

Modeling the impact of drought on canopy carbon and water fluxes for a subtropical evergreen coniferous plantation in southern China through parameter optimization using an ensemble Kalman filter

W. Ju¹, S. Wang², G. Yu², Y. Zhou³, and H. Wang²

¹International Institute for Earth System Science, Nanjing University, Nanjing, 210093, China

²Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing, 100101, China

³School of Geography and Oceanography, Nanjing University, Nanjing, 210093, China

Received: 6 July 2009 – Published in Biogeosciences Discuss.: 21 August 2009

Revised: 11 February 2010 – Accepted: 19 February 2010 – Published: 3 March 2010

Abstract. Soil and atmospheric water deficits have significant influences on CO₂ and energy exchanges between the atmosphere and terrestrial ecosystems. Model parameterization significantly affects the ability of a model to simulate carbon, water, and energy fluxes. In this study, an ensemble Kalman filter (EnKF) and observations of gross primary productivity (GPP) and latent heat (LE) fluxes were used to optimize model parameters significantly affecting the calculation of these fluxes for a subtropical coniferous plantation in southeastern China. The optimized parameters include the maximum carboxylation rate ($V_{c_{max}}$), the slope in the modified Ball-Berry model (M) and the coefficient determining the sensitivity of stomatal conductance to atmospheric water vapor deficit (D_0). Optimized $V_{c_{max}}$ and M showed larger variations than D_0 . Seasonal variations of $V_{c_{max}}$ and M were more pronounced than the variations between the two years. $V_{c_{max}}$ and M were associated with soil water content (SWC). During dry periods, SWC at the 20 cm depth explained 61% and 64% of variations of $V_{c_{max}}$ and M , respectively. EnKF parameter optimization improved the simulations of GPP, LE and SH, mainly during dry periods. After parameter optimization using EnKF, the variations of GPP, LE and SH explained by the model increased by 1% to 4% at half-hourly steps and by 3% to 5% at daily time steps. Further efforts are needed to differentiate the real causes of parameter variations and improve the ability of models to describe the change of stomatal conductance with net photosynthesis rate and the sensitivity of photosynthesis capacity to soil water stress under different environmental conditions.

1 Introduction

Carbon (C) and water fluxes between the atmosphere and terrestrial ecosystems are interactively linked at various temporal and spatial scales (Rodrigues-Iturbe, 2000). Two major components of the terrestrial C cycle (C fixation through photosynthesis and C release through heterotrophic respiration) are strongly regulated by soil water content (SWC) (Barr et al., 2006). Consequently, SWC is a key determinant of net ecosystem productivity (NEP) of a terrestrial ecosystem (Grainer et al, 2003). Photosynthesis peaks when SWC is near the field capacity and decreases with the departure of SWC from this optimum. When soil or atmospheric water is insufficient, leaf stomatal conductance reduces and correspondingly CO₂ fixation is limited (Dang et al., 1997; Hogg et al., 2000; Grant et al., 2006a). Extensive studies have demonstrated the influence of SWC on C fixation at leaf (Infante et al., 1999; Lawlor, 1995) and canopy (Reichstein et al., 2002; Rambal et al., 2003) levels. For three Mediterranean evergreen forests, drought caused light-saturated ecosystem gross C fixation and day-time averaged canopy conductance to decline by up to 90% and ecosystem water-use efficiency relative to the gross C fixation to decrease (Reichstein et al., 2002). The heat and drought hitting Europe in 2003 caused a 30% reduction in the continental gross primary productivity (GPP) (Ciais et al., 2005). The sensitivity of GPP to drought depends on vegetation species. In the boreal region of Canada, the decreasing degree of GPP caused by drought during 2001 to 2003 was larger for Aspen than for Jack Pine and Black Spruce (Kljun et al., 2005). The heat and drought in 2003 in Europe caused larger reductions in GPP in temperate deciduous beech and northern Mediterranean forests than in other ecosystems (Ciais et al., 2005; Granier et al., 2007).



Correspondence to: W. Ju
(juweimin@nju.edu.cn)

Models are useful tools to estimate regional/global terrestrial C budget. However, large discrepancy exists in outputs by models due to differences in model structure, input data, and parameters. The reliability of a model to simulate terrestrial C and energy fluxes depends, to a great extent, on its ability to simulate SWC dynamics and the influence of SWC on C sequestration. Performance of models in simulating the decline of C sequestration caused by soil and atmospheric dryness is quite different (Grant et al., 2006b). Accurate estimation of model parameters is critically important for modeling surface fluxes (Wolf et al., 2006). However, not all model parameters are measurable, especially at canopy level. And some parameters are not temporally constant. Properly determining parameter values is always a big challenge for modelers.

The availability of long-term measurements of CO₂, water and energy fluxes using the eddy covariance (EC) technique in different ecosystems provides opportunities to optimize model parameters to which simulated CO₂, water, and energy fluxes are very sensitive. Various parameter optimization methods have been successfully adopted in combination with EC measurements to optimize model parameters and to analyze the seasonality of parameters. Parameter optimization can be implemented by minimizing a cost function constructed on the basis of one or several criteria quantifying the differences between simulated fluxes and corresponding measurements (Aakto et al., 2004; Owen et al., 2007; Reichstein et al., 2003; Wang et al., 2007; Wolf et al., 2006) or by using the ensemble Kalman filter based approach (Mo et al., 2008). The cost function can be resolved at different temporal intervals to identify the seasonal variations of parameters. Through inverting a mechanistic model every five days, Reichstein et al. (2003) found that both active leaf area and photosynthetic capacity ($V_{c_{max}}$) declined during the drought period for three Mediterranean forest ecosystems. With the inclusion of drought-dependent parameter variations, the model's ability to simulate hourly gross CO₂ uptake and transpiration was greatly improved. In a pristine grassland-forb steppe, inverted $V_{c_{max}}$ and m (the Ball-Berry coefficient) also had large seasonal variations (Wolf et al., 2006). Recently, Mo et al. (2008) studied the trajectories of model parameters for an old aspen stand in Canada at daily time steps using an ensemble Kalman filter-based algorithm with EC measurements of GPP, ecosystem respiration and latent heat. Inverted parameter values (clumping index, $V_{c_{max}}$ and m) showed distinct interannual and seasonal variations. Keenan et al. (2008) declared that for Mediterranean forest, changes in photosynthetic capacity not related to stomatal closure under water stressed conditions are very important for simulating surface carbon and water fluxes.

Water availability is an important ecological factor affecting C sequestration of terrestrial ecosystems in China (Yu et al., 2006). Long-term CO₂ flux measurements at 8 stations in China show a positive linear relationship between annual NEP and precipitation across biomes with different

water availability conditions. In tropical and subtropical regions of China with monsoon climates, seasonal and inter-annual variability of precipitation are considerable. In these regions, although annual precipitation is normally plentiful, seasonal droughts occur frequently and influence terrestrial C sequestration. The decrease in terrestrial C sequestration under seasonal drought conditions is determined by the accumulation of soil water deficits and a co-occurrence of high temperatures (Sun et al., 2006). On the basis of modeling analysis, Gu et al. (2008) found that drought caused NEP of a subtropical coniferous plantation in southern China to decrease by 63% and 47% in 2003 and 2004, respectively. At this site, C fixation was more sensitive to drought than ecosystem respiration. Soil drought has a much larger influence on NEP than atmospheric drought. Therefore, it is of importance for reliable estimation of terrestrial C balance in China to study the impact on C sequestration by soil and atmospheric water deficits. Although some observational and modeling research have been conducted to study the response of C sequestration by forests to drought in subtropical region of China (Sun et al., 2006; Gu et al., 2008), drought driven changes of model parameters have not been studied yet.

The objectives of this study are: (1) to study the inter-annual and seasonal variations of model parameters significantly affecting the calculations of canopy C and water exchange; (2) to analyze the linkage between variations of parameters and SWC; (3) to investigate the improvement in simulated canopy C and water fluxes by the inclusion of drought-dependent parameters. To achieve these objectives, the BEPS (Boreal Ecosystem Productivity Simulator) model (Ju et al., 2006) was optimized using eddy covariance measurements of GPP and latent heat fluxes (LE) taken over a subtropical coniferous plantation at QianYanZhou ecological station (QYZ), located in southeastern China.

2 Materials and methods

2.1 Site description

The QYZ ecological station (115°01'13" E, 26°44'48" N) is located at the southwest portion of Jiangxi province (Fig. 1). This site belongs to the typical red earth hilly region in the mid-subtropical monsoon landscape zone of southeastern China. The mean annual temperature is 17.9°C and annual precipitation is 1542.4 mm during 1985–2002. The vegetation is mainly evergreen coniferous trees planted after 1985, including *Pinus massoniana*, *Pinus elliottii engelm*, and *Cunninghama Lanceolata*. An above-canopy flux system mounted in a 39.6 m tower has been in operation to record half-hourly exchanges of CO₂, H₂O and energy fluxes between the ecosystem and atmosphere and meteorological conditions since September, 2002 (Liu et al., 2006). This site is a typical plantation ecosystem in Jiangxi province, in which vegetation restoration (mainly reforestation and

afforestation) has been widely and successfully practiced in the past three decades. Therefore, parameters optimized at this site can be used for investigating the effect of vegetation restoration on C sequestration in this region.

2.2 Data used

Half-hourly measurements of air temperature, incoming solar radiation, relative humidity, wind speed and precipitation during 2003 and 2004 were used for driving the BEPS model. The forest at QYZ is an evergreen coniferous plantation. The seasonal variability of leaf area index (LAI) is relative small (Huang et al., 2007). LAI was estimated from photosynthetically active radiation (PAR) measured above and below the canopy in clear days (Baldocchi et al., 1994). These estimated LAI values were averaged to produce monthly mean LAI, which was used to drive the model. Figure 2 shows the temporal trend of LAI, varying from 3.2 to 3.9 in two years. The maximum of LAI is larger in 2004 than in 2003.

Measurements of latent heat (LE) and CO₂ fluxes using the EC method (Liu et al., 2006) are used for parameter optimization. The missed NEP data were filled using the Michaelis-Menten equation (Liu et al., 2006). Missed LE data were filled using the Penman-Monteith equation. In order to reduce the influence of observation noises on parameter optimization, the flux data were checked in two steps. The methodology of Song et al. (2006) was first used to exclude abnormal records of half-hourly NEP and LE data. Then, if the summation of LE and sensible heat fluxes are below 70% or above 125% of the measured above-canopy net energy flux, the LE data was marked as abnormal values. GPP was derived from measured NEP, air temperature, and SWC (Wen et al., 2006). The averages of measured GPP and LE for the period between 9:00 and 17:00 were calculated for parameter optimization.

2.3 Model description

The BEPS model used in this study includes a module for photosynthesis calculation (Chen et al., 1999), a soil biogeochemical module for soil C, N and heterotrophic respiration simulations following CENTURY (Parton et al., 1993), and a land surface scheme for the computations of energy balance, sensible and latent heat fluxes, soil water and soil temperature status (Ju et al., 2006). GPP is calculated by scaling leaf-level Farquhar's biochemical model (Farquhar et al., 1980) up to canopy-level implemented through a sunlit and shaded leaves separation algorithm (Chen et al., 1999). Fluxes of C, water, and energy are separately simulated for sunlit and shaded leaves. Details about the model are described in Ju et al. (2006). We only highlight processes directly related to parameter optimization here.

GPP is calculated as:

$$\text{GPP} = A_{\text{net,sunlit}}\text{LAI}_{\text{sunlit}} + A_{\text{net,shaded}}\text{LAI}_{\text{shaded}} \quad (1)$$

where $A_{\text{net,sunlit}}$ and $A_{\text{net,shaded}}$ are net photosynthesis rates of sunlit and shaded leaves ($\text{mol m}^{-2} \text{s}^{-1}$), respectively, calculated using the leaf level Farquhar model (Farquhar et al., 1980; Chen et al., 1997); $\text{LAI}_{\text{sunlit}}$ and $\text{LAI}_{\text{shaded}}$ are the leaf area index of sunlit and shaded leaves, respectively.

The bulk stomatal conductance of the sunlit and shaded leaves for water vapor ($G_{s,i}$, $\text{mol m}^{-2} \text{s}^{-1}$) is calculated using a modified version of Ball-Woodrow-Berry (Ball et al., 1987) empirical model following Leuning (1995):

$$G_{s,i} = G_{o,i} + \frac{f_w m A_{\text{net},i}}{(C_{s,i} - \Gamma)(1 + D_{s,i}/D_0)} \quad (2)$$

where $G_{o,i}$ is the residual conductance ($\text{mol m}^{-2} \text{s}^{-1}$); f_w is a parameter describing the sensitivity of $G_{o,i}$ to soil water availability, m is the Ball-Berry coefficient; $C_{s,i}$ is the CO₂ concentration at the leaf surface ($\mu\text{mol mol}^{-1}$); $D_{s,i}$ is the vapor pressure deficit at the leaf surface (kPa); and D_0 is an empirical parameter determining the sensitivity of stomatal conductance to vapor pressure deficit (kPa), and Γ is the compensation point ($\mu\text{mol mol}^{-1}$).

In Eq. (2), parameters f_w and m work together to link stomatal conductance with the net photosynthesis rate. f_w can be empirically determined by soil water content (Wang and Leuning, 1998), soil water potential (Zierl, 2003) or leaf water potential (Tuzet et al., 2003). In the optimization, f_w and m are grouped together and Eq. (2) was rewritten as:

$$G_{s,i} = G_{o,i} + \frac{M A_{\text{net},i}}{(C_{s,i} - \Gamma)(1 + D_{s,i}/D_0)} \quad (3)$$

where M is a parameter representing the sensitivity of stomatal conductance to net photosynthesis rate, named as the slope of the modified Ball-Berry model in the flowing sections.

LE is simulated as:

$$\text{LE} = (T_r + E_i + E_g)\lambda \quad (4)$$

where T_r is the transpiration rate from canopy ($\text{kg m}^{-2} \text{s}^{-1}$); E_i and E_g are evaporation rates of intercepted water from canopy and ground surface ($\text{kg m}^{-2} \text{s}^{-1}$), respectively; and λ is the latent heat of water vaporization. Sublimation is not considered at this subtropical forest site.

Canopy transpiration is calculated as the summation of transpired loss from sunlit and shaded leaves. Following Wang and Leuning (1998), transpiration from sunlit ($i = 0$) and shaded ($i = 1$) leaves is computed as:

$$T_{r,i} = \rho C_p / \gamma [(D_a + \Delta(T_{s,i} - T_a)) / (r_b + r_a + 1/G_{s,i})] \quad (5)$$

where ρ is the air density (kg m^{-3}); C_p is the specific heat of air at constant temperature ($=1010 \text{ J kg}^{-1} \text{ }^\circ\text{C}^{-1}$); γ the psychrometric constant ($\text{kPa }^\circ\text{C}^{-1}$); D_a is the atmospheric vapor pressure deficit (kPa); Δ is the rate of change of the saturated vapor pressure with temperature ($\text{kPa }^\circ\text{C}^{-1}$); $T_{s,i}$ and T_a are temperatures at leaf surface and of air ($^\circ\text{C}$), respectively; r_a and r_b are boundary layer and aerodynamic resistance (s m^{-1}), respectively.

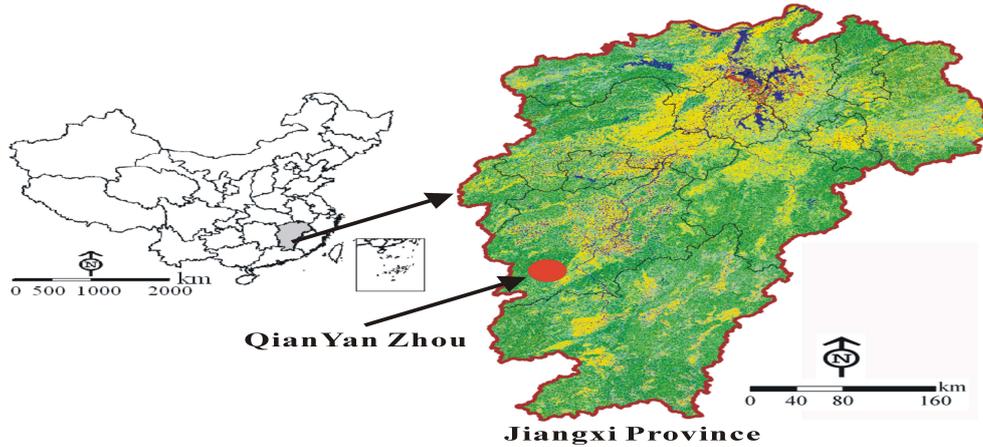


Fig. 1. The location of the study site. Green colored areas are forests. The red solid circle represent the QianYanZhou Ecological station.

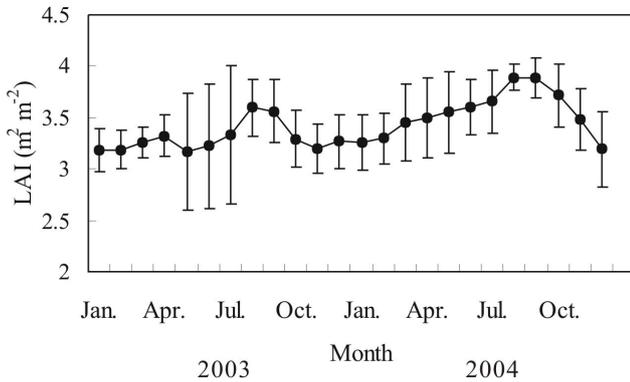


Fig. 2. Monthly LAI derived from photosynthetically active radiation measured above and below the canopy in years 2003 and 2004. Error bars represent standard deviations of estimated LAI in each month.

2.4 Parameter optimization

Model parameter optimization was implemented using a dual state-parameter estimation method based on the ensemble Kalman filter (Moradkani et al., 2005; Mo et al., 2008). The parameter ensembles are updated as:

$$\theta_{t+1}^{i+} = \theta_{t+1}^{i-} + K_{t+1}^{\theta} (y_{t+1}^i - \hat{y}_{t+1}^i) \quad (6)$$

where θ_{t+1}^{i+} is the updated parameter ensemble member at time step $t+1$; θ_{t+1}^{i-} is the parameter sample generated with an assumption that model parameters follow a random walk in the space prescribed (Moradkani et al., 2005); K_{t+1}^{θ} is the Kalman gain matrix for correcting the parameter trajectories; and y_{t+1}^i and \hat{y}_{t+1}^i are the ensemble members of observations and predictions, respectively

Parameter sample θ_{t+1}^{i-} is made as:

$$\theta_{t+1}^{i-} = \theta_t^{i+} + \tau_t^i, \quad \tau_t^i \sim N(0, \Sigma_t^{\theta}) \quad (7)$$

In above Eq. (6), the Kalman gain matrix K_{t+1}^{θ} is calculated as:

$$K_{t+1}^{\theta} = \Sigma_{t+1}^{\theta y} [\Sigma_{t+1}^{yy} + \Sigma_{t+1}^y]^{-1} \quad (8)$$

where $\Sigma_{t+1}^{\theta y}$ is the cross covariance between parameter ensemble and prediction ensemble; Σ_{t+1}^{yy} is the error covariance matrix of the prediction \hat{y}_{t+1}^i ; and Σ_{t+1}^y is the error covariance of observation.

2.5 Parameters optimized and ensemble

Through sensitivity analysis, three parameters (i.e., V_{cmax} , M , and D_0) are selected for optimization. These parameters have significant impacts on simulated GPP and LE. Although the electron transport rate (J_{max}) is also an important parameter for calculating GPP and LE, it was calculated according to V_{cmax} in the BEPS model (Chen et al., 1999). Therefore, J_{max} was not optimized in this study. The ranges and standard deviations of these parameters are listed in Table 1. The ensemble members of predicted GPP and LE are generated by disturbing these parameters using Eq. (7) with an assumption that data used to force the model are perfect.

Estimation of observational errors is important for EnKF data assimilation since the observational errors determine the degree to which the simulated results are to be corrected (Mo et al., 2008). Studies show that the observation errors of flux data are related to flux magnitudes (Lasslop et al., 2008; Richardson et al., 2008). According to the previous study on the uncertainties of observed flux data conducted by Liu et al. (2009) for this site, the uncertainties of GPP and LE are set as 15% of their daily averages and assumed to be independent of each other. The ensemble size is set to 200 to ensure the correct estimate of cross covariance between parameter and prediction ensembles and that of the prediction error covariance. Parameter optimization is conducted in days when both GPP and LE measurements are available. The parameters are updated by adding up corrections calculated using

Table 1. The standard deviations and ranges of three parameters optimized

Symbol	Unit	Standard deviation	Range
$V_{c_{\max}}$	$\mu\text{mol m}^{-2} \text{s}^{-1}$	4	10–60
M	Dimensionless	0.8	4–14
D_0	kPa	0.15	1.2–2.2

Eq. (6). Then the new parameters are used to simulate fluxes at half-hourly time steps in the following days until next parameter optimization is conducted.

3 Results

3.1 Interannual and seasonal variations of the parameters

The seasonal variations of three optimized parameters were analyzed with 10-day averages since there are certain daily fluctuations of retrieved parameters. Figure 3 shows the seasonal variations of $V_{c_{\max}}$ in years 2003 and 2004. This parameter was in the range from 14.4 to $29.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ in 2003 and from 13.3 to $28.6 \mu\text{mol m}^{-2} \text{s}^{-1}$ in 2004, respectively. The averages of $V_{c_{\max}}$ were 19.2 and $20.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ in 2003 and 2004, respectively. In 2003, this parameter gradually increased to a peak value of $29.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the middle of June and then quickly decreased due to the impact of severe summer drought. It started to recover with the increase of precipitation in mid August and approached the second peak of $23.9 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the middle of September. Then this parameter declined again and showed a relatively small variation after middle October. The seasonality of $V_{c_{\max}}$ in 2004 was very similar to that in 2003. The summer decrease of $V_{c_{\max}}$ was smaller in 2004 than in 2003. Starting from late September, this parameter was larger in 2004 than in 2003.

The parameter of $V_{c_{\max}}$ represents the foliage photosynthetic capacity at a reference temperature (25°C in this study) and is believed to be linearly related with leaf nitrogen content (Chen et al., 1999). It is also affected by other factors including photosynthetic enzyme capacity, leaf mass area ratio, and leaf age, soil water stress, acclimation to seasonal change of environmental conditions (Wilson et al., 2006; Mo et al., 2008; Keenan et al., 2009). Many studies have demonstrated the seasonal variations of $V_{c_{\max}}$ (Reichstein et al., 2003; Wolf et al., 2006; Wang et al., 2007; Mo et al., 2008). However, the reported seasonal patterns of $V_{c_{\max}}$ varied considerably in different ecosystems. The seasonal changes of $V_{c_{\max}}$ identified in this study are similar to those in three Mediterranean forests reported by Reichstein et al (2003). In both cases, $V_{c_{\max}}$ showed increasing trends in the spring

and early summer and a noticeable decline during a summer drought period.

The slope in the Ball-Berry model (M) ranged from 7.5 to 13.4 in 2003 and from 7.0 to 12.9 in 2004, respectively (Fig. 4). It averaged 10.3 and 10.7 in these two years. In 2003, it showed an increasing trend prior to the end of March and a decreasing trend after April. It dropped during the summer drought and recovered when the soil was getting wet after the middle of August. This parameter reached the second peak of 11.7 in mid September. Then, it continuously decreased as the soil was getting dry again. The seasonal pattern of M in 2004 is different from that in 2003. In 2004, this parameter gradually increased from mid March to early September and then slowly decreased. It did not decrease during the summer of 2004.

The seasonal and interannual variations of parameter M have been confirmed in many studies (Sala and Tenhunen, 1996; Lai et al., 2000; Wolf et al., 2006; Mo et al., 2008). There is still no consistent conclusion on the seasonal pattern of this parameter and its association with SWC. Sala and Tenhunen (1996) used single values of LAI and $V_{c_{\max}}$ for the entire growing season to invert M and found that this parameter changed dramatically. Lai et al. (2000) found that M was associated with SWC. Wolf et al. (2006) demonstrated that M could vary seasonally in the range from 15.4 to 23.8 and the association between M and SWC was not strong. Mo et al. (2008) indicated that M was smaller in dry years than in wet years for an aspen forest in the southern study area of BOREAS, Canada. The variations of M between two years in this study were similar to the results reported by Mo et al. (2008). Both of studies found that M was smaller in dry than in wet years.

The annual averages of D_0 were almost identical in 2003 and 2004, equal to 1.47. This value is close to those used in many modeling studies (Wang and Leuning, 1998; Arrain et al., 2003; Ju et al., 2006). This parameter showed similar seasonal patterns in 2003 and 2004. The seasonal variations of this parameter were relatively small, ranging from 1.35 to 1.64 kPa in 2003 and from 1.33 to 1.62 kPa in 2004 (Fig. 5), respectively. During the summer drought period in 2003, it decreased slightly and had smaller values than those in the same period of 2004. D_0 was slightly below the average during the periods from April to early August in 2003 and from mid February to late May in 2004.

3.2 The relationship between the parameters and soil water content

As expected, parameters $V_{c_{\max}}$ and M showed a certain degree of association with SWC (Fig. 6). These two parameters started to decline when SWC decreased. They are more tightly linked with SWC in deep layers than with SWC in the surface layer. $V_{c_{\max}}$ kept increasing when SWC at 5 cm depth started to decrease and SWC at depths of 20 cm and 40 cm remained above the field capacity. This confirms

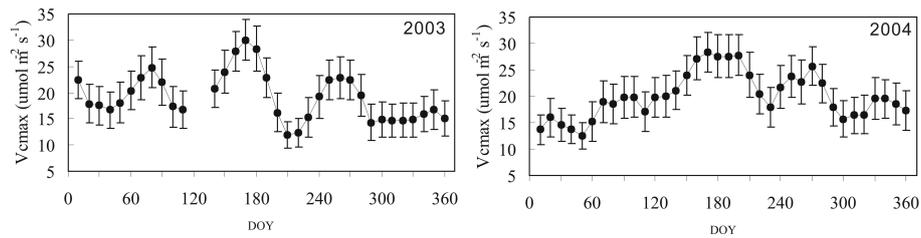


Fig. 3. Seasonal variations of optimized $V_{c_{\max}}$ in 2003 (left) and 2004 (right). Error bars represent standard deviations of optimized $V_{c_{\max}}$ within 10 days.

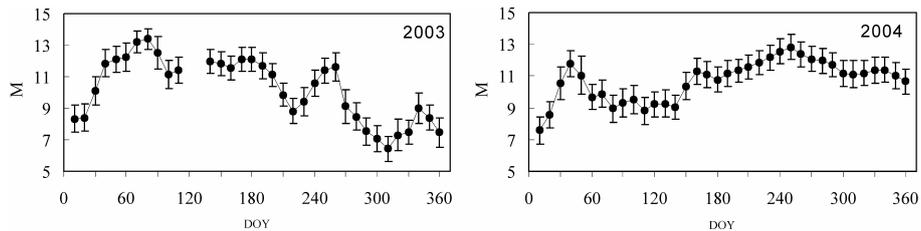


Fig. 4. Seasonal variations of optimized M in 2003 (left) and 2004 (right). Error bars represent standard deviations of optimized M within 10 days.

the hypothesis that forest is able to uptake deep water to maintain normal photosynthesis and transpiration rates during the initial stage of drought. With the continuation of drought, deep soil water is consumed and the stomatal conductance decreases (Ju et al., 2006). Consequently, the photosynthetic capacity (parameterized as $V_{c_{\max}}$ in the model) showed a considerable reduction (Reichstein et al., 2003). $V_{c_{\max}}$ showed a stronger response to decrease in SWC in mid summer of 2003 than in mid summer of 2004 due to co-occurrence of drought and high temperature in 2003 (Sun et al., 2006). $V_{c_{\max}}$ and SWC at depths of 20 cm and 40 cm almost started to decrease simultaneously. However, the recovering rate of $V_{c_{\max}}$ was slower than that of SWC, indicating drought has a lagged effect on the photosynthetic capacity. In years 2003 and 2004, the lags with maximum correlation with $V_{c_{\max}}$ were about 20 days and 10 days for SWC at depths of 20 cm and 40 cm, respectively. Parameter M decreased during the summer drought period in 2003. This decrease of M did not occur during the summer of 2004 although $V_{c_{\max}}$ showed a moderate decrease because SWC of deep layers were relatively high.

When SWC at 20 cm depth was below the field capacity, both M and $V_{c_{\max}}$ linearly increased with SWC. If SWC was above the field capacity, its change had no detectable influence on M and $V_{c_{\max}}$ (Fig. 7). This is similar to the findings of the impact of SWC on M in previous studies (Lai et al., 2000; Wolf et al., 2006; Kennan et al., 2009) and on $V_{c_{\max}}$ by Reichstein et al. (2003) and Wang et al. (2007). SWC alone explained 61% and 64% of the variations in $V_{c_{\max}}$ and M when SWC was below the field capacity. $V_{c_{\max}}$ and M showed very large variations when SWC was above the field

capacity, indicating that SWC was the key determinant of $V_{c_{\max}}$ and M when SWC was low, causing stress on forest growth. However, when SWC was high, other factors may also have significant influences on them.

3.3 Performance of the optimized BEPS model in flux simulation

Because fluxes of GPP, LE and sensible heat flux (SH) were predicted with the corrected parameters on the previous day, the efficiency of model parameter optimization in improving flux estimation was evaluated by comparing measured and simulated fluxes. Figure 8 shows the comparisons for half-hourly GPP, LE and SH. The simulated fluxes are the averages of 200 ensemble predictions. With the optimized parameters, the BEPS model explained 83%, 81% and 83% of variations of measured half-hourly LE, SH and GPP in 2003, respectively. In 2004, the optimized model captured 83%, 79% and 83% of variations in measurements of LE, SH and GPP. The model tends to overestimate smaller values of LE and GPP and underestimate their large values. In contrast, the small (or large) values of SH were underestimated (or overestimated) by the model, respectively.

These results are significant improvements over the results simulated with stomatal conductance calculated using Eq. (2) with calibrated parameter set ($D_0=1.58$ kPa, $m=11$, $V_{c_{\max}}=25$ $\mu\text{mol m}^{-2} \text{s}^{-1}$) (Table 2). The biggest improvement was achieved for GPP, followed by LE and SH. The RMSE (root mean square error) values of GPP with EnKF parameter optimization decreased to 0.17 and 0.19 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in 2003 and 2004, respectively, from 0.21

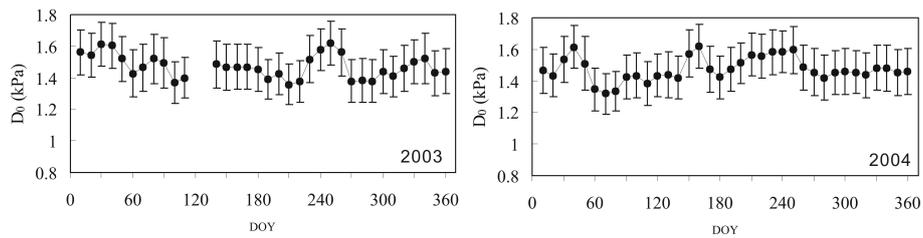


Fig. 5. Seasonal variations of optimized D_0 in 2003 (left) and 2004 (right). Error bars represent standard deviations of optimized D_0 within 10 days.

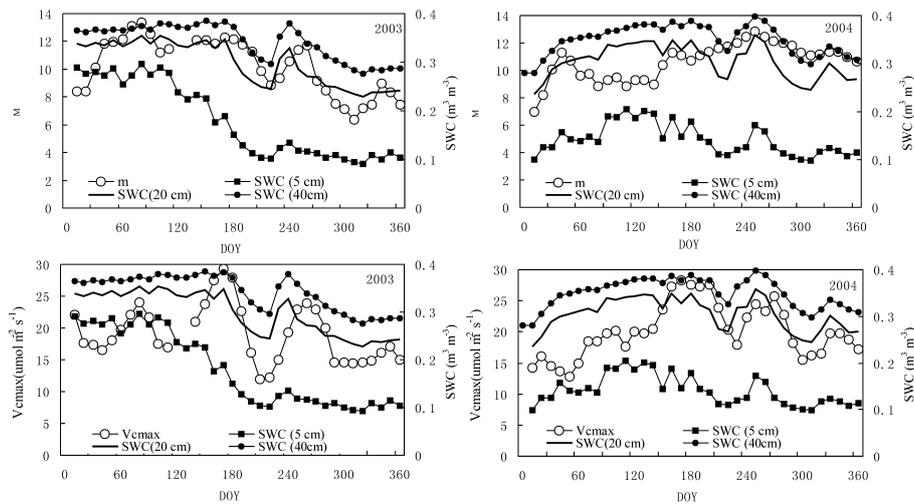


Fig. 6. Seasonal variations of optimized parameters of V_{cmax} and M and measured soil water content at depths of 5 cm, 20 cm and 40 cm. The left panel is for year 2003 and the right one is for year 2004.

and $0.21 \mu\text{mol m}^{-2} \text{s}^{-1}$ based on the calibrated parameter set. Correspondingly, the EnKF parameter optimization made the RMSE of LE decrease from 42 to 36 W m^{-2} in 2003 and from 47 to 40 W m^{-2} in 2004.

At daily steps, the optimized model was able to explain 90% and 91% variations of daily GPP in 2003 and 2004, respectively (Fig. 9). These percentages for the simulations using the calibrated parameter set were 86% and 89%. The improvement for daily GPP simulation was mainly in the periods of the summer and autumn droughts of 2003 and 2004. The improvement in simulated GPP after EnKF parameter optimization was smaller in 2004 than in 2003. With the optimized parameters, the model greatly reduced the overestimation of GPP during the drought periods (Fig. 9).

The improvement in the simulation by the EnKF parameter optimization was greater for LE than GPP (Figs. 9 and 10). 93% and 90% of variations of day time LE were captured by the BEPS model optimized using EnKF in 2003 and 2004, respectively while corresponding values were 89% and 85% for simulations using the calibrated parameter set in 2003 and 2004. The improvements in LE simulations were also mainly during the drought periods in 2003 and 2004. During the serious drought period from day 171 to

day 232 in 2003, the RMSE of simulated LE was 31 W m^{-2} using the optimized parameters while it was 43 W m^{-2} using the calibrated parameters. During the drought period from day 188 to day 221 in 2004, the RMSE of simulated LE was 41 W m^{-2} using the optimized parameters while it was 56 W m^{-2} using the calibrated parameters.

The model using the optimized parameters was unable to capture some peaks of GPP and LE in the midday since the adjustments of parameters was carried out using daily values of observation GPP and LE.

4 Discussions

Parameters in the ecosystem models are temporally and spatially interlinked in nonlinear forms. Parameter values derived from measurements taken at leaf or canopy scales may lead to incorrect predictions at other scales (Mo et al., 2008). Eddy covariance measurements represent the information at 100–1000 m footprint distance, similar to the spatial resolution of many hydrological and ecological models. Therefore, parameter values optimized using eddy covariance measurement will improve the simulations at regional scales.

Table 2. Statistics from the regression ($Y=aX+b$) of observed (as Y) on simulated (as X) half-hourly fluxes of GPP ($\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), LE (W m^{-2}) and SH (W m^{-2})

ITEM	Year	Parameters optimized using EnKF				Parameters calibrated			
		a	b	R^2	RMSE	a	b	R^2	RMSE
LE	2003	1.003	-0.234	0.827	36.3	0.845	-1.462	0.822	42.2
	2004	1.008	-1.958	0.831	40.4	0.823	-1.14	0.810	46.9
SH	2003	0.714	19.314	0.813	41.3	0.716	21.536	0.814	42.9
	2004	0.696	19.941	0.787	36.4	0.712	21.836	0.752	39.4
GPP	2003	0.960	0.011	0.826	0.173	0.764	0.012	0.797	0.209
	2004	1.003	0.011	0.829	0.187	0.822	0.012	0.809	0.212

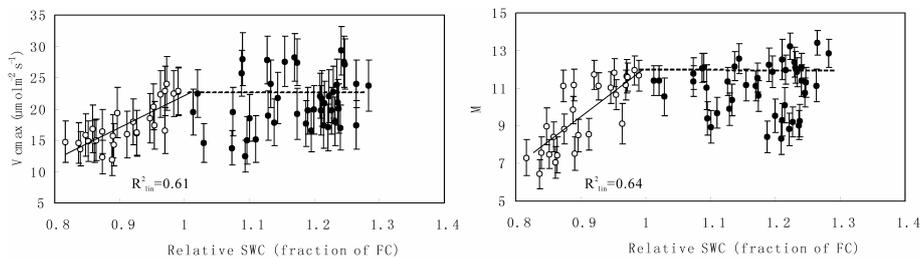


Fig. 7. Association of optimized $V_{c_{\max}}$ and M with measured relative soil water content (fraction of field capacity) at 20 cm depth in 2003 and 2004. Values shown are 10-day averages. Curves are linear functions with upper threshold, fitted to unfilled symbols. Also indicated are the R^2 values of fitted linear functions. Error bars are the standard deviations of optimized parameters within 10 days.

Many studies have demonstrated the applicability of eddy covariance measurements to optimizing model parameters (Reichstein et al., 2003; Wolf et al., 2006; Wang et al., 2007; Santaren et al., 2007; Mo et al., 2008). EnKF sequential data assimilation is an effective technique for model parameter optimization, which is able to track the seasonal variations of the parameters representing the photosynthetic capacity indicated by $V_{c_{\max}}$ and the sensitivity of stomatal conductance to net photosynthesis rate indicated by M . The estimation of observation errors is critical to the EnKF parameter optimization algorithm. If larger observation errors are used in the calculation of Kalman gain matrix, the trajectories of model parameters will be corrected to a smaller degree. Using the daily-differencing approach, Liu et al. (2009) found that relative errors of observed GPP decreased with temporal scales and the overall uncertainties of observed GPP at half-hourly and daily time scales are about 10% during 2003 to 2005 at this site. Richardson et al. (2008) and Lasslop et al. (2008) proposed practical methods to estimate observational errors of flux data and pointed out that the observation errors of flux data increased with flux magnitudes. In this study, the errors of GPP and LE were set as 15% of their daily values, which are in the range of reported uncertainties of GPP and LE measurements (Santaren et al., 2007; Richardson et al., 2008) and close to the numbers reported by Liu et al. (2009). The assumption ignores the effects of meteorological conditions on

the proportion of observational error of flux data to flux magnitudes, possibly inducing some uncertainties in optimized parameters. The application of estimated observational errors of flux data for each day will increase the confidence of optimized parameters. The construction of the second eddy covariance tower in July, 2008 at this site will make it possible to estimate uncertainties of GPP and LE measurements more reasonably.

Current conclusions on the statistical properties of random flux errors are not inconsistent. Hollinger and Richardson (2005) indicated that flux measurement errors are more close to a double exponential distribution. Liu et al. (2009) declared a similar conclusion about the statistical distribution of random errors of observed fluxes for the QYZ site. Recently, Lasslop et al. (2008) indicated that the double exponential distribution of random errors of observed errors is mostly due to the superposition of normal distributions with varying standard deviation. In this current study, the observation error is assumed to be Gaussian distributed and independent between GPP and LE. The effects of this assumption about the distribution of observation errors on optimized parameters need further investigation.

Compared with the global optimization algorithms, which use eddy covariance measurements in long time periods to invert parameters, the EnKF optimization method updates the model parameters using measurements in one day. Although

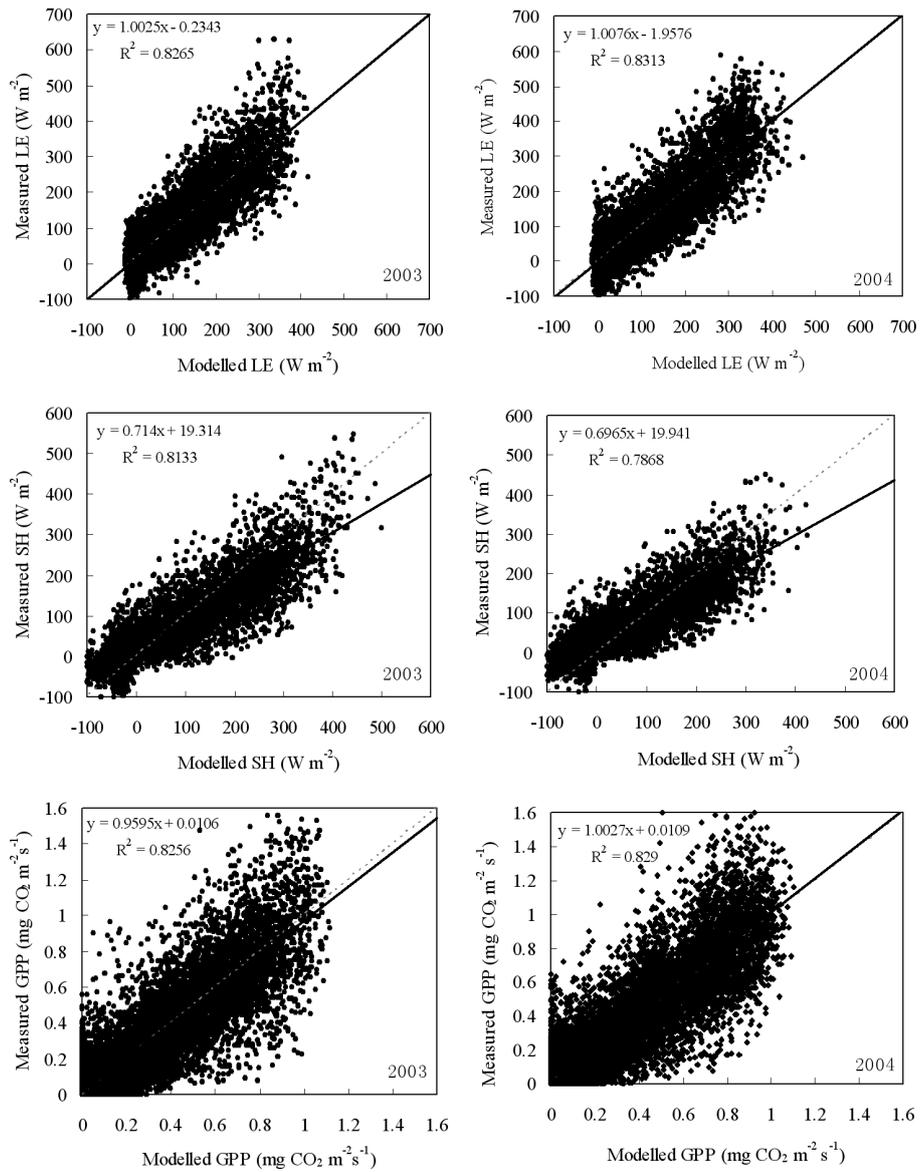


Fig. 8. Comparison between observed and simulated half-hourly fluxes of GPP, LE, and SH. The grey dashed line is the 1:1 line and dark solid one is the regression line. The left panel is for 2003 and right one is for 2004.

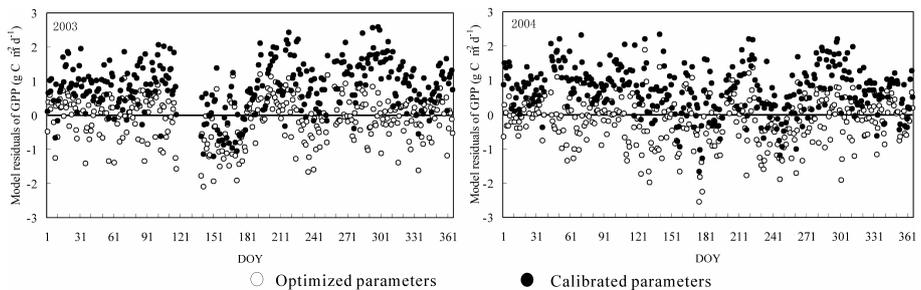


Fig. 9. Residuals of simulated daily GPP using parameters optimized by EnKF and parameters determined through model calibration for years 2003 (left) and 2004 (right).

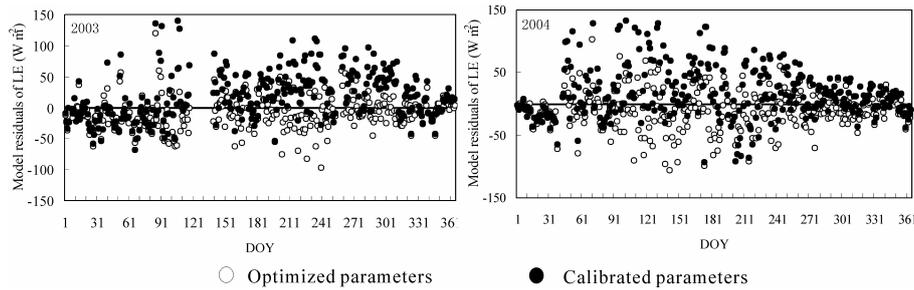


Fig. 10. Residuals of simulated daily mean LE using parameters optimized by EnKF and parameters determined through model calibration for years 2003 (left) and 2004 (right).

this strategy is able to trace day to day variations of parameters, it makes the optimization results sensitive to the quality of observation. One or several abnormal observational values in one day might cause the parameters to vary unrealistically. Therefore, careful quality control of observation data is of importance prior to the implementation of the EnKF parameter optimization scheme. Since the daily averages of observed and simulated GPP and LE are used to correct the parameters, the simulation accuracy is more improved at daily time steps than at half-hourly time steps. This is because in the calculations of daily values, the underestimation/overestimation of large GPP or LE values will be possibly compensated by overestimation/underestimation of small GPP or LE values. The model with optimized parameters still tends to underestimate large GPP and LE fluxes at noon.

Similar to findings in other studies, considerable seasonal variations of $V_{c_{max}}$ and M are derived through assimilating eddy covariance. They also show noticeable changes between the two years used in our study. There are many possible mechanisms causing the changes of these parameters. In addition to water stress, changes in photosynthetic enzyme capacities, foliage N concentration status, leaf mass per area, leaf age and the acclimation of forest to environmental conditions might cause the seasonal variations of $V_{c_{max}}$ (Wilson et al., 2000; Reichstein et al., 2003; Mo et al., 2008). Carlhais et al. (2008) indicated that model structure and estimation method can also cause the temporal variations of optimized parameters. In this study, the model structure and optimization method are assumed to be perfect. The robustness of this assumption needs further study.

Development of algorithms to quantify the variations of these parameters ($V_{c_{max}}$ and M) is of importance for improving the simulations of carbon and water fluxes at various scales since they are used in models to represent the photosynthetic capacity and the sensitivity of stomatal conductance to net photosynthetic rates. Previous studies indicated that the allowance of the change in photosynthetic capacity ($V_{c_{max}}$) with soil water stress was required to improve the agreement between simulated and observed fluxes during dry periods (Reichstein et al., 2003; Wang et al., 2007). Current

study found that both responses of the sensitivity of stomatal conductance to net photosynthesis rates (indicated by the reduction of M) and photosynthetic capacity to soil water stress (indicated by the reduction of $V_{c_{max}}$) are necessary for reliable simulations of GPP and LE for this subtropical coniferous forest ecosystem. This is similar to the findings for the Mediterranean forest ecosystem reported by Keenan et al. (2009).

It was found that SWC is a good predictor for $V_{c_{max}}$ and M during dry periods for this coniferous plantation ecosystem in subtropical zone of southeastern China. During wet periods, $V_{c_{max}}$ and M showed large variations around the averages (Fig. 7). The simultaneous observations of nitrogen content, $V_{c_{max}}$, M , photosynthesis rate are required to understand the mechanisms underlying the variations of $V_{c_{max}}$ and M and to develop methodologies to describe the variations of $V_{c_{max}}$ and M for bettering the simulations of surface fluxes.

5 Conclusions

From this study, following conclusions can be drawn:

1. The EnKF data assimilation is an effective technique for model parameter optimization, which is able to track the seasonal and interannual variations of the parameters. The optimized parameter values are sensitive to the estimation of observation errors and quality of observation data.
2. Optimized $V_{c_{max}}$ and M showed considerable seasonal variations and also changed noticeably between two years. The seasonal variations of parameters were larger than their variations between the two years. The variations of $V_{c_{max}}$ and M indicate that soil water stress reduced the sensitivity of stomatal conductance to net photosynthesis rates and photosynthesis capacity. SWC is a good predictor of $V_{c_{max}}$ and M during dry periods with SWC of 20 cm depth below the field capacity. SWC of 20 cm depth alone explained 61% and 64% variations of $V_{c_{max}}$ and M , respectively. During

wet periods, the dependence of these two parameters on SWC were not significant and other factors (e.g., photosynthetic enzyme capacities, foliage N concentration status, and leaf mass per area, acclimation of forest to environmental conditions and leaf aging) can cause these parameters to vary largely.

3. The inclusions of responses of both the sensitivity of stomatal conductance to net photosynthesis rate (M) and photosynthetic capacity ($V_{c_{max}}$) to soil water stress improved the simulation of GPP, LE and SH under different soil water conditions. After parameter optimization using EnKF, the variations of GPP, LE and SH explained by the model increased by 1% to 4% at half-hourly steps and increased by 3% to 5% at daily time steps.
4. In this study, the effects of model structure and optimization method (causing stochastic variations) on the optimization of parameters were not investigated. In addition, the observational errors can be split into systematic and random components. Only the random components of observational errors were currently included. Further efforts are required to consider these effects of model structure and optimization methods on parameter optimization to identify the real mechanisms underlying the temporal variations of parameters.

Acknowledgements. This study was supported by the A3 Foresight Program under National Science Foundation of China (30721140307) and National Science Foundation of China (40871240/D011004). We also greatly thank the ChinaFLUX for the provision of flux and meteorological data. We also acknowledged the constructive comments from two anonymous reviewers which greatly improved the quality of this manuscript.

Edited by: J. Kim

References

- Aalto, T., Ciais, P., Chevillard, A., and Moulin, C.: Optimal determination of the parameters controlling biospheric CO₂ fluxes over Europe using eddy covariance fluxes and satellite NDVI measurements, *Tellus* 56B, 93–104, 2004.
- Arrian, M. A., Black, T. A., Barr, A. G., Javis, P. G., Massheder, J. M., Versghy, D. L., and Nescic, Z.: Effects of seasonal and inter-annual climate variability on net ecosystem productivity of boreal deciduous and conifer forests, *Can. J. Forest Res.*, 32, 878–891, 2002.
- Baldocchi, D. A.: comparative study of mass and energy exchange rates over a closed C₃ (wheat) and an open C₄ (corn) crop: II, CO₂ exchange and water use efficiency, *Agr. Forest Meteorol.*, 67, 291–321, 1994.
- Barr, A. G., Black, T. A., Hogg, E. H., Griffis, T., Morgenstern, K., Kljun, N., Theede, A., and Nescic, Z.: Climatic controls on the carbon and water budgets of a boreal aspen forest, 1994–2003, *Glob. Change Biol.*, 12, 10–16, 2006.
- Ball, J. T., Woodrow, I. E., and Berry, J. A.: A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions, edited by: Biggins, J., Martinus Nijhoff Publishers, Dordrecht, 221–224, 1987.
- Carvalho, N., Reichstein, M., Seixas, J., Collatz, G. J., Pereira, J. S., Berbigier, P., Carrara, A., Granier, A., Montagnani, K., Papale, D., Rambal, S., Sanz, M. J., and Valentini, R.: Implications of the carbon cycle steady state assumption for biogeochemical modeling performance and inverse parameter retrieval, *Global Biogeochem. Cy.*, 22, GB2007, doi:10.1029/2007GB003033, 2008.
- Chen, J. M., Liu, J., Cihlar, J., and Goulden, M. L.: Daily canopy photosynthesis model through temporal and spatial scaling for remote sensing applications, *Ecol. Model.*, 124, 99–119, 1999.
- Ciais, P., Reichstein, M., and Viovy, N.: Europe-wide reduction in primary productivity caused by the heat and drought in 2003, *Nature*, 437, 529–533, 2005.
- Dang, Q. L., Margolis, H. A., Coyea, M. R., Sy, M., and Collatz, G. J.: Regulation of branch-level gas exchange of boreal trees: roles of shoot water potential and vapour pressure difference, *Tree Physiol.*, 17, 521–535, 1997.
- Evenson, G.: The ensemble Kalman filter: theoretical formulation and practical implementation, *Ocean Dynam.*, 53, 343–367, 2003.
- Farquhar, G. D., Caemmerer, S. V., and Berry, J. A.: A biochemical model of photosynthetic CO₂ assimilation in leaves of C-3 Species, *Planta*, 149, 78–90, 1980.
- Grainer, A., Reichstein, M., Bréda, N., Janssens, I. A., Ealge, E., Ciais, P., Grünwald, T., Aubinet, M., Berbigier, P., Bernhofer, C., Buchmann, N., Facini, O., Grassi, G., Heinesch, B., Ilvesniemi, H., Keronen, P., Knohl, A., Köstner, B., Lagergren, F., Lindroth, A., Longdoz, B., Loustau, D., Mateus, J., Montagnani, L., Nys, C., Moors, E., Papale, D., Peiffer, M., Pilegaard, K., Pita, G., Pumpanen, J., Rambal, S., Rebmann, C., Rodrigues, A., Seufert, G., Tenhunen, J., Vesala, T., Wang, Q.: Evidence for soil water control on carbon and water dynamics in European forests during the extremely dry year 2003, *Agr. Forest Meteorol.*, 143, 123–145, 2007.
- Grant, R. F., Black, T. A., Gaumont-Guay, D., Klujn, N., Barr, A. G., Morgenstern, K., and Nescic, Z.: Net ecosystem productivity of boreal aspen forests under drought and climate change: Mathematical modelling with Ecosys, *Agr. Forest Meteorol.*, 140, 152–170, 2006a.
- Grant, R. F., Zhang, Y., Yuan, F., Wang, S., Handson, P. J., Gaumont-Guay, D., Chen, J., Black, T. A., Barr, A., Baldocchi, D. D., and Arain, A.: Modelling water stress effects on CO₂ and energy exchange in temperate and boreal deciduous forests, *Ecol. Model.*, 196, 289–312, 2006b.
- Gu, F. X., Yu, G. R., Wen, X. F., Tao, B., Li, K. R., and Liu, Y. F.: Drought effects on carbon exchange in a subtropical coniferous plantation in China, *J. Plant Ecol.* (in chinese with english abstract), 32(5), 1041–1051, 2008.
- Hogg, E. H., Saugier, B., Pontailier, J. Y., Black, T. A., Chen, W., Hurdle, P. A., Wu, A.: Response of trembling aspen and hazelnut to vapour pressure deficit in a boreal deciduous forest, *Tree Physiol.*, 20(11), 725–734, 2000.
- Hollinger, D. Y. and Richardson, A. D.: Uncertainties in eddy covariance measurements and its application to physiological models, *Tree Physiol.*, 25, 873–885, 2005.

- Huang, M., Ji, J. J., Li, K. R., Liu, Y. F., and Yang, F. T.: The ecosystem carbon accumulation after conversion of grasslands to pine plantations in subtropical red soil of South China, *Tellus B*, 59, 439–448, 2007.
- Infante, J. M., Damesin, C., Rambal, S., and Fernandez-Ales, R.: Modelling leaf gas exchange in holm-oak trees in southern Spain, *Agr. Forest Meteorol.*, 95, 203–223, 1999.
- Ju, W. M., Chen, J. M., Black, T. A., Barr, A. G., Liu, J., Chen, B.: Modelling multi-year coupled carbon and water fluxes in a boreal aspen forest, *Agr. Forest Meteorol.*, 140, 136–151, 2006.
- Keenan, T., Garca, R., Friend, A. D., Zaehle, S., Gracia, C., and Sabate, S.: Improved understanding of drought controls on seasonal variation in Mediterranean forest canopy CO₂ and water fluxes through combined in situ measurements and ecosystem modelling, *Biogeosciences*, 6, 1423–1444, 2009, <http://www.biogeosciences.net/6/1423/2009/>.
- Kljun, N., Black, T. A., Griffis, T. J., Barr, A. G., Gaumont-Guay, D., Morgentern, K., McCaughey, J. H., and Nesic, Z.: Response of net ecosystem productivity of three boreal forest stands to drought, *Ecosystems*, 10, 1039–1055, 2005.
- Lasslop, G., Reichstein, M., Kattge, J., and Papale, D.: Influences of observation errors in eddy flux data on inverse model parameter estimation, *Biogeosciences*, 5, 1311–1324, 2008, <http://www.biogeosciences.net/5/1311/2008/>.
- Lawlor, D. W.: The effects of water deficit on photosynthesis, in: *Environmental and Plant Metabolism-Flexibility and Acclimation*, edited by: Smirnoff, N., Bioscience Scientific Publishers, Oxford, 129–160, 1995.
- Leuning, R.: A critical appraisal of a coupled stomatal photosynthesis model for C₃ plants, *Plant Cell Environ.*, 18, 339–357, 1995.
- Liu, M., He, H. L., Yu, G. R., Luo Y. Q., Sun, X. M., and Wang, H. M.: Uncertainty analysis of CO₂ flux components in sub-tropical evergreen coniferous plantation, *Science in China D: Earth Science*, 52(2), 257–268, 2008.
- Liu, Y. F., Yu, G. Y., Wen, X. F., Wang, Y. H., Song, X., Li, J., Sun, X. M., Yang, F. T., Chen, Y. R., and Liu, Q. J.: Seasonal dynamics of CO₂ fluxes from subtropical plantation coniferous ecosystem, *Science in China Series D: Earth Science*, 49 Supp II, 99–109, 2006.
- Mo, X. G., Chen, J. M., Ju, W. M., and Black, T. A.: Optimization of ecosystem model parameters through assimilating eddy covariance flux data with an ensemble Kalman filter, *Ecol. Model.*, 217, 157–173, 2008.
- Moradkhani, H., Sorooshian, S., Gupta, H. V., and Houser, P. R.: Dual-state-parameter estimation of hydrological models using ensemble Kalman filter, *Adv. Water Res.*, 28, 135–147, 2005.
- Owen, K. E., Tenhunen, J., Reichstein, M., Wang, Q., Falge, E., Geyer, R., Xiao, X., Story, P., Ammann, C., Arain, A., Aubinet, M., Aurela, M., Bernhofer, C.: Lining flux network measurements to continental scale simulations: ecosystem carbon dioxide exchange capacity under non-water-stressed conditions, *Glob. Change Biol.*, 13, 1–27, 2007.
- Parton, W. J., Scurlock, J. M. O., Ojima, D. S., Gilmanov, T. G., Scholes, R. J., Schimel, D. S., Kirchner, T., Menaut, J. C., Seastedt, T., Moya, E. G., Kamnalrut, A., and Kinyamario, J. I.: Observations and modeling of biomass and soil organic-matter dynamics for the grassland biome worldwide, *Global Biogeochem. Cy.*, 7, 785–809, 1993.
- Rambal, S., Ourcival, J. M., Joffre, R., Mouillot, F., Nouvellon, Y., Reichstein, M., and Rocheteau, A.: Drought controls over conductance and assimilation of a Mediterranean evergreen ecosystem: scaling from leaf to canopy, *Glob. Change Biol.*, 9, 1813–1824, 2003.
- Reichstein, M., Tenhunen, J., Rouspard, O., Ourcival, J. M., Rambal, S., Miglietta, F., Peressotti, A., Pecchiari, M., Tirone, G., and Valentini, R.: Inverse modeling of seasonal drought effects on canopy CO₂/H₂O exchange in three Mediterranean ecosystems, *J. Geophys. Res.*, 108, D23, 4726, doi:10.1209/2003JD003430, 2003.
- Reichstein, M., Tenhunen, J. D., Rouspard, O., Ourcival, J. M., Rambal, S., Miglietta, F., Peressotti, A., Pecchiari, M., Tirone, G., and Valentini, R.: Severe drought effects on ecosystem CO₂ and H₂O fluxes at three Mediterranean evergreen sites: revision of current hypotheses?, *Glob. Change Biol.*, 8, 999–1017, 2002.
- Richardson, A. D., Mahecha M. D., Falge E., Kattge, J., Moffat, A. M., Papale, D., Reichstein, M., Stauch, V. J., Braswell, B. H., Churkina, G., Kruuft, B., and Hollinger, D. Y.: Statistical properties of random CO₂ flux measurement uncertainties inferred from model residuals, *Agr. Forest Meteorol.*, 148, 38–50, 2008.
- Rodrigues-Iturbe, I., Ecohydrology: a hydrologic perspective of climate-soil-vegetation dynamics, *Water Resour. Res.*, 36, 3–9, 2000.
- Santaren, D., Peylin, P., Viovs, N., and Ciais, P.: Optimize a process-based ecosystem model with eddy-covariance flux measurement: a pine forest in southern France, *Glob. Biogeochem. Cy.*, 21, GB2013, doi:10.1029/2006GB002834, 2007.
- Sala, A. M. and Tenhunen, I. D.: Simulations of canopy net photosynthesis and transpiration in *Quercus ilex* L under the seasonal drought, *Agr. Forest Meteorol.*, 78, 203–222, 1996.
- Song, X., Yu, G. R., Liu, Y. F., Sun, X. M., Lin, Y. M., and Wen, X. F.: Seasonal variations and environmental control of water use efficiency in subtropical plantation, *Science in China Series D*, 49, Supp. II, 119–126, 2006.
- Sun, X., Wen, X. F., Yu, G. R., Liu, Y. F., and Liu, Q. J.: Seasonal drought effects on carbon sequestration of a mid-subtropical planted forest of southeastern China, *Science in China Series D: Earth Science*, 49 Supp. II 110–118, 2006.
- Tuzet, A., Perrier, A., and Leuning, R.: A coupled model of stomatal conductance, photosynthesis and transpiration, *Plant Cell Environ.*, 26, 1097–1116, 2003.
- Wang, Y. P. and Leuning, R.: A two-leaf model for canopy conductance, photosynthesis and partitioning of available energy I: Model description and comparison with a multi-layered model, *Agr. Forest Meteorol.*, 91, 89–111, 1998.
- Wang, Y. P., Baldocchi, D., Leuning, R., Falge, E., and Vesal, T.: Estimating parameters in a land-surface model by applying nonlinear inversion to eddy covariance flux measurements from eight FLUXNET sites, *Glob. Change Biol.*, 13, 652–670, doi:10.1111/j.1365-2486.2006.01225.x, 2007.
- Wen, X. F., Yu, G. R., Sun, X. M., Li, Q. K., Liu, Y. F., Zhang, L. M., Ren, C. Y., Fu, Y. L. and Li, Z. Q.: Soil moisture effect on the temperature dependence of ecosystem respiration in a subtropical *Pinus* plantation of southeastern China, *Agr. Forest Meteorol.*, 137, 166–175, 2006.
- Wilson, K. B., Baldocchi, D. D., and Hanson, P. J.: Spatial and seasonal variability of photosynthetic parameters and their relationship to leaf nitrogen in a deciduous forest, *Tree Physiol.*, 20, 565–578, 2000.

- Wolf, A., Akshalov, K., Saliendra, N., Johnson, D. A., and Laca, E. A.: Inverse estimation of V_{cmax} , leaf area index, and the Ball-Berry parameter from carbon and energy fluxes, *J. Geophys. Res.*, 111, D08S08, doi:10.1029/2005JD005927, 2006.
- Yu, G. R., Fu, Y. L., Sun, X. M., Wen, X. F., and Zhang, L. M.: Recent progress and future directions of ChinaFlux, *Science in China Series D*, 49, Supp II, 1–23, 2006.
- Zierl, B.: A water balance model to simulate drought in forested ecosystem and its application to entire forested area in Switzerland, *J. Hydrol.*, 242, 115–136, 2001.