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Examination of model-estimated ecosystem respiration using flux measurements from a cool-temperate deciduous broad-leaved forest in central Japan

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ABSTRACT

Reducing uncertainty in the emission of carbon dioxide (CO_2) from plants and microbes is critically important in determining carbon budgets. We examined properties of net ecosystem CO_2 exchange (*NEE*) derived from a process-based model that simulates an ecosystem carbon cycle, focusing on nighttime flux determined from ecosystem respiration and soil efflux. The model simulated autotrophic and heterotrophic respiration using semi-empirical ecophysiological parameterizations. In a cool-temperate deciduous broad-leaved forest in central Japan, simulation results from 1998 to 2005 were compared with measurement of the forest made using eddy-covariance and chamber methods. The model estimated annual ecosystem respiration as 1397 g Cm^{-2} yr^{-1}, of which 67% was from the soil surface, with a clear seasonal cycle. Compared to flux observations, the model appropriately captured daytime *NEE*, but produced substantial differences from the observed nighttime *NEE*. The differences were evident under stable atmospheric conditions (at low friction velocity), implying a problem with the observations. With regard to soil-surface CO_2 efflux (soil respiration), the model estimation was consistent with chamber observations, except in winter periods with thick snow cover. We discuss whether the model is applicable for estimating ecosystem respiration rates, and what is required to improve the predictability of the model.

1. Introduction

Quantification and elucidation of the terrestrial carbon dioxide (CO_2) budget is a critical issue in understanding the global carbon cycle and climate change. An increasing number of FLUXNET measurement sites (Baldocchi et al., 2001), which use micrometeorological methods (i.e., eddy-covariance method; Aubinet et al., 2000), are providing invaluable plot-scale net ecosystem CO_2 exchange (*NEE*) data. Several studies have used process-based models to interpret the observed *NEE* in relation to gross carbon flows and environmental conditions (e.g., Arora, 2003; Wang et al., 2004; Ito et al., 2005, 2006). Although *NEE* is determined as the difference between photosynthetic assimilation and respiratory catalysis, observational and modelling studies have primarily emphasized the uptake process. It is expected that this process may primarily determine the ecosystem carbon budget and is related to interesting ecophysiological phenomena. However, many recent studies (e.g., Ryan et al., 1997; Valentini et al., 2000; Reichstein et al., 2005) have suggested that respiratory processes have different properties and are also important in determining the ecosystem carbon budget.

Unfortunately, significant uncertainties remain in the present observation and modelling of respiratory CO_2 emission from plants and soil organic matter (Gifford, 2003; Trumbore et al., 2006). In modeling, the respiration processes have been parameterized more simply than photosynthetic assimilation, although their magnitude of contribution is comparable to that of ecosystem carbon budgets. Specifically, plant autotrophic respiration (dark respiration) consumes approximately one-half of the carbon fixed from the atmosphere, but is estimated using phenomenological schemes. For example, many carbon cycle

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models use the two-component scheme (McCree, 1970; Amthor, 2000), in which autotrophic respiration is estimated as the sum of maintenance (proportional to standing biomass) and construction (proportional to biomass increment) components. The two-component respiration model is less mechanistic than biochemical photosynthetic models used in many carbon cycle models. This makes simulations easy, but decreases the accuracy because the process comprises complicated environmental and biological regulations. Many studies have revealed complexity in the regulation of autotrophic respiration such as in acclimatization and size-dependence, implying the necessity for more mechanistic respiration models. The situation is the same for heterotrophic soil microbial respiration. Most carbon cycle models use extremely simplified soil models compared to the complexity and heterogeneity of soil systems. In these models, responses of soil decomposition to temperature and moisture conditions are evaluated using empirical parameterizations: e.g. exponential increase with soil temperature and optimal curve for moisture. Microbial properties and activities are seldom included in an explicit manner. Therefore, a new mechanistic model is required to estimate respiration rates and their environmental response with higher reliability. Although a few modelling studies (e.g. Thornley and Cannell, 2000) have focused on the respiration processes, most of recent models still use some simplified parameterizations. For global environmental change, a model comparison study (Jones et al., 2005) has implied that the difference in respiration parameterization among land models accounts for part of the uncertainty in the carbon cycle feedback to climate change.

On the other hand, many flux measurements (e.g. Lavigne et al., 1997; Aubinet et al., 2000) suggest that the eddy-covariance method may not provide reliable data for complex terrain, heterogeneous surfaces and unsuitable atmospheric conditions. In particular, nighttime CO_2 flux, which should represent the ecosystem respiration rate, can be strongly affected by stable, i.e. insufficiently turbulent atmospheric conditions. Although several techniques have been developed to remove inappropriate data and fill the data gaps (e.g. Falge et al., 2001; Gu et al., 2005), it is still difficult to measure continuous nighttime CO_2 flux with high accuracy. *In situ* measurements using the chamber method provide more accurate data for specific respiration components, such as CO_2 efflux from the soil surface (soil respiration). However, this method cannot provide data at spatial scales larger than a small plot.

Therefore, we examined how well the present respiration parameterization, used in a carbon cycle model developed by Ito et al. (2005), simulates ecosystem respiration by comparing its results to observational data from a cool-temperate forest on complex terrain in central Japan. We focused on nighttime CO_2 flux because we could directly compare the model-estimated ecosystem respiration to the flux measurements, and because larger uncertainties may remain in both modelling and observation of nighttime CO_2 flux.

2. Methods

2.1. Site description

The study was conducted in a cool-temperate deciduous broad-leaved forest near Takayama, central Japan (36°08′N, 137°25′E, 1420 m above sea level), at an AsiaFlux site. The physiognomy of this forest was fully described by Ohtsuka et al. (2005); this is a secondary forest mainly composed of birch (*Betula platyphylla* Sukaczev var. *japonica* Hara and *Betula ermanii* Cham) and oak (*Quercus crispula* Blume) trees. The survey by Ohtsuka et al. (2005) shows that the canopy-top height is about 20 m, the density of deciduous species is about 1379 trees ha^{-1}, and the total biomass is 163.8 Mg dry matter ha^{-1} (equivalent to 74 Mg C ha^{-1}). This forest was affected by human logging, and the stand age is about 50 years. The soil is classified as a dystric cambisol (brown forest soil) with depths of 33 cm in the A-horizon and 95 cm in the whole soil column, and is covered by a surface organic layer (Jia and Akiyama, 2005; Uchida et al., 2005). The soil survey by Jia and Akiyama (2005) shows that below ground carbon storage is spatially heterogeneous, but on average, litter and mineral soil store up to 23.2 and 318.3 Mg C ha^{-1}, respectively.

2.2. Observational data

2.2.1. Eddy-covariance measurements. Since 1998, heat, vapour and CO_2 fluxes at the Takayama site have been measured using the eddy-covariance method (Saigusa et al. 2002, 2005). A 27-m tower was installed by the National Institute of Advanced Industrial Science and Technology, Japan. A closed-path infrared gas analyzer (IRGA; model LI-6262, Li-Cor, Lincoln, NE, USA) was used to measure CO_2 and vapour concentrations at a height of 25 m (approximately 5 m above the canopy). The wind velocity at this height was measured using an ultrasonic anemometer (DAT-600, Kaijo Corp., Tokyo, Japan). Data were recorded at 5 Hz and averaged for 30-min periods, and appropriate quality controls were applied to the data for the effect of slope on vertical wind velocity, time lags in the closed-path vapour and CO_2 sensors, linear trends and the effect of fluctuations in air density. We used 30-min average gap-filled data of net ecosystem CO_2 exchange (*NEE*) and micrometeorology during the period from 1998 to 2005.

2.2.2. Chamber measurements. CO_2 efflux from the soil surface (*SR*, or soil respiration) near the flux tower was measured using the open-flow chamber method from 1999 to 2002 (Lee et al., 2002; Mo et al., 2005). The measurements were made for 24 to 48 h, once or twice a month, to capture diurnal and seasonal changes. During the snow-free periods, four chambers (internal diameter 21 cm, height 15 cm) were used for measurement. Measurements were conducted on a 25-min cycle, using an IRGA (LI-6262, Li-Cor). During the snow-covered periods, a modified chamber method (Mariko et al., 2000) was used to measure CO_2 efflux from the snow surface. At each measurement, soil temperature at 1 cm below the soil surface was monitored using a thermocouple.

2.3. Model description

2.3.1. Ecosystem carbon cycle model. A process-based terrestrial ecosystem model (Ito et al., 2005, 2006) was used to simulate the carbon cycle of the Takayama site. The model included a hydrological scheme derived by Ito and Oikawa (2002) and a box-flow carbon cycle scheme composed of four sectors (tall trees, floor plants, litter and humus) subdivided into 15 carbon pools. The carbon cycle scheme included two modules: an atmospheric CO_2 exchange module and an intraecosystem carbon dynamics module. The atmospheric CO_2 exchange module simulated gross primary production (*GPP*) using a two-layer canopy model (de Pury and Farquhar, 1997), autotrophic respiration and litter decomposition at 30-min time steps. The intraecosystem carbon dynamics module simulated leaf phenology, allocation, litter fall and humus decomposition at daily time steps. Parameters used in this model are described in Ito et al. (2005).

2.3.2. Autotrophic respiration. In the deciduous broad-leaved forest, leaf respiration rate (*RF*) was estimated using an Arrhenius-type function of temperature:

$$RF = f_{LAI} \cdot RF_{T=25} \cdot \exp\left[\frac{E_a \cdot (T - 25)}{8.314 \cdot 298 \cdot (T + 273)}\right], \tag{1}$$

where f_{LAI} is a scaling coefficient for canopy leaf area index (Ito et al., 2006), E_a is activation energy (J mol^{-1}), and T is temperature (°C). Table 1 shows parameter values that are related to environmental responsiveness. The respiration activity at 25°C, $RF_{T=\Theta\Pi}$, varies with leaf aging during the growing period (Ito et al., 2006), based on chamber measurements by Muraoka and Koizumi (2005). Plant stem (*RS*) and root (*RR*) respiration rates were estimated using a two-component model (maintenance respiration with subscript M and construction respiration with subscript C).

$$RS = WS \cdot RS_M \cdot Q_{10}^{(T-15)/10} + \Delta WS \cdot RS_C, \tag{2}$$

$$RR = WR \cdot RR_M \cdot Q_{10}^{(T-15)/10} + \Delta WR \cdot RR_C, \tag{3}$$

Table 1. Sensitivity of estimated ecosystem respiration (ER) to ±10% changes in the value of parameters used in the respiration model

		Change in annual *ER* (%)	
Parameter	Value	+10%	−10%
E_a	66400	−1.84	+2.05
Q_{10}	2.0	+0.48	−0.43
E_0	308.56	+0.15	−0.17
T_0	46.02	−0.28	+0.29
KL_M	14.1	+0.001	−0.001
KH_M	80.9	0.0	0.0
KH_P	56.6	−0.007	+0.008

where *WS* and *WR* denote the amount of carbon storage (Δrepresents growth rate from the daily-step scheme), and RS_M, RR_M, RS_C and RR_C are specific respiration rates. The construction terms were calculated only when the biomass growth rate was positive. The temperature dependence parameter, $Q_{\Delta\Gamma}$, takes a typical value of 2.0 at 15°C and higher values at lower temperatures because of acclimatization (Yokota and Hagihara, 1996). In addition, the specific maintenance respiration rates (RS_M and RR_M) decrease with the amount of carbon storage (Yokota and Hagihara, 1998) because a larger part of stems and roots is composed of heartwood with low respiratory activity (see Ito and Oikawa (2002) for parameterization).

2.3.3. Heterotrophic respiration. The rates of litter (*RL*) and humus (*RH*) decomposition are functions of soil temperature and soil moisture content. Each carbon pool of litter (from tree and forest floor plants for leaves, stems and roots) and humus (active, intermediate and passive) has different decomposability (RL_Γ and RH_Γ) and is calculated separately:

$$RL = RL_0 \cdot f_T \cdot f_M \cdot WL, \tag{4}$$

$$RH = RH_0 \cdot f_T \cdot f_M \cdot WH, \tag{5}$$

where *W*L and *W*H denote the amount of carbon storage in litter and humus. The temperature dependence followed a parameterization by Lloyd and Taylor (1994):

$$f_T = \exp\left[E_0 \cdot \left(\frac{1}{T_0 + 10} - \frac{1}{T_0 + T_{soil}}\right)\right], \tag{6}$$

where E_Γ and T_Γ are parameters, T_{soil} represents soil temperature: i.e., for litter, the observed 1-cm soil temperature, and for humus, the lower soil (10–200 cm depth) temperature estimated from daily climate data (described below). The moisture dependence parameterization differs between the two soil components; humus decomposition can be restricted not only by dryness, but also by water saturation:

$$f_M\,(litter) = \frac{ML}{KL_M + ML}, \tag{7}$$

$$f_M\,(humus) = \min\left\{\frac{MH}{KH_M + MH}, \frac{PH}{KH_P + PH}\right\}, \tag{8}$$

where *ML* and *MH* are the soil water contents of the litter and humus layers estimated using the hydrology module, and *PH* is the soil porosity index defined as the difference between *MH* and soil water-holding capacity. KL_M, KH_M, and KH_P are parameters (see Table 1 for values). Because the environmental conditions and carbon storage of the humus pool are satisfactorily stable, calculating *RH* at a daily time step may not result in a substantial estimation error.

2.3.4. Ecosystem respiration and soil respiration. Total CO_2 emission, or ecosystem respiration (*ER*), was obtained using the following equation:

$$ER = RF + RS + RR + RL + RH. \tag{9}$$

Similarly, CO_2 emission from the soil surface, or soil respiration (*SR*), was obtained as:

$$SR = RR + RL + RH. \tag{10}$$

The ecosystem carbon budget, or net ecosystem production (*NEP*), was obtained as the difference between photosynthetic assimilation *GPP* and *ER*. During the nighttime, *NEP* is quantitatively identical to *ER*.

2.3.5. Parameters and sensitivity analysis. Parameters for leaf respiration were derived from observations by Muraoka and Koizumi (2005), whereas most parameters for stem, root and heterotrophic respiration were determined through calibration. Ito et al. (2005) described the parameter calibration and provided a list of parameter values used in the model. Here, we performed a sensitivity analysis of the parameters that determine the responsiveness of the respiration rate to environmental conditions to provide the responses of the estimated annual *ER* to ±10% change in each of the parameter values (Table 1). In general, *ER* responded more strongly to parameters for temperature dependence (E_a, $Q_{\Delta\Gamma}$, E_Γ and T_Γ) than those for moisture dependence (KL_M, KH_M and KH_P). The low sensitivity for moisture is attributable to the abundant of annual precipitation.

2.4. Simulation and analyses

2.4.1. Simulation configuration. A model simulation is driven by time, climatic condition, atmospheric CO_2 concentration and disturbance events. Daily climate data for central Japan from 1 January 1948 to 31 December 2005 were generated from data from the US National Center for Atmospheric Research and the US National Centers for Environmental Prediction (Kistler et al., 2001). The large-scale climate data were corrected using temperature and precipitation recorded near the flux tower. In particular, soil temperatures during the snow-covered periods were corrected carefully to include snow-pack thermal effects (McGuire et al., 2000). First, for spinning-up the model to reach an equilibrium state, the model was run for 2900 years under a fixed atmospheric CO_2 condition (around 310 ppmv). A transitional simulation was performed using time-series climate and CO_2 conditions from 1948 to 2005. To include the disturbance effects of logging in the 1960s (Ito et al., 2005), removal of aboveground biomass was simulated for 1964. We examined the simulation results of ecosystem respiration from 1998 to 2005, when the eddy-covariance and chamber measurements were conducted. For that period, we performed a 30-min-step model simulation using observed meteorological data for air temperature, humidity, photosynthetically active radiation and 1-cm soil temperature.

2.4.2. Comparison with observations. The estimated *NEE* and *ER* were compared to the flux measurements from 1998 to 2005 at 30-min, daytime, nighttime, daily and annual time steps. Daily *SR* was compared to chamber observations from 1999 to 2002. Diurnal changes in correlation coefficients between model estimated and observed *NEE* were examined. For nighttime *NEE*, the difference between model estimation and observation was correlated with air temperature and friction velocity (u*), an index of atmospheric stability.

Table 2. Summary of the estimated respiratory CO_2 fluxes at the Takayama site for 1998–2005

Respiration term	Mean (g Cm^{-2} year^{-1})	Contribution (% ER)
RF, leaves	328	23.5
RS, stems	134	9.6
RR, roots	290	20.8
RL, litter	432	30.9
RH, humus	212	15.2
SR, soil respiration	934	66.9
ER, ecosystem respiration	1397	100.0

3. Results and discussion

3.1. Simulated ecosystem respiration

In 1998–2005, the average annual ecosystem respiration *ER* at the Takayama site was estimated as 1397 g Cm^{-2} yr^{-1} (Table 2), ranging from 1346 g Cm^{-2} yr^{-1} in 2003 to 1469 g Cm^{-2} yr^{-1} in 1998. Evidently, *ER* has quantitative importance equivalent to *GPP* making it one of the most important carbon flows in the ecosystem carbon budget. Approximately two-thirds of *ER* was soil respiration (*SR*), of which 31% was root respiration (*RR*). The simulated *RR* contribution to *SR* was slightly lower than that estimated empirically by Lee et al. (2003) using the trenching method. Fig. 1 shows that the seasonal change in *ER*

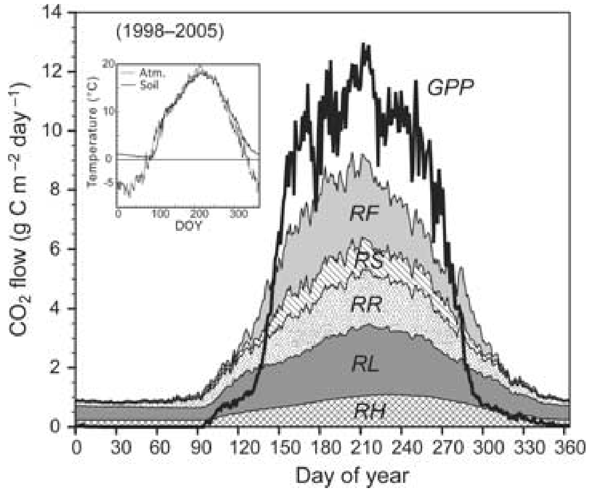

Fig. 1. Estimated seasonal changes in the ecosystem respiration components at the Takayama site: respiration by leaves (*RF*), stems (*RS*), roots (*RR*), litter (*RL*), and humus (*RH*). For comparison, the estimated seasonality in gross primary production (*GPP*) is also shown. Inset, seasonal changes in air temperature and 0-1 cm soil temperature.

and specific respiration flows were simulated clearly, especially in leaf respiration (*RF*) by mainly deciduous broad-leaved trees. *ER* was stable during winters with snow cover and increased during the growing period in parallel with temperature. Because of the abundance of precipitation throughout the year (about 2400 mm), soil moisture variability was so small that it did not exert evident effects on *SR* or *ER*. Fig. 1 clearly shows that the different seasonal changes in *GPP* and *ER* are responsible for the seasonal change in *NEE*. Almost half (49%) of the annual *ER* occurred at nighttime; note that the plant construction respiration rates (eq. 2 and eq. 3) are based on the daily allocation and growth rate. The nighttime contribution to daily rates was higher (about 65%) in winter and lower (about 35%) in early summer because of the variation in day length and temperature.

The years of lowest and highest *ER* corresponded to the cooler and warmer years, respectively, because ecosystem respiration is strongly regulated by temperature. To elucidate the temperature dependence, we examined the correlation of daily *ER* with daily mean air temperature (Fig. 2). The model estimation shows a non-linear curve with some scattering because it includes construction respiration components and soil decomposition, which are affected by soil temperature. Leaf respiration (*RF*) was also affected by the leaf phenology and aging effect, leading to apparently greater seasonal changes. The temperature dependence parameter value calculated by using regression, i.e. $Q_{10} = 2.54$, was close to that obtained using flux measurements, $Q_{10} = 2.57$ (Saigusa et al., 2002). The simulated *T–ER* relationship carried several important implications. First, two regimes appear in the *T–ER* relationship between the growing period (10 to 22°C), which was dominated by plant respiration, and the dormancy period (–13 to 10°C), which was dominated by soil respiration. The estimated ER had higher temperature dependence during the cooler term ($Q_{10} = 2.7$) than the warmer term ($Q_{10} = 2.1$). Second, the ecosystem respiration rate may not be estimated accurately using air temperature alone, although the relationship is used frequently to estimate *ER*. For example, around 10°C, the estimated *ER* ranged from 1.5 to 5.5 g $\mathrm{Cm^{-2}\ day^{-1}}$ because of variation in the leaf mass of deciduous trees, construction respiration and soil temperature and water conditions. Third, process-based models would be useful to interpret the observed *NEE* flux as the balance between gross uptake and release flows, and especially *ER*, for each of the individual respiratory components.

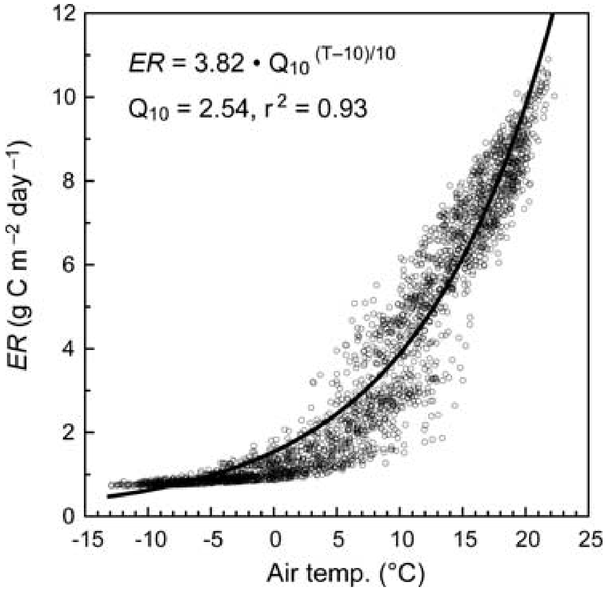

Fig. 2. Response of daily ecosystem respiration (*ER*) to daily mean air temperature at the Takayama site. The exponential regression curve is shown.

3.2. Comparison with observations

Fig. 3 shows the comparison of the estimated soil CO_2 efflux (*SR*) to observations in 1999–2002. The model captured the seasonal change in *SR* properly, ranging from low rates in winter to high rates in summer, as observed using the chamber method. The component flows (*RR*, *RL* and *RH*) had higher values in summer, and root respiration (*RR*) contributed greatly to *SR* during the growing period. However, the model simulation gave higher *SR* values than the observations in winter. The model estimation did not include several potentially important mechanisms to reduce *SR* in winter, i.e. the effect of snow packing on CO_2 diffusion, carbon substrate limitation and changes in the microbial community (Sommerfeld et al., 1993; Hirano, 2005; Takagi et al., 2005; Monson et al., 2006).

Fig. 4b compares the typical diurnal change in *NEE* simulated using the 30-min-step scheme to the flux observations. The

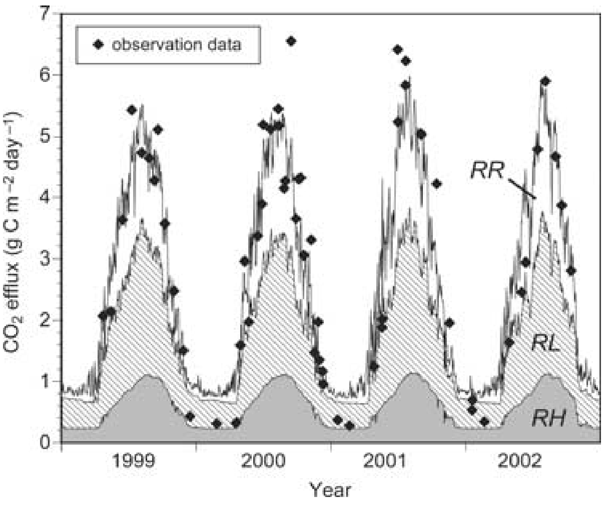

Fig. 3. Seasonal changes in the components of soil respiration (*SR*) by roots (*RR*), litter (*RL*), and humus (*RH*) at the Takayama site. The estimated *SR* is compared to observations made using the chamber method (Mo et al., 2005).

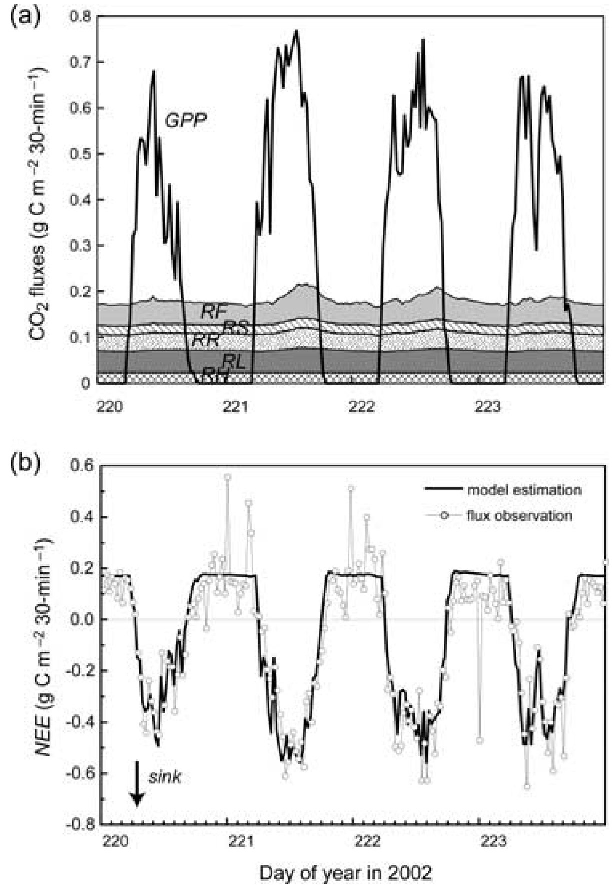

Fig. 4. Typical diurnal changes in (a) estimated gross CO_2 fluxes and (b) net CO_2 exchange at the Takayama site compared to the flux observations of Saigusa et al. (2002). Gross primary production (*GPP*), net ecosystem exchange (*NEE*), and respiration by leaves (*RF*), stems (*RS*), roots (*RR*), litter (*RL*), and humus (*RH*).

model satisfactorily reproduced daytime CO_2 uptake, but produced a nighttime CO_2 release that was very stable and higher than the observations on many occasions. Using the 8-year data, we calculated coefficients of correlation between the model-estimated and observed *NEE* at each time of day (Fig. 5). The correlation, i.e. the ability of the model to explain the variability in the observed *NEE*, appeared to be lower during nighttime hours. This implies that it is difficult to accurately capture the nighttime *NEE*, which is determined by *ER*, using the process-based model. However, as mentioned previously, nighttime flux measurement remains difficult under unsuitable atmospheric conditions. We therefore analyzed the difference in nighttime *NEE* between the model estimation and flux observation (Δ*NEE*), correlating it with atmospheric conditions. Fig. 6a shows the relationship between the nighttime Δ*NEE* and friction velocity (u*, an index of atmospheric turbulence) obtained from the flux measurements. Under relatively stable atmospheric conditions with $u^* < 1\ \mathrm{m\,s^{-1}}$, the difference was so evident that the model could not determine the nighttime *NEE* or *ER* as observed using the eddy-covariance method. As the atmosphere became turbulent, the difference became small, implying an observational problem under stable atmospheric conditions. Indeed, several studies (e.g., Law et al., 1999; Gu et al., 2005) pointed out that it is still difficult to relate u* with nighttime *NEE* and determine appropriate u* thresholds. This model-based analysis also suggests the necessity of further researches. Similarly, the relationship between Δ*NEE* and air temperature (Fig. 6b) shows that larger differences were apt to occur under warmer conditions, because of the exponential increase in *ER* with temperature (Fig. 2).

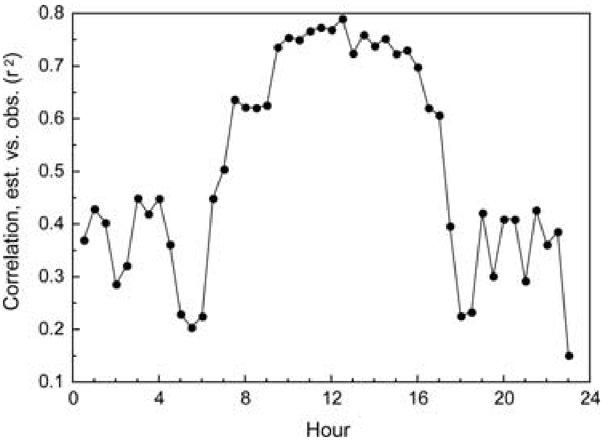

Fig. 5. Diurnal changes in the coefficients of correlation between the model estimation and flux observations for 30-min time step net ecosystem exchange (*NEE*) at the Takayama site for 1998–2005. Note that data from different seasons were used.

3.3. Concluding remarks

We studied the properties of ecosystem CO_2 efflux simulated with a process-based model using observational data. The model captured major features of *NEE* and component CO_2 fluxes, but often provided higher nighttime *ER*. The mean annual *ER* estimated in this study (1397 $\mathrm{g\,Cm^{-2}\,yr^{-1}}$) is higher than estimated from flux observations (Saigusa et al., 2005) and our previous model study (Ito et al., 2005), i.e. about 1000 $\mathrm{g\,Cm^{-2}\,yr^{-1}}$. These former studies used daily climate data and a daily-step model; however, using a 30-min step scheme, we were able to provide a finer estimation of ecosystem CO_2 emission. If the updated model estimation is confirmed by direct observations, we should revise the annual carbon budget of the Takayama forest mainly based on indirect *ER* observation using flux measurements.

In the Takayama forest, the interannual variability in the model-estimated *ER* (range of 123 $\mathrm{g\ Cm^{-2}\ yr^{-1}}$) was much smaller than that in the observed *NEE* (range of 287 $\mathrm{g\ Cm^{-2}\ yr^{-1}}$; Saigusa et al., 2005), implying that respiratory CO_2 emission may not be the determinant factor of interannual variability. This is consistent with the observation-based analysis by Saigusa et al. (2005) that the interannual change in *NEE* appears

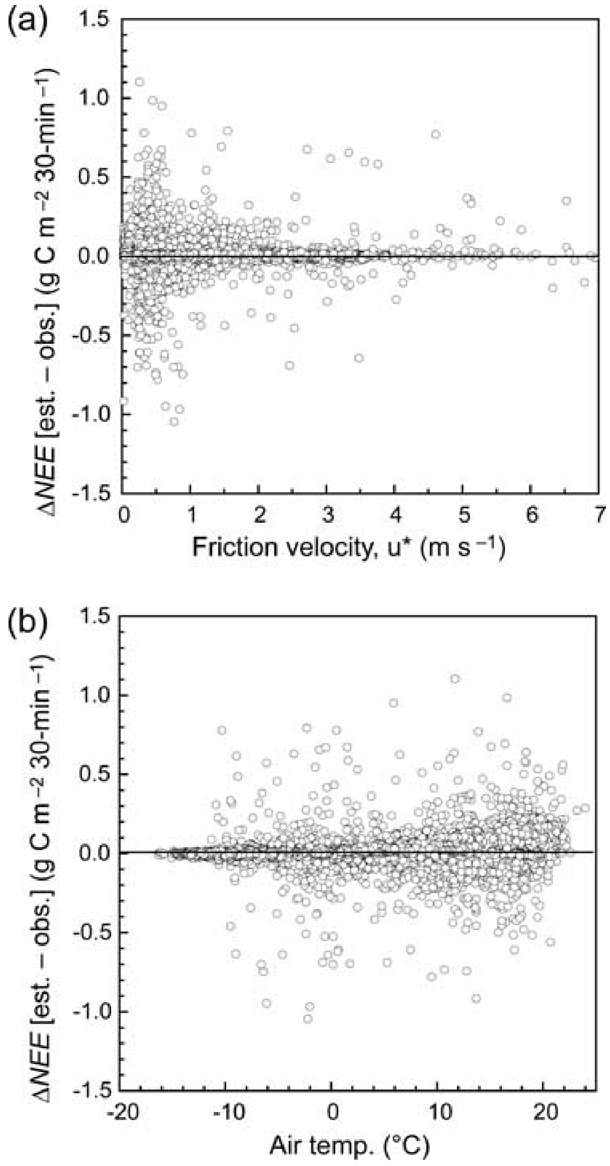

Fig. 6. Distributions of the difference in the 30-min net ecosystem exchange (*NEE*) between the model estimation and flux observation (Δ*NEE*) as functions of (a) friction velocity (u*) and (b) air temperature.

to be caused variability in photosynthetic productivity rather than respiration. However, in our 58-year simulation, the estimated *ER* varied substantially, especially after the simulated biomass removal by logging in 1964 (Ito et al., 2005). The decadal variability of *ER* contrasted with that of *GPP*, which became stable after canopy-closure, and was so large that it almost determined the long-term carbon budget of the forest, implying the characteristics and importance of respiration processes.

The model using semi-empirical parameterizations of respiratory processes captured the average magnitude and temporal variability in the ecosystem-scale respiration rate appropriately, allowing us to analyze the temporal variability and compositional change in the context of the carbon cycle. The good agreement implies that environmental responses were properly assumed in the model, although many parameters, e.g. respiratory activity of stems and roots, were obtained not by direct observation but by calibration. Additional observations of stem and root respiration and soil decomposition are necessary to develop a model to analyze the underlying mechanisms of carbon dynamics. The current parameterizations of respiratory processes used in ecosystem models are less mechanistic and more empirical than those in photosynthetic models. However, recent observations have pointed out the importance of the mechanistic parameterization of respiration, especially when we consider long-term carbon budgets (Ryan, 1991). With regard to the parameterization of plant respiration, insufficiencies remain in the response to elevated CO_2 levels, scaling of size dependent components and physiological linkages between respiratory processes including acclimation (Atkin et al., 2005). For example, several studies (e.g. Lavigne and Ryan, 1997; Noguchi et al., 2001) have suggested that the respiration coefficients (RS_M and RR_M in eq. 2 and eq. 3) are dependent on plant growth rates and light intensity. In relation to future global change, no consensus exists yet on whether elevated CO_2 concentration significantly inhibits mitochondrial respiration (Amthor and Baldocchi, 2001); acclimation makes its modelling more difficult. Correspondingly, several studies (e.g. Giardina and Ryan, 2000; Kirschbaum, 2004; Fang et al., 2005; Knorr et al., 2005) have suggested that soils can respond to long-term temperature change in a different manner from the response to changes over the short-term, a scale at which most experiments have been conducted. Unfortunately, these studies have reported inconsistent results for the acclimatization of soil decomposition to long-term temperature change (Davidson and Janssens, 2006). Further studies are required to include qualitative changes in soil organic matter and microbial acclimatization in ecosystem models.

We are convinced that collaborative studies such as those conducted in the Takayama site, including process observation, flux measurement and modelling, are the most effective approach by which to reduce the uncertainty in our understanding of the carbon cycle. This study may carry implications to field researchers for facilitating observations of parameters and fluxes related to respiration processes. Namely, further observations to determine parameter values in terms of sensitive environmental responses (Table 1) and large contribution to the ecosystem budget (Table 2) may improve the reliability of ecosystem carbon cycle models.

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