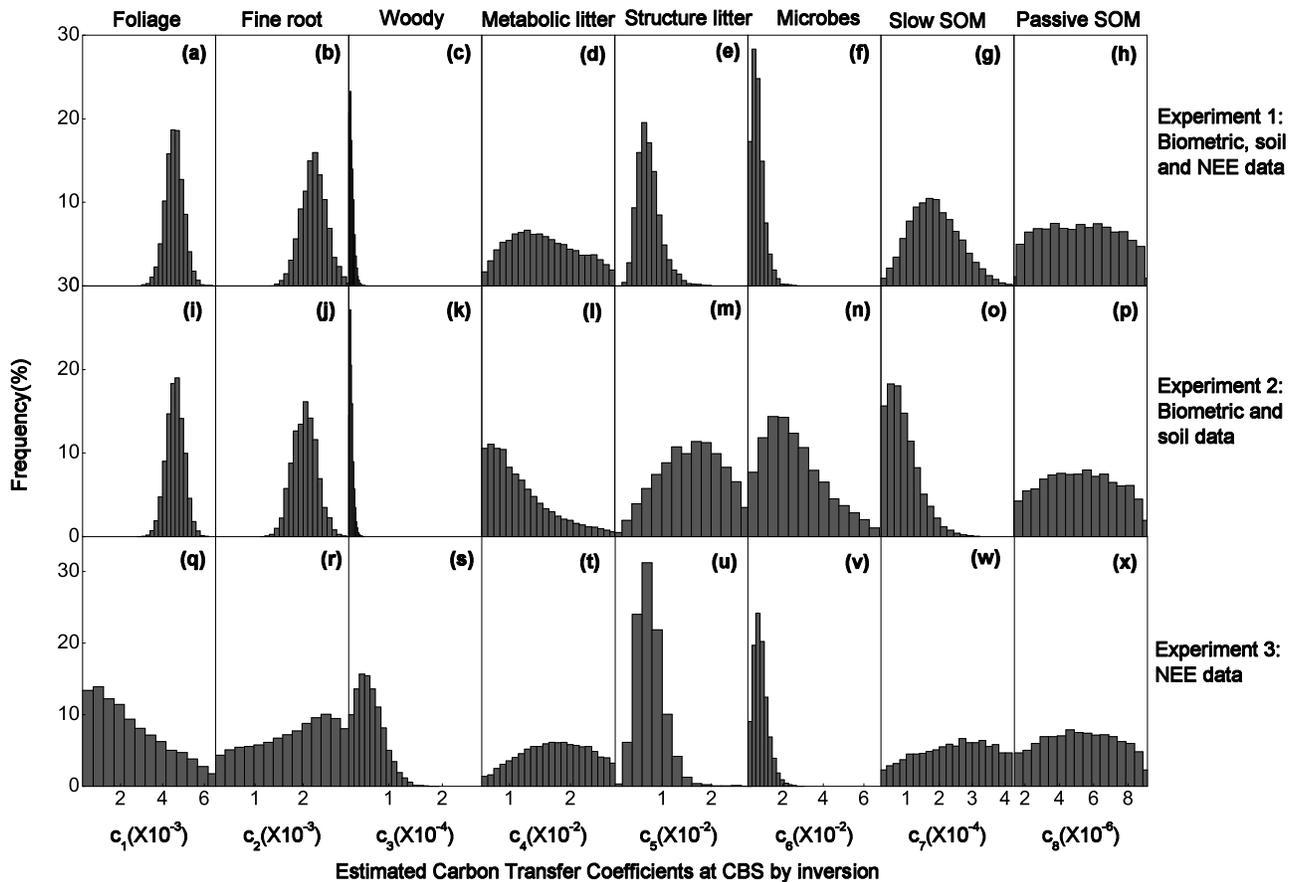


Figure 2. Posterior distributions of carbon transfer coefficients from the eight pools using all biometric, soil, and NEE data (experiment 1), biometric and soil data only (experiment 2), and NEE data only (experiment 3) for parameter constraints using the MCMC optimization approach at the Changbaishan forest site.

improvement in the agreement of modeled and observed NEE data was at the cost of lower fitness of biometric and soil variables. For instance, the RMSE between modeled and observed soil respiration were 0.89, 0.78 and 0.69 $\text{g C m}^{-2} \text{d}^{-1}$ in experiment 1 versus that of 0.84, 0.60 and 0.61 $\text{g C m}^{-2} \text{d}^{-1}$ in experiment 2 at the respective three sites (Table S2). The model overestimated soil respiration in its low range and underestimated it in the high range (Figures 1p–1r). The model underestimation in the high range was mainly reflected by 3–4 data points of high values of observed soil respiration during summers, which likely resulted from fluctuation of wind speed at the time of measurements [Luo and Zhou, 2006]. In addition, monthly measurements of litterfall were aggregated yearly for the data assimilation so that the model may not accurately simulate the seasonal variation of carbon input to soil via litterfall.

3.2. Estimated Carbon Cycle Parameters

[25] Generally, estimated parameter by probabilistic inversion can be divided into three groups: “well-constrained,” “poorly constrained,” and “edge-hitting,” depending on the shape of posterior distributions. At the Changbaishan site, for example, exit rates of carbon from foliage, fine root pools, structural litter, microbes, and slow SOM (i.e., parameters c_1 , c_2 , c_5 , c_6 , and c_7) were well

constrained by biometric, soil and NEE data in experiment 1 (Figures 2a, 2b, 2e, 2f, and 2g) and by biometric and soil data in experiment 2 (Figures 2i, 2j, 2m, 2n, and 2o). Exit rates of carbon from metabolic litter and passive SOM (parameters c_4 and c_8) were poorly constrained in three experiments (Figures 2d, 2h, 2p, 2t, and 2x) except for parameter c_4 in experiment 2 (Figure 2l). Estimated exit rate of carbon from wood pool (parameter c_3) hit the lower limit in experiments 1 and 2 (Figures 2c and 2k) but was well constrained by NEE data in experiment 3 (Figure 2s).

[26] Exit rates of carbon from foliage, fine root and woody biomass pools (parameters c_1 , c_2 , and c_3) were well constrained in experiments 1 and 2 when assimilating biometric and soil data, but cannot be constrained by assimilating NEE data alone as shown in experiment 3 (Figures 2–4). In addition, biometric and soil data provided more information of exit rate of carbon from slow SOM (c_7) than NEE data at Changbaishan and Dinghushan but Qianyanzhou. In contrast, NEE data contained more information than biometric and soil data on exit rates of carbon from structural litter and microbes, i.e., parameters c_5 and c_6 (Figures 2m, 2n, 2u, and 2v). Parameter c_4 was poorly constrained by either biometric and soil or NEE data or all data at Changbaishan and Qianyanzhou but well constrained using NEE data in experiments 1 and 3 at Dinghushan. However, NEE data was found having a strongly

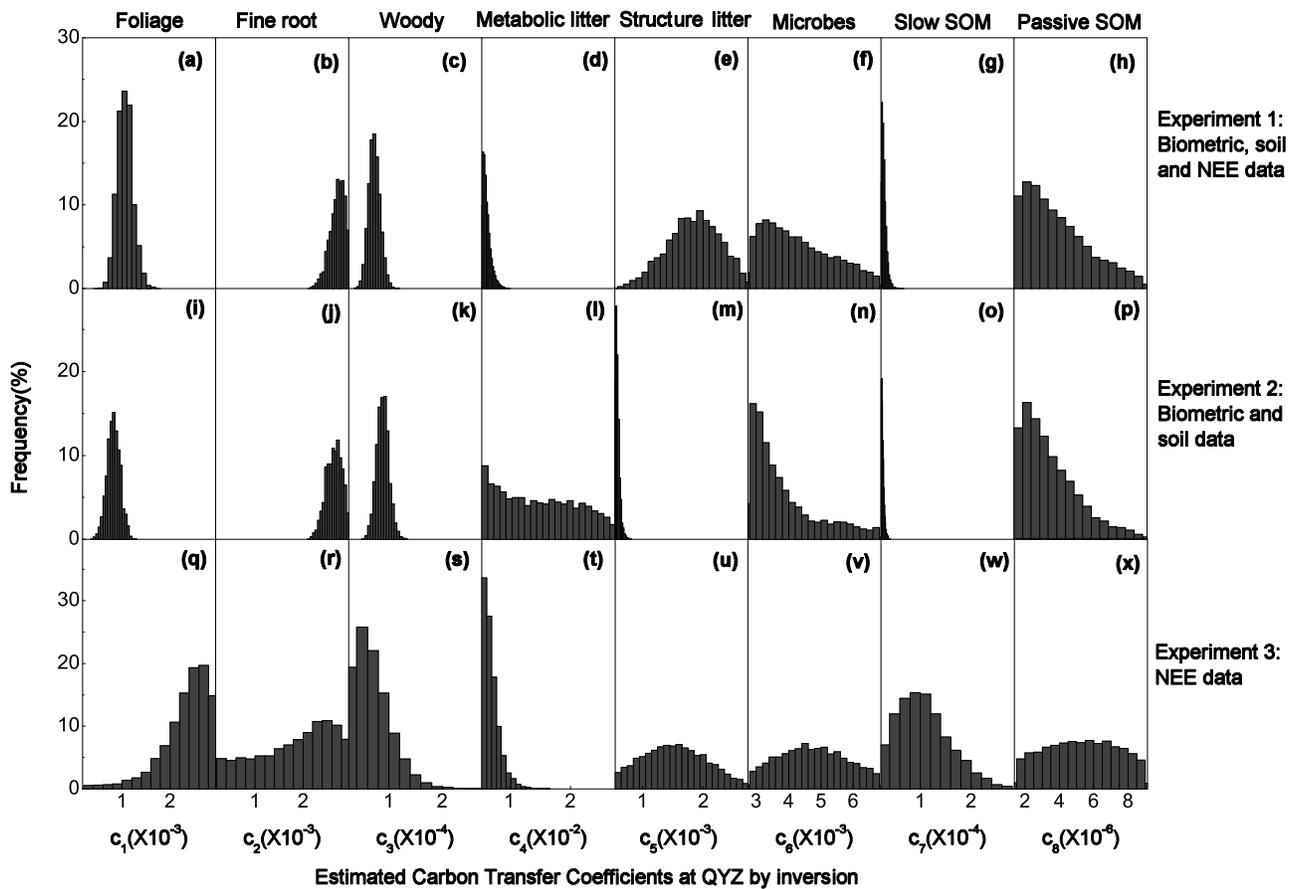


Figure 3. Posterior distributions of carbon transfer coefficients constrained by biometric, soil, and NEE data (experiment 1), biometric and soil data (experiment 2), and NEE data (experiment 3) from MCMC simulations at the Qianyanzhou site.

influence on posterior PDF of parameter c_4 at Changbaishan and Qianyanzhou (Figures 2 and 3). Either biometric and soil or NEE data or all data did not contain enough information to constrain the exit rate of carbon from passive SOM (parameter c_8) in all cases.

[27] Among eight initial carbon pools, only three initial plant pools were well constrained in experiment 1 (Figure S2) and experiment 2, other initial carbon pools cannot be estimated effectively when biometric and soil data were assimilated. Similar to carbon transfer coefficients, even initial condition of three plant pools cannot be identified in experiment 3 if only daily NEE data were assimilated. For 11 parameters in matrix A , neither biometric and soil nor daily NEE data could provide useful information to estimate them (Figure S2).

3.3. Estimated Mean Residence Times of Carbon Among the Three Sites

[28] The mean residence times of carbon are the inverse of exit rates of carbon from the pool ($1/c$). Since not all posterior distributions of the eight parameters followed Gaussian distributions, we chose the mode of the posterior distribution as the best estimate for each parameter, associated with 90% confidence interval (Table 5). The estimated mean residence times ranged from 2 to 10 months for metabolic litter and microbial biomass pools; from 1 to 3

years for foliage, fine root biomass, and structural litter pools; and from 17 to 1361 years for woody biomass, slow and passive SOM pools.

[29] Differences in the mean residence times were found among three forest ecosystems in the study (Table 5). Overall, the residence times of carbon were longer for leaf, litter and microbes pools but shorter for fine root and wood pools in the young evergreen coniferous plantation at Qianyanzhou site than the two mature mixed forests at Changbaishan and Dinghushan sites. Carbon in slow and passive organic matter pools had shorter residence times at the Changbaishan site than at the other two forest sites. Leaves stayed longer in Qianyanzhou forest (2.63 years) than in Changbaishan (1.86 years) and Dinghushan (1.85 years) forests. Mean residence times of carbon in fine root biomass at the Dinghushan site (3.02 years) was about two to three times those at the Changbaishan (1.27 years) and Qianyanzhou site (0.97 years). Moreover, mean residence times of woody biomass in the Changbaishan forest (99 years) and Dinghushan forest (104 years) were over twice that in Qianyanzhou forest (38 years). The mean residence time of carbon in the metabolic litter pool at Qianyanzhou (0.47 years) was about twice those at Changbaishan (0.22 years) and Dinghushan (0.22 years). Carbon in microbial biomass pool had a longer residence time at the Qianyanzhou site (0.82 years) than Dinghushan (0.70 years) and Chang-

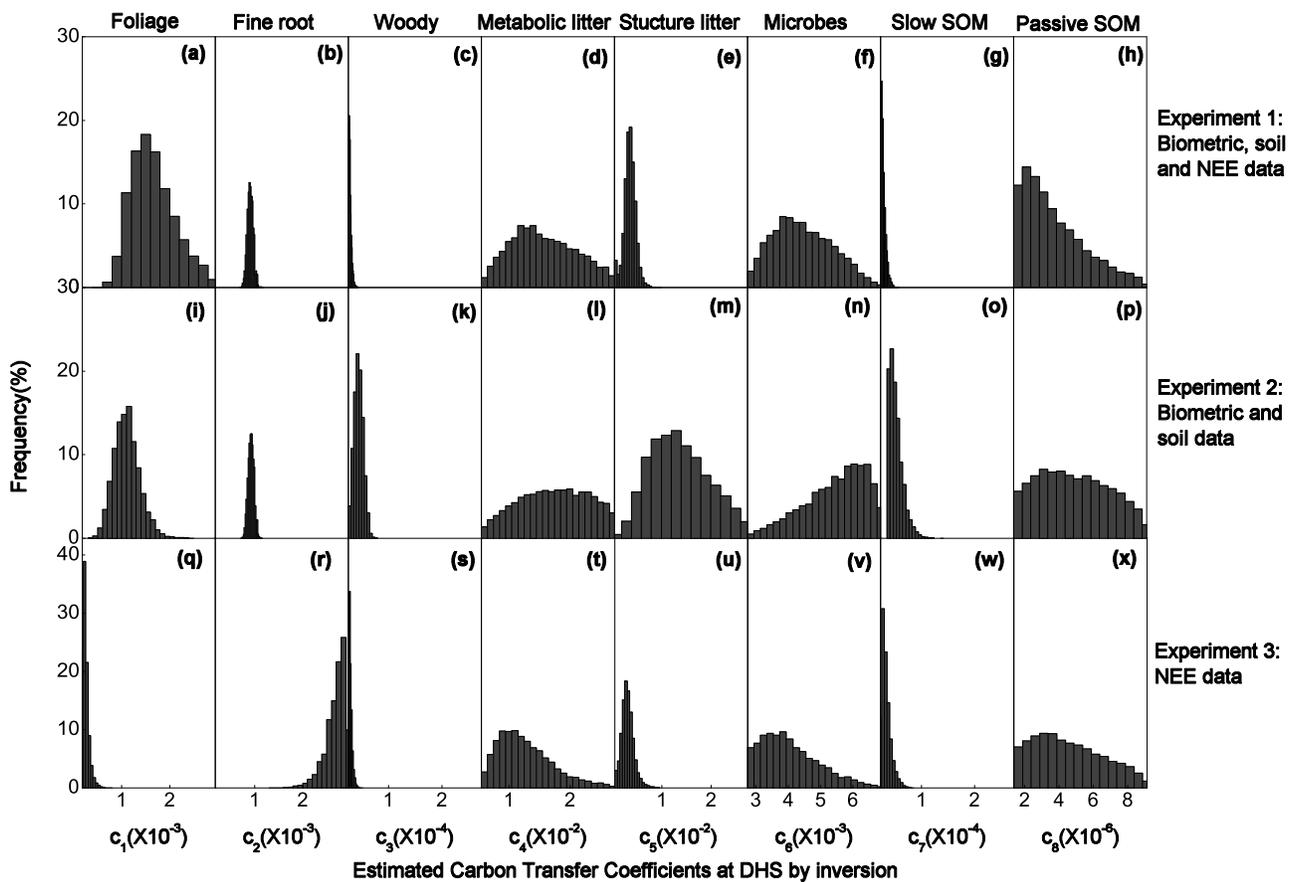


Figure 4. Posterior distributions of carbon transfer coefficients constrained by biometric, soil and NEE data (experiment 1), biometric and soil data (experiment 2), and NEE data (experiment 3) from MCMC simulations at the Dinghushan site.

baishan sites (0.48 years). Slow soil organic carbon turned over at a much slower rate about at Qianyanzhou (110 years) and Dinghushan (112 years) than at Changbaishan (17 years).

3.4. Sensitivity Analysis

[30] To examine effects of prior ranges on posterior PDFs of poorly constrained parameters, we decreased the lower limits by 1/5 and increased by fivefold the upper limits as defined in Table 2 for parameters c_4 and c_8 at the Changbaishan site. Histograms of parameters c_4 and c_8 still appeared uniform distributions (Figures 5d and 5h) given large prior ranges, and posterior estimate of parameter c_3 was also close to the lower limit (Figure 5c). Furthermore,

we decreased the standard deviations of woody biomass, litterfall, and SOC data by half (i.e., increased their weights in likelihood function by four times) to examine their effects on parameters c_3 , c_4 and c_8 . Similar to Figure 2, well-constrained parameters (i.e., parameters c_1 , c_2 , c_5 , c_6 and c_7) were not influenced. Parameter c_3 was still edge-hitting within its prior range, and parameters c_4 and c_8 also followed the similar distributions as Figure 2 (data not presented).

[31] In addition, estimated parameters were influenced by sample sizes of NEE data. When we decreased the sample size of NEE data with, for example, only 59 data points without gap filling over three years at the Changbaishan site in combination with biometric and soil data, posterior

Table 5. Estimated Modes and Confidence Intervals of Potential Carbon Residence Times in Eight Pools at Three Forest Sites^a

Pool	Changbaishan		Qianyanzhou		Dinghushan	
	Mode	90% CI	Mode	90% CI	Mode	90% CI
Foliage biomass	1.86	(1.58, 2.16)	2.63	(2.06, 3.40)	1.85	(1.08, 2.70)
Fine root biomass	1.27	(1.03, 1.52)	0.97	(0.94, 1.13)	3.02	(2.71, 3.39)
Woody biomass	99.2	(71.0, 108.3)	37.7	(29.9, 49.0)	104.1	(82.2, 109.2)
Metabolic litter	0.22	(0.11, 0.36)	0.47	(0.36, 0.49)	0.22	(0.11, 0.35)
Structural litter	0.41	(0.23, 0.64)	1.44	(1.09, 2.50)	0.73	(0.50, 1.72)
Microbial biomass	0.48	(0.20, 0.76)	0.82	(0.44, 0.94)	0.70	(0.45, 0.88)
Slow soil organic matter	16.7	(8.7, 37.6)	109.7	(72.8, 117.8)	111.7	(73.3, 117.9)
Passive soil organic matter	715.8	(320.0, 1446.5)	1081.7	(357.8, 1699.3)	1361.2	(369.4, 1712.7)

^aCI, confidence intervals. Units are in years. Note: We assumed that the carbon in leaf biomass transferred to litter pools from August to November at Changbaishan site.

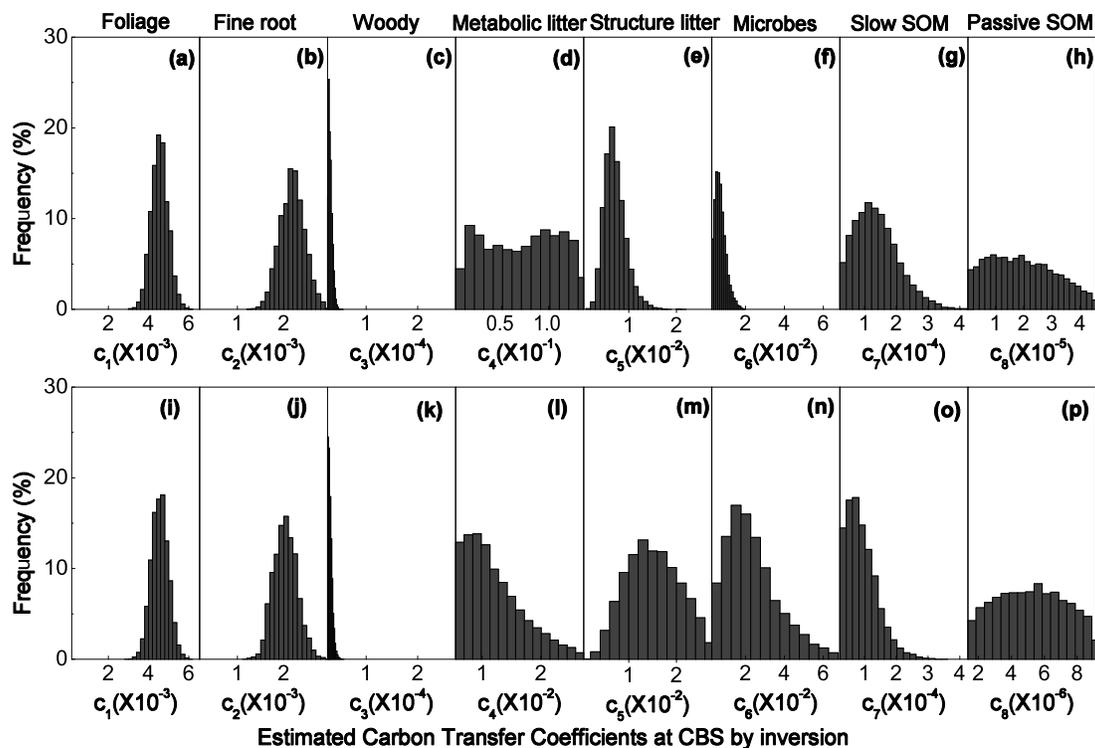


Figure 5. Posterior distributions of carbon transfer coefficients when (a–h) the lower limits of parameters c_4 and c_8 are reduced by 1/5 and the upper limits of parameters c_4 and c_8 are increased fivefold and (i–p) constrained by biometric and soil in combination with non-gap-filled NEE data (i.e., 59 observed NEE data only) at the Changbaishan site.

estimation of parameters (Figures 5i–5p) appeared similar to that using biometric and soil data only (Figures 2i–2p). The negative log likelihood value for NEE data decreased from 252.3 to 19.3 (Table S3), indicating substantially weakened contribution of NEE data to parameter estimation.

[32] Estimation of carbon transfer coefficients among plant and soil pools is influenced by carbon input from photosynthesis. Accordingly, parameters of the GPP model were another source of uncertainty in determining the posterior distributions of carbon transfer coefficients. Among eight parameters of the GPP model (Table S1), predicted GPP was most sensitive to optimum temperature for photosynthesis (T_{opt}) and quantum yield (α) (Table S4). When T_{opt} increased or decreased by 10% and 20%, predicted GPP changed by 6.5–8.9% and 11.9–16.5%, respectively. Consequently, variations in GPP introduced uncertainties to estimated carbon transfer coefficients, especially for parameters c_4 , c_7 , and c_8 (Figure 6a).

[33] We also evaluated the possible influences of observation errors and allometric equations on estimated parameters. Increases in standard deviations of foliage, fine root, and woody biomass by 10% and 20% did not affect much transfer coefficients from three plant pools but influenced the transfer coefficient from the microbial carbon pool by 40.5% and 67.4% (Figure 6b). The two Monte-Carlo simulations showed that Gaussian random errors added to the allometric equations resulted in large variations in posterior estimates of c_8 by 33.7% in Monte-Carlo simulation 1 and 40.7% in Monte-Carlo simulation 2 (Figure 6b). Cross-correlation analysis for posterior parameters showed

less significant correlations between pairs of the 27 parameters in the probabilistic inversion, except for the pair of parameters $X_0(7)$ and $X_0(8)$ with a strong negative correlation (Text S3).

4. Discussion

4.1. Constraints of Carbon Transfer Coefficients by NEE, Biometric, and Soil Data

[34] This study compared the effectiveness of biometric and soil versus daily NEE data for estimation of carbon exit rates from individual plant and soil pools. Biometric data were found to be effective in constraining exit rates of carbon from plant pools (parameters c_1 , c_2 , and c_3). Biomass in those foliage, fine root, wood pools and litterfall (i.e., flux) can be directly measured and corresponded to variables in the model. Even limited data points can provide enough information on carbon transfer from plant to litter.

[35] As for the estimation of transfer coefficients of litter and soil carbon, *Xu et al.* [2006] used six biometric and soil data sets to estimate carbon transfer coefficients and found that the transfer coefficients of metabolic litter, microbes, and passive SOM pools were poorly constrained. Our inverse analysis with either biometric and soil or all data in the three forest ecosystems of China showed that NEE data contain substantial information on constraints of exit rates of carbon from metabolic litter (c_4), structural litter (c_5), and microbes (c_6). It suggests that NEE data can be used to help estimate transfer coefficients of litter and microbial biomass together with biometric and soil data. Because eddy covariance systems measure exchange of

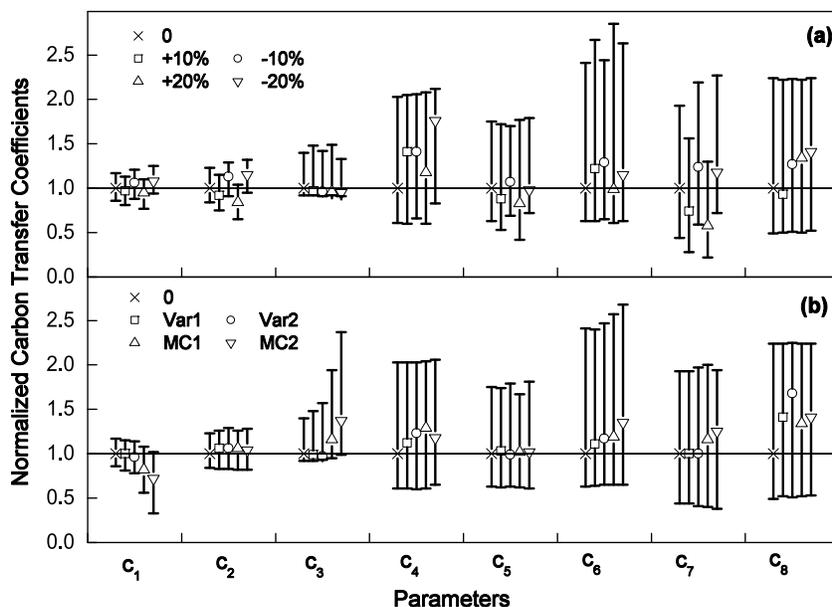


Figure 6. Sensitivity analysis of estimated carbon transfer coefficients with (a) optimum temperature for photosynthesis (T_{opt}) varying by $\pm 10\%$ and $\pm 20\%$; (b) variances of foliage, fine root, and woody biomass data increasing by 10% (Var1) and 20% (Var2), and added random errors to allometric relationships by Monte-Carlo simulations 1 (MC1) and 2 (MC2). Symbols show posterior modes, and error bars represent 90% confidence interval.

CO_2 between the atmosphere and ecosystems with high frequency, daily NEE data provide more information on fast turnover pools (with residence times of several months) than the biometric and soil measurements as showed in this study.

[36] Biometric and soil data also provided some information for constraints of carbon exit rate from slow SOM (c_7), as shown in Figures 2o and 4o. When NEE data were used together with biometric and soil data, the posterior estimate of c_7 differs from that with biometric and soil data alone, probably because NEE provided information to differentiate some cross correlations between c_7 and other parameters. Due to lack of long-term observation of soil carbon, neither biometric and soil, nor NEE data were effective to constrain the exit rate of carbon from passive SOM pool (c_8). Therefore, the estimate of c_8 was strongly influenced by the prior range assigned. A better estimate of this parameter requires long-term SOM observation.

4.2. Estimated Carbon Residence Times

[37] Our best estimates of carbon mean residence times of about 1.9–2.6 years in foliage biomass for three forest ecosystems are well consistent with the inversion result from tall forest, open woodland and arid shrubland biomes in Australia (1.2–2.5 years) [Barrett, 2002]. Results from this probabilistic inversion showed that leaves of vegetation in the evergreen coniferous forest (Qianyanzhou) turned over slower than in coniferous and broad-leaved mixed forest (Changbaishan and Dinghushan), which reflected the variations in leaf life spans with forest types and climatic regimes. Leaf life span of conifers is generally longer than broadleaves, and increases with higher altitude and elevation. The woody tissues at three forest sites in eastern China are shorter-lived than that in tall forest biome in Australia

(138–227 years) [Barrett, 2002] but longer than that in southeast Sweden forests (10–50 years) [Karlberg *et al.*, 2006]. Among the three sites, the turnover time of wood in plantation (Qianyanzhou) was less than in natural mixed forest (Changbaishan) and seminatural mixed forest (Dinghushan), probably due to the differences in forest age and woody biomass pool size.

[38] Carbon was decomposed more slowly and resided longer in Qianyanzhou evergreen plantation, compared with that in Duke Forest with a similar age [Luo *et al.*, 2003; Xu *et al.*, 2006]. The differences in estimated residence time could result from more carbon inputs ($1610 \text{ g m}^{-2} \text{ a}^{-1}$ for Qianyanzhou forest versus $1307 \text{ g m}^{-2} \text{ a}^{-1}$ for Duke Forest) and less aboveground biomass and litterfall ($300\text{--}340 \text{ g m}^{-2} \text{ a}^{-1}$ for Qianyanzhou forest versus $350\text{--}550 \text{ g m}^{-2} \text{ a}^{-1}$ for Duke Forest) under seasonal drought in summer at Qianyanzhou.

[39] To compare inverted residence time of fine root with that estimated from isotope techniques, we calculated average mean residence times at Changbaishan (1.7 years), Qianyanzhou (0.3 years), and Dinghushan (0.7 years) using local mean annual temperature and mean soil moisture together with the environmental scaler $\xi(t)$ in equation (1). Fine root turnover time usually ranges from weeks to three years [Edwards and Harris, 1977; Hendrick and Pregitzer, 1992; Matamala and Schlesinger, 2000]. Our estimated residence time for fine root is well within this range but lower than the residence time (4.2–5.7 years) estimated from $\delta^{13}\text{C}$ signals [Johnsen *et al.*, 2005; Matamala *et al.*, 2003]. Recent studies also found that isotope techniques tended to systematically overestimate residence times of fine roots due to sampling biases of different root cohorts by missing the smallest and most ephemeral roots from soil cores [Luo, 2003; Strand *et al.*, 2008].

[40] Our results also showed that soil organic carbon in the natural mature forest at Changbaishan was decomposed faster than that in the evergreen plantation at Qianyanzhou and seminatural successional forest at Dinghushan. Especially, the potential residence times of slow SOM pools varied by 1 order of magnitude among the three forests. The differences may stem from soil physical and chemical properties and microbial community structure for different soil types (dark brown forest soil at Changbaishan while red soil at Qianyanzhou and latosolic red soil at Dinghushan), since the climatic effects on decomposition have been considered in the probabilistic inversion. It was still difficult to identify and quantify how these factors influence decomposition of litter and soil organic carbon among the three forest ecosystems.

4.3. Uncertainties in Estimating Carbon Residence Times

[41] Uncertainties of carbon residence times estimated by probabilistic inversion primarily derived from prior estimates for parameters, data properties such as error type and magnitude, fixed parameters, cross correlations among different data and self-correlations with time, and model structure [Luo *et al.*, 2009]. In this study, we examined the effects of priors, error variance of observations, and carbon input on estimated parameters by sensitivity analysis. Overall, the constraints of NEE, biometric and soil data on carbon transfer coefficients or residence times were not weakened under various parameter ranges, observation error variances, and carbon input, but the best estimates of parameters did change, especially for litter and soil carbon pools (Figure 6). Among these possible uncertainty sources, posterior estimation of transfer coefficients was most sensitive to parameters of the GPP model and observation errors. The sensitivities of estimated transfer coefficients to parameters of the GPP model and observation errors of biomass increased if additional 19 parameters were included with eight carbon transfer coefficients in Monte Carlo sampling, which probably resulted from the equifinality of parameters. In that case, the utilization of additional information on prior estimates for the parameters and other kinds of observations, or the fixation of some parameters might reduce the uncertainty [Wang *et al.*, 2009]. Estimated transfer coefficients were also influenced by sample sizes of NEE data in multiple constraints (Figure 5). We need more studies to determine how much information provided by each data set would be enough to constrain parameter estimation in future.

[42] Estimated residence times in this study varied with parameterization of the GPP model, error properties and their covariance of data sets, and model structure of TECO. It is still a difficult task to determine error types, cross correlations among different data and self-correlations with time, and model errors. Commonly the assumption of a Gaussian error distribution was used when we knew nothing about error properties, as did in this study. However, eddy flux measurement error was found follow a double exponential distribution [Hollinger and Richardson, 2005; Richardson *et al.*, 2006] due to a superposition of almost Gaussian distributions with standard deviations varying by flux magnitude [Lasslop *et al.*, 2008]. Different choices of cost functions according to error distribution of NEE

measurement led to big variations in parameter estimates and model predictions [Richardson and Hollinger, 2005]. It is yet to be determined how much variation of parameter estimates will result from different error distributions for NEE in multiple constraints. In addition, Sacks *et al.* [2006] compared different model structures of SIPNET using best estimates of parameters, which could be another source of uncertainty in parameter estimation.

5. Conclusions

[43] We conducted three parameter estimation experiments with different data sets to estimate carbon residence times based on an eight-pool terrestrial ecosystem (TECO) model. We found that biometric, soil and NEE data are complementary in constraining mean residence times. Residence times of three plant pools and slow soil organic matter were well constrained by biometric and soil data, whereas residence times of metabolic and structural litter, and microbial biomass pools were constrained by NEE data. We therefore suggest that combined measurements of slow carbon pools and fast fluxes are most effective to constrain estimation of model parameters and state variables. Our sensitivity analysis suggested that estimated carbon residence times varied with gross primary production and the volume of NEE data. It is highly desirable in future study to use an integrated canopy photosynthesis and ecosystem carbon cycle model to evaluate the confidence of parameter estimation and model predictions.

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