Functional Consequences of Differences in Canopy Phenology for the Carbon Budgets of Two Cool-Temperate Forest Types: Simulations Using the NCAR/LSM Model and Validation Using Tower Flux and Biometric Data

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SAITOH Taku M.1*, NAGAI Shin2, YOSHINO Jun3, MURAOKA Hiroyuki1, SAIGUSA Nobuko4 and TAMAGAWA Ichiro1

1 River Basin Research Center, Gifu University, 1-1 Yanagido, Gifu 501-1193, Japan
2 Research Institute for Global Change, Japan Agency for Marine-Earth Science and Technology, 3173-25 Showa-machi Kanazawa-Ku, Yokohama 236-0001, Japan
3 Graduate School of Engineering, Gifu University, 1-1 Yanagido, Gifu 501-1193, Japan
4 Center for Environmental Biology and Ecosystem Studies, National Institute for Environmental Studies, 16-2 Onogawa, Tsukuba 305-8506, Japan

Abstract
We quantified the sensitivity of estimated carbon budgets in Japanese evergreen coniferous and deciduous broad-leaved forests using NCAR/LSM simulations under two climatic conditions: the relatively warm end of the cool-temperate zone (i.e., 800 m a.s.l., annual average temperature of 9.4°C, annual average precipitation of 1700 mm), and the relatively cold end of this zone (i.e., 1420 m a.s.l., 7.2°C, and 2400 mm). To improve the model's performance for both forests, we modified parameters such as biomass and plant area index (PAI) based on measured values and calibrated the model using field-measured tower flux and biometric data at two AsiaFlux sites near Takayama City, Japan. The seasonal patterns and annual cumulative values of gross primary production (GPP), ecosystem respiration (RE), and net ecosystem production (NEP) predicted by the model agreed well with field measurements at the two sites. Our sensitivity analysis of the impact of growing period length on the carbon budget in the deciduous broad-leaved forest showed that GPP and NEP increased by 12.7% and 48.0%, respectively, when we considered the temperature dependency of the growing period length. In simulations under both climatic conditions, NEP peaked between April and June in the evergreen coniferous forest, and between July and September in the deciduous broad-leaved forest. The different seasonal patterns of NEP between the two forest types were determined primarily by differences in GPP that resulted from differences in PAI from April to June. The annual values of GPP, RE, and light-use efficiency were clearly greater in the evergreen coniferous forest than in the deciduous broad-leaved forest. Our simulation results suggest that the evergreen coniferous forest has higher metabolic activity than the deciduous broad-leaved forest in this region due to its larger biomass.

Key words: carbon budget, deciduous broad-leaved forest; evergreen coniferous forest; modeling

Introduction
Quantification of carbon budgets and their responses to environmental changes in several forest types will be crucial for predicting future carbon cycling under changing climate (e.g., Bonan 2008). The evergreen coniferous and deciduous broad-leaved forests are dominant forest types in Far East Asia (Ito 2008). Because these forests are expected to experience broad environmental fluctuations over seasons and years under a range of geographical and climatic conditions, analyses of the functional consequences of their different canopy characteristics for ecosystem carbon gain would provide deeper insights into the possible influence of climate change. The carbon budget of a forest ecosystem consists mainly of photosynthetic CO2 uptake and respiratory CO2 release, and ecophysiological regulation of the CO2 cycle is largely responsible for the environmental responses of ecosystem-scale carbon budgets (e.g., Muraoka and Koizumi 2009; Muraoka et al. 2010). Quantification of the carbon budget of forest ecosystems has been attempted using eddy-covariance measurements of the CO2 flux around a forest tower (e.g., Saigusa et al. 2005) and biometric analysis of vegetation, which provided a more detailed understanding of carbon cycling in the associated ecosystems (Ohtsuka et al. 2007).

Flux data measured from towers provide components of the carbon budget such as gross primary production (GPP), ecosystem respiration (RE), and net ecosystem exchange (NEE = –NEP, where NEP is net ecosystem production) (Baldocchi 2008). Biometric data provide components of the carbon budget such as NEP, net primary production (NPP), soil respiration (Rsoil), heterotrophic respiration (Rh), and root respiration (Rroot) (Litton et al. 2007). In addition to these in situ measurements, modeling analysis is useful for examining the ecophysiological and micrometeorological processes that occur in ecosystems and the integrated effects of these phenomena on...
carbon budgets. These kinds of analyses can deepen our understanding of carbon dynamics from both mechanistic (process-based simulations) and empirical (plant- or stand-scale observations) perspectives, especially in terms of the responses of carbon budgets to changes in climatic variables (e.g., Ito et al. 2005; Sitch et al. 2008).

The monsoon climate that characterizes Far East Asia differs from the dominant climates of Europe, North America, and South America (Kim et al. 2006; Yu et al. 2006; Saigusa et al. 2008). To monitor ecosystem carbon budgets in widely areas, Asian researchers require validated model simulations based on a combination of tower flux and biometric data at a range of forest sites. Some previous studies conducted these validations at individual sites in Far East Asia (e.g., Ito et al. 2007; Toda et al. 2011; Xue et al. 2011). However, to clarify and understand the differences in carbon budgets between evergreen coniferous and deciduous broad-leaved forests and the major causes of these differences, it will be necessary to compare two or more ecosystems. Previous studies have described the differences in carbon budgets among several terrestrial ecosystems using model simulations that were calibrated using either tower flux data or biometric measurement data (Ito 2008; Ichii et al. 2010; Ueyama et al. 2010; Sasai et al. 2011). However, we found no examples of comparisons of carbon budgets between two forest types using a model calibrated using both data types.

To provide such a comparison, we performed a long-term, continuous field study using both tower flux and biometric measurements in an evergreen coniferous forest at the AsiaFlux TKC site (Lee et al. 2008; Saitoh et al. 2010; Yashiro et al. 2010) and in a deciduous broad-leaved forest at the AsiaFlux TKY site (Saigusa et al. 2002; Ohtsuka et al. 2005, 2009). To reveal differences in the carbon budgets of the two forest types and the major causes of these differences, we used the National Center for Atmospheric Research / Land Surface Model (NCAR/LSM; Bonan 1996), which simulates carbon, energy, and water fluxes. We focused on three points: (1) To improve the model’s predictions, we evaluated the effects of model calibration using both the tower flux data and the biometric data from the two sites. (2) To clarify the influence of the growing period length on the carbon budget in the deciduous broad-leaved forest, we investigated the temperature dependency of the forest’s plant area index (PAI), because PAI is one of the key physiological parameters in the model (Bonan 1993) and because the timings of leaf expansion and leaf-fall were correlated well with seasonal changes of air temperature (Polgar and Primack 2011). (3) To compare the carbon budgets in the two forest types and to determine the sensitivity of the model outputs to climatic factors, we evaluated the budgets simulated with the micrometeorological data from each site at the two forest types.

2. Methods
2.1. Site description
The study was conducted at an evergreen coniferous forest site (TKC; 36°08’N, 137°22’E; 800 m a.s.l.) and a deciduous broad-leaved forest site (TKY; 36°08’N, 137°25’E; 1420 m a.s.l.) belonging to the AsiaFlux network (http://asiaflux.net) and the Japan Long-Term Ecological Research network (JaLTER, http://www.jalter.org). The horizontal distance between the sites is about 10 km. Both sites are located near Takayama City, in the central part of Japan’s main island. This region has a cool-temperate climate that is influenced by the Asian monsoon. It is characterized by mild, humid springs and autumns; hot, humid summers; and cold, snowy winters (Lee et al. 2008). Table 1 summarizes the vegetation and climate characteristics of the sites. PAI shows a clear seasonal pattern in the deciduous broad-leaved forest (Nasahara et al. 2008) but shows little seasonality in the evergreen coniferous forest (Saitoh et al. 2010). The difference in annual average temperature between the two altitudes (800 and 1420 m a.s.l.) was 2.2°C (Table 1). Saigusa et al. (2002) and Saitoh et al. (2010) provide more detailed descriptions of the TKY and TKC sites, respectively.

2.2. Ecosystem model
We used version 1.0 of the NCAR/LSM model (Bonan 1996). Here, we briefly describe the carbon flux calculations. In this model, the carbon budget is divided into CO₂ uptake by photosynthesis and CO₂ release by plant and heterotrophic respiration. Photosynthesis is coupled to stomatal resistance via parameterization of the model based on the models of Farquhar et al. (1980) and Collatz et al. (1991) for C₃ plants (see Appendix A for a detailed description). CO₂ release by the ecosystem consists of maintenance respiration, growth respiration, and heterotrophic respiration (see Appendix A for a detailed description). The model is driven at an hourly time step by the values of shortwave and longwave radiation, air temperature, wind speed, precipitation, and relative humidity. The outputs used in this study were carbon budget components (i.e., GPP, RE, NEP, NPP, Rsoil, Rn, and Rroot; see Appendix A for a detailed description). The micro-meteorological measurements at the TKY and TKC sites were described in Saigusa et al. (2002) and Saitoh et al. (2010), respectively.

2.3. Model simulations
To improve the model’s performance for both forests, we replaced default parameter values with values based on data from our study sites (Table 2). First, we improved the tree height, bottom of canopy, stem biomass, root biomass, PAI, displacement height, and roughness length parameters with measured values at the two sites. Second, we adjusted the maximum rate of carboxylation at 25°C, foliage maintenance respiration at 25°C, stem maintenance respiration at 25°C, root maintenance respiration at 25°C, and the heterotrophic respiration at 10°C and growth respiration parameters, and further calibrated the model, using tower flux data (i.e., seasonal patterns and the annual values of GPP, RE, and NEP) and biometric data (i.e., annual values of NPP, Rsoil, Rn, and Rroot) from the evergreen coniferous
Carbon budgets of two forests

The measured and adjusted parameters in our detailed comparison. The values used for calibration of the carbon budget were obtained from previously published data (Saigusa et al. 2005; Ohtsuka et al. 2007; Saitoh et al. 2010; Yashiro et al. 2010; Sasai et al. 2011).

To compare the carbon budgets between the two forest types, we ran the model under four scenarios: For

Table 1. Summary of the vegetation and climate characteristics at the AsiaFlux TKC and TKY sites, near Takayama City, Japan

<table>
<thead>
<tr>
<th>Parameters</th>
<th>TKC</th>
<th>TKY</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vegetation type</td>
<td>Evergreen coniferous forest</td>
<td>Deciduous broad-leaved forest</td>
</tr>
<tr>
<td>Dominant species</td>
<td>Cryptomeria japonica D. Don,</td>
<td>Betula ermanii Cham.</td>
</tr>
<tr>
<td></td>
<td>Chamaecyparis obtusa Sieb. et Zucc.(1)</td>
<td>Quercus crispula Blume(d)</td>
</tr>
<tr>
<td>Height of the tree canopy</td>
<td>20 to 25 m(a)</td>
<td>13 to 20 m(e)</td>
</tr>
<tr>
<td>Tree age</td>
<td>About 40 to 50 years(b)</td>
<td>About 50 years(f)</td>
</tr>
<tr>
<td>Annual maximum plant area index</td>
<td>PAI = 5 m² m⁻²(b)</td>
<td>PAI = 6 m² m⁻²(e)</td>
</tr>
<tr>
<td>(PAI, excluding understory)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Forest-floor vegetation</td>
<td>sparse shrubs, herbs, and ferns(c)</td>
<td>evergreen dwarf bamboo ([Sasa senanensis](Franch. et Sav.) Rehder)²</td>
</tr>
<tr>
<td>Annual mean air temperature</td>
<td>9.4 °C(c)</td>
<td>7.2 °C(d)</td>
</tr>
<tr>
<td>Annual mean rainfall</td>
<td>About 1700 mm(e)</td>
<td>About 2400 mm(d)</td>
</tr>
<tr>
<td>Snow period</td>
<td>December to April(e)</td>
<td>December to April(d)</td>
</tr>
</tbody>
</table>

(a) Lee et al. (2008), (b) Saitoh et al. (2010), (c) Average values from 2006 to 2010, (d) Ohtsuka et al. (2005), (e) Nasahara et al. (2008), (f) Saigusa et al. (2002)

Table 2. Representative default values and modified values for the parameters used in the model simulation in the evergreen coniferous forest at the TKC site and deciduous broad-leaved forest at the TKY site

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Evergreen coniferous forest at the TKC site</th>
<th>Deciduous broad-leaved forest at the TKY site</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Default Modified</td>
<td>Default Modified</td>
</tr>
<tr>
<td>Measured parameters</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tree height (m)</td>
<td>17</td>
<td>20.2(a)</td>
</tr>
<tr>
<td>Bottom of canopy (m)</td>
<td>8.5</td>
<td>10.0(a)</td>
</tr>
</tbody>
</table>
| Stem biomass (Vₚₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑехал

| Adjusted parameters                    |                                             |                                             |
| Max. rate of carboxylation at 25 °C (Vₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑ𝚎typing) | 33                                          | 33                                          | 33                                          | 40                                          |
| Foliage maintenance respiration rate at 25 °C (Rₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑ𝚎typing) | 0.5                                         | 0.7                                         | 0.5                                         | 0.3                                          |
| Stem maintenance respiration at 25 °C (Rₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑ𝚎typing) | 0.94                                        | 0.09                                        | 0.02                                        | 0.001                                        |
| Root maintenance respiration at 25 °C (Rₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑᵉtyping) | 0.36                                        | 0.30                                        | 0.01                                        | 0.45                                        |
| Heterotrophic respiration parameter at 10 °C (αₗ, μmol kg⁻¹ s⁻¹) | 0.37                                        | 0.37                                        | 0.40                                        | 0.32                                        |
| Proportionality coefficient of Growth respiration (αₖ) | 0.25                                        | 0.25                                        | 0.25                                        | 0.10                                        |

(a) Megumi Ishida, unpublished data, (b) Yashiro et al. (2010), (c) Saitoh et al. (2010), (d) Taku M. Saitoh, unpublished data, (e) Ohtsuka et al. (2005), (f) Nasahara et al. (2008), (g) Ichiro Tamagawa, unpublished data
the carbon budget of the evergreen coniferous forest, Simulation 1 used the climatic data recorded in that warmer forest (800 m a.s.l., 2006 and 2007), whereas Simulation 3 used the colder TKY climatic data (1420 m a.s.l., 2002 and 2003). For the carbon budget of the deciduous broad-leaved forest, Simulation 2 used the warmer TKC climatic data (800 m a.s.l., 2006 and 2007), whereas Simulation 4 used the data recorded within the colder deciduous forest (1420 m a.s.l., 2002 and 2003).

We compared simulation 1 with simulation 2 (which had an “expanded growing period” due to the use of warmer temperatures as mentioned below), and simulation 3 with simulation 4. Because PAI of broad-leaved forests depends on growing period length, in simulation 2 we calculated the carbon budget using two different seasonal variations in PAI: one used “modified growing period” based on the measured data at 1420 m a.s.l. (i.e., we assumed no temperature dependency of PAI and used the parameters in Table 2), and the other used adjusted parameters that accounted for the effects of changes in leaf phenology as a function of temperature (i.e., we used an “expanded growing period” that accounted for warmer temperatures at the lower elevation of the TKC site). In simulation 4, we used the seasonal pattern of PAI measured in the deciduous broad-leaved forest at the TKY site as the modified model parameters for PAI (i.e., we used the modified parameters in Table 2). In simulations 1 and 3, we used the seasonal pattern of PAI measured in the evergreen coniferous forest at the TKC site as the model parameters for PAI (i.e., we used the modified parameters in Table 2) at the two altitudes, because PAI exhibits little seasonality in evergreen coniferous forests (Saitoh et al. 2010).

3. Results and Discussion

3.1. Model calibration and estimation errors

The simulated seasonal patterns of GPP, RE, and NEP coincided well with the tower-flux measurements at both sites (R² 0.71–0.97 at the TKC site, 0.90–0.98 at the TKY site; Figs. 1, 2; Table 3). The annual errors in GPP, RE, and NEP ranged from 0.1 to 1.0 Mg C ha⁻¹ yr⁻¹ (Table 4).

The differences in GPP, RE, and NEP between the model estimate and the measured data, especially during the leaf-expansion and leaf-fall periods, might result from the model's simple treatment of ecophysiological variables such as the maximum carboxylation rate at 25°C ($V_{cmax25}$) and leaf nitrogen (N) content, both of which are key parameters that affect carbon dynamics in terrestrial ecosystems. The NCAR/LSM assumes that the values of $V_{cmax25}$ and leaf N content are constant throughout the year. However, Ito et al. (2006) and Muraoka et al. (2010) examined the effects of seasonal and inter-annual variations in canopy LAI and $V_{cmax25}$ on the GPP of a cool-temperate deciduous broad-leaved forest, and found seasonal variations in $V_{cmax25}$ that affected GPP. Kosugi et al. (2003) also concluded that the description of seasonal
variations in resulted from the model's failure to account for seasonal results suggest that some of our estimation errors improved by accounting for the seasonal pattern of N content in a cool-temperate, deciduous broad-leaved forest. Other studies have reported that N content was not constant throughout the year in evergreen coniferous (e.g., Kobayashi et al. 2010) forests. These analyses indicated that the two approaches differed by about 1.0 Mg C ha–1 yr–1. In addition, Yashiro et al. (2010) compared the eddy-covariance and biometric-based NEP at six Asian forest sites, including the TKY site, and found that the difference between the modeled and measured carbon fluxes at the TKC site (Table 4). The differences were of the same order of magnitude as the differences in measured NEP between the eddy-covariance and biometric approaches: Hirata et al. (2008) compared a tower flux–based NEP with a biometric-based NEP at six Asian forest sites, including the TKY site, and found that the difference (tower flux–biometric) in the NEPs at each site ranged from –1.0 to +1.5 Mg C ha–1 yr–1. In addition, Yashiro et al. (2010) compared the eddy-covariance and biometric estimates of NEP at the TKC site and found that the two approaches differed by about 1.0 Mg C associated with energy-imbalance problems (Wilson et al. 2002; Foken 2008) and may also underestimate the nocturnal ecosystem flux under stable atmospheric conditions (van Gorsel et al. 2007, 2009). The differences between the modeled and measured carbon fluxes were <1.0 Mg C ha–1 yr–1, except for Rsoil at the TKC site (Table 4). The differences were of the same order of magnitude as the differences in measured NEP between the eddy-covariance and biometric approaches: Hirata et al. (2008) compared a tower flux–based NEP with a biometric-based NEP at six Asian forest sites, including the TKY site, and found that the difference (tower flux–biometric) in the NEPs at each site ranged from –1.0 to +1.5 Mg C ha–1 yr–1. In addition, Yashiro et al. (2010) compared the eddy-covariance and biometric estimates of NEP at the TKC site and found that the two approaches differed by about 1.0 Mg C

<table>
<thead>
<tr>
<th>Site</th>
<th>Carbon flux</th>
<th>Model simulation (Mg C ha–1 yr–1)</th>
<th>Measurement (g C m–2 mon–1)</th>
</tr>
</thead>
<tbody>
<tr>
<td>TKC</td>
<td>GPP</td>
<td>22.3</td>
<td>22.1(b)</td>
</tr>
<tr>
<td></td>
<td>RE</td>
<td>18.9</td>
<td>16.8(b)</td>
</tr>
<tr>
<td></td>
<td>NEP</td>
<td>3.5</td>
<td>3.4(b)</td>
</tr>
<tr>
<td></td>
<td>NPP</td>
<td>7.7</td>
<td>7.9(b)</td>
</tr>
<tr>
<td></td>
<td>Rsoil</td>
<td>8.3</td>
<td>6.8(b)</td>
</tr>
<tr>
<td></td>
<td>Rh</td>
<td>4.1</td>
<td>3.6(b)</td>
</tr>
<tr>
<td></td>
<td>Rroot</td>
<td>4.2</td>
<td>3.3(b)</td>
</tr>
<tr>
<td>TKY</td>
<td>GPP</td>
<td>11.3</td>
<td>10.3(b)</td>
</tr>
<tr>
<td></td>
<td>RE</td>
<td>8.3</td>
<td>7.3(b)</td>
</tr>
<tr>
<td></td>
<td>NEP</td>
<td>3.0</td>
<td>2.9(b)</td>
</tr>
<tr>
<td></td>
<td>NPP</td>
<td>6.3</td>
<td>6.5(b)</td>
</tr>
<tr>
<td></td>
<td>Rsoil</td>
<td>6.2</td>
<td>6.8(b)</td>
</tr>
<tr>
<td></td>
<td>Rh</td>
<td>3.3</td>
<td>3.7(b)</td>
</tr>
<tr>
<td></td>
<td>Rroot</td>
<td>2.9</td>
<td>3.1(b)</td>
</tr>
</tbody>
</table>

RMSE = root-mean-square error; MBE = mean bias error; \( R^2 \) = coefficient of determination.

Although measurement data are useful for model calibration and validation, it's important to remember that they usually include estimation errors. Previous studies indicated that random measurement errors in estimates of the annual carbon budget by the eddy-covariance approach are typically on the order of ±0.3 to 0.5 Mg C ha–1 yr–1 (Baldocchi 2003; Richardson and Hollinger 2007). However, the errors sometimes exceed ±1.0 Mg C ha–1 yr–1 at mountain sites (Baldocchi 2003). Carbon budget estimation based on the eddy-covariance approach has been carefully evaluated at the TKC and TKY sites by means of “quality control and quality assurance” and gap-filling (Saigusa et al. 2002; Saitoh et al. 2010). These analyses showed that the eddy-covariance measurements have uncertainties due to a potential systematic bias

**Table 3.** Errors in monthly gross primary production (GPP), ecosystem respiration (RE), and net ecosystem production (NEP) simulated by the model in the evergreen coniferous forest at the TKC site and the deciduous broad-leaved forest at the TKY site.

<table>
<thead>
<tr>
<th>Site</th>
<th>Carbon flux</th>
<th>Error (g C m–2 mon–1)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>RMSE</td>
</tr>
<tr>
<td>TKC</td>
<td>GPP</td>
<td>26.7</td>
</tr>
<tr>
<td></td>
<td>RE</td>
<td>21.7</td>
</tr>
<tr>
<td></td>
<td>NEP</td>
<td>18.0</td>
</tr>
<tr>
<td>TKY</td>
<td>GPP</td>
<td>24.6</td>
</tr>
<tr>
<td></td>
<td>RE</td>
<td>10.6</td>
</tr>
<tr>
<td></td>
<td>NEP</td>
<td>19.6</td>
</tr>
</tbody>
</table>

**Table 4.** Validation of the simulated (model) annual cumulative carbon fluxes in the evergreen coniferous forest at the TKC site and the deciduous broad-leaved forest at the TKY site. Note that this validation includes some uncertainty arising from the difference in the periods used for the model and the measurement data in (b) and (d).

GPP = gross primary production; RE = ecosystem respiration; NEP = net ecosystem production; NPP = net primary production; Rsoil = soil respiration; Rh = heterotrophic respiration; Rroot = root respiration.

(a) 2-year average from 2006 to 2007 estimated using the tower flux–based (eddy-covariance) method (Saitoh et al. 2010).
(b) 4-year average from May 2005 to March 2009 estimated using biometric (Yashiro et al. 2010).
(c) 2-year average from 2002 to 2003 estimated using the tower flux–based (eddy-covariance) method (Saitoh et al. 2010).
(d) 5-year average from 1999 to 2003 estimated using biometric data (Ohtsuka et al. 2007).
(e) 2-year average from 2002 to 2003 estimated using biometric data (Ohtsuka et al. 2007).

physiological changes in \( V_{\text{max25}} \) by a biochemical model of photosynthesis will affect estimates of the long-term CO2 gas exchange. In addition, Ueyama et al. (2010) indicated that the BIOME-BGC model's accuracy of estimation of the carbon budget was improved by accounting for the seasonal pattern of N content in a cool-temperate, deciduous broad-leaved forest. Other studies have reported that N content was not constant throughout the year in evergreen coniferous (e.g., Kobayashi et al. 2010) and deciduous broad-leaved (e.g., Wilson et al. 2000) forests. These results suggest that some of our estimation errors resulted from the model's failure to account for seasonal variations in \( V_{\text{max25}} \) and N content.

The differences in GPP, RE, and NEP between model estimates and the measured data, especially in summer at the TKC site, might similarly result from the model's parameters for the water cycle. Saitoh et al. (2010) reported that soil dryness influenced the maximum GPP estimated by non-linear curve fitting of the relationship between light intensity (photosynthetic photon flux density, PPFD) and GPP in August 2007 at the TKC site. The model might overestimate the effects of soil moisture stress on GPP and RE. To improve the model's accuracy, it will be necessary to calibrate the water budget against field measurements.

Although measurement data are useful for model calibration and validation, it's important to remember that they usually include estimation errors. Previous studies indicated that random measurement errors in estimates of the annual carbon budget by the eddy-covariance approach are typically on the order of ±0.3 to 0.5 Mg C ha–1 yr–1 (Baldocchi 2003; Richardson and Hollinger 2007). However, the errors sometimes exceed ±1.0 Mg C ha–1 yr–1 at mountain sites (Baldocchi 2003). Carbon budget estimation based on the eddy-covariance approach has been carefully evaluated at the TKC and TKY sites by means of “quality control and quality assurance” and gap-filling (Saigusa et al. 2002; Saitoh et al. 2010). These analyses showed that the eddy-covariance measurements have uncertainties due to a potential systematic bias associated with energy-imbalance problems (Wilson et al. 2002; Foken 2008) and may also underestimate the nocturnal ecosystem flux under stable atmospheric conditions (van Gorsel et al. 2007, 2009). The differences between the modeled and measured carbon fluxes were <1.0 Mg C ha–1 yr–1, except for Rsoil at the TKC site (Table 4). The differences were of the same order of magnitude as the differences in measured NEP between the eddy-covariance and biometric approaches: Hirata et al. (2008) compared a tower flux–based NEP with a biometric-based NEP at six Asian forest sites, including the TKY site, and found that the difference (tower flux–biometric) in the NEPs at each site ranged from –1.0 to +1.5 Mg C ha–1 yr–1. In addition, Yashiro et al. (2010) compared the eddy-covariance and biometric estimates of NEP at the TKC site and found that the two approaches differed by about 1.0 Mg C
We conclude that the simulated carbon budget in our forests was within these levels of measurement error.

Yashiro et al. (2010) indicated that the measurement errors in a biometric approach may be caused by (1) an insufficient number of sample points for measurement components such as soil respiration and biomass (mainly due to spatial and temporal heterogeneity of the variables), (2) uncertainty in root growth and respiration, and (3) footprint differences between the tower flux and biometric approaches. For instance, Liang et al. (2004) found large differences in CO$_2$ efflux among four observational approaches. These reports suggest the need for a more robust approach to measuring soil respiration so that this parameter can be divided into root and heterotrophic respiration, and the need to calibrate the relationship between measurements obtained using different instruments.

### 3.2. Sensitivity analysis of the impact of growing period length on the carbon budget

Using daily canopy surface images and air temperature data at the TKY site (1420 m a.s.l.) from 2004 to 2009 (Nagai et al. 2011), we examined the dates of the beginning of leaf expansion, the beginning of autumn leaf color development, and the end of leaf-fall, and their relationships with air temperature. We found that (1) leaf expansion began when the accumulated effective air temperature from the first day of the year (based on a 5°C threshold) exceeded 140.0 ± 13.5°C (average ± standard deviation) during spring; (2) leaf color development began when the 5-day moving-average daily temperature fell below 10.8 ± 1.3°C during autumn; and (3) the leaf-fall period, which was defined as the period between the beginning of autumn leaf color development and the end of leaf-fall, was 30.7 ± 4.0 days.

We adapted these relationships between leaf phenology in the deciduous broad-leaved forest and air temperature to account for the seasonal variation of PAI at the warmer TKC site (800 m a.s.l.). As a result, the beginning of leaf expansion and the end of leaf-fall were 12.7 days earlier and 9.9 days later, respectively, at 800 m a.s.l. than they were at 1420 m a.s.l. In total, the potential growing period was therefore about 23 days longer at the lower altitude. We defined this expanded period of tree phenology as one of the two sets of model parameters for PAI at 800 m a.s.l. In simulation 2, the carbon budget differed between the “modified growing period” and “expanded growing period” simulations: the latter GPP, NPP, and NEP values from April to June that are similar to those from May and LAI does not reach its maximum value during this period (Nasahara et al. 2008). In contrast, evergreen coniferous forests of this region have PAI values from April to June that are similar to those from July to September (Saitoh et al. 2010). Therefore, the difference in GPP from April to June may be influenced by differences in the seasonal patterns of PAI between the two forest types.

The difference in GPP between the two forest types from April to June affected the seasonal variation in NEP: NEP peaked from April to June in the evergreen coniferous forest but from July to September in the deciduous broad-leaved forest. Our results confirm previous studies of the seasonal patterns of NEP in evergreen coniferous and deciduous broad-leaved forests in East Asia (e.g., Saigusa et al. 2008). In addition, the biomass in the evergreen coniferous forest was more than twice that in the deciduous broad-leaved forest, with corresponding values of 8.2 and 1.2 Mg C ha$^{-1}$ yr$^{-1}$ in two years with the lowest mean annual air temperature, in 1995 and 1996 (i.e., average values of 5.6°C) (Saigusa et al. 2005; Ohtsuka et al. 2009).

### Fig. 3. Annual carbon budget simulated by using “modified growing period” and “expanded growing period” in the deciduous broad-leaved forest under the TKC meteorological conditions. GPP is gross primary production, RE is ecosystem respiration, NPP is net ecosystem production, NEP is net primary production, Rs is soil respiration, Rh is heterotrophic respiration, and Rroot is root respiration.
forest (Table 2). As a result, under the microclimatic conditions at both altitudes, the annual values of GPP, RE, and light-use efficiency (LUE), which we calculated as the ratio of GPP to PPFD measured at the flux towers in the two forests, were clearly greater in the evergreen coniferous forest than in the deciduous broad-leaved forest, and the differences (coniferous – deciduous) in NEP, NPP, $R_{\text{soil}}$, $R_{\text{in}}$, and $R_{\text{root}}$ between the forests ranged from −0.2 to +2.1 Mg C ha$^{-1}$ yr$^{-1}$ (Figure 5). Our findings suggest that the evergreen coniferous forest has higher metabolic activity than the deciduous broad-leaved forest in this cool-temperate region of Japan.

Fig. 4. Comparison of the carbon budget between the evergreen coniferous forest and the deciduous broad-leaved forest under the different meteorological conditions at the two altitudes for four periods during the year. GPP is gross primary production, RE is ecosystem respiration, and NEP is net ecosystem production. JFM, AMJ, JAS, and OND indicate the average values from the corresponding months of the year. Note that “expanded growing period” was used in simulation 2 (the carbon budget in the deciduous broad-leaved forest at 800 m a.s.l.).
3.4. Implications for future studies

This study is the first step in evaluating differences in the carbon budget characteristics between evergreen coniferous and deciduous broad-leaved forests in the cool-temperate region of Japan. Our analytical approach to determining the carbon budgets based on calibration of the simulation model using both tower flux and biometric data can be conducted at various spatial scales. To apply the calibration approach to other ecosystems and to evaluate the carbon budget with improved accuracy from regional to global scales, researchers will require general, long-term, continuous, and comprehensive biometric information, such as NPP and biomass values, and phenological information, such as PAI, from tower flux sites. To achieve this goal, it will be necessary to share ecosystem databases, as has been done by the International Long Term Ecological Research project (ILTER; http://www.ilternet.edu/) and the Phenological Eyes Network (PEN; http://www.pheno-eye.org). It will be also necessary to confirm the present results by determining carbon budgets for the same forest types at three or more elevations or three or more latitudes at the same elevation to confirm the differences as a function of altitude that we observed here.

Recent studies indicate that estimates based on a fine spatial resolution (a 1-km grid) were much more effective for evaluating ecosystem carbon cycles than simulations at a coarser spatial resolution (about a 100-km grid) for landscapes with complex topography (Ito 2008; Sasai et al. 2011). Our results revealed clear differences in growing period length and in carbon budget estimates between the two altitudes, even though the horizontal distance between the two sites was less than 10 km. Furthermore, the tree phenology characteristics in deciduous broad-leaved forests at different altitudes clearly affected the carbon budget estimation. Our results therefore indicate the importance of determining the optimal spatial resolution for use in evaluating the carbon budget of regions such as Japan that have complex topography.
Appendix A: Estimation of carbon budget components in NCAR/LSM

NCAR/LSM is a sun and shade model that does not account for the effects of the understory vegetation. The sunlit fraction of the canopy \( f_{\text{sun}} \) is given by:

\[
f_{\text{sun}} = \int_0^{L+S} e^{-K(L+S)} \frac{dx}{L+S} = 1 - e^{-K(L+S)} \tag{A1}
\]

where \( e^{-K(L+S)} \) is the fractional area of sunflecks on a horizontal plane below the leaf and stem areas (represented by the indices \( L \) and \( S \), respectively), and \( K \) represents scattering within canopy. The shaded fraction \( f_{\text{shade}} \) equals \( [1 - f_{\text{sun}}] \) and the sunlit and shaded LAIs are \( [L_{\text{sun}} = f_{\text{sun}} L] \) and \( [L_{\text{shade}} = f_{\text{shade}} L] \), respectively. Bonan (1996) provides details of the calculation scheme for incident solar radiation at the canopy level and for the energy budget resulting from the radiation and the water vapor balances.

The photosynthesis part of LSM (Bonan 1996) is based on those of Farquhar et al. (1980) and Collatz et al. (1991). Single-leaf photosynthesis of \( C_3 \) plant is determined as:

\[
A = \min(w_c, w_j, w_c) \tag{A2}
\]

where \( w_c \) is the RuBP carboxylase–limited rate of carboxylation, \( w_j \) is the maximum rate of carboxylation allowed by the capacity to regenerate RuBP, and \( w_c \) is the export-limited rate of carboxylation:

\[
w_c = \frac{\left(c_i - \Gamma^* \right) V_{\text{max}}}{c_i + K_c \left(1 + \frac{O_j}{K_o}\right)} \tag{A3}
\]

\[
w_j = \frac{\left(c_i - \Gamma^* \right) 4.6 \varphi \alpha}{c_i + 2 \Gamma^*} \tag{A4}
\]

where \( \varphi \) is the absorbed photosynthetically active radiation calculated in LSM, \( \alpha \) is the quantum yield of photosynthesis (\( \mu \text{mol} \text{CO}_2 \mu \text{mol}^{-1} \text{photons} \)), \( c_i \) is the initial leaf \( \text{CO}_2 \) concentration (Pa), \( \Gamma^* \) is the \( \text{CO}_2 \) compensation point (Pa), \( O_j \) is \( \text{O}_2 \) concentration (Pa), \( K_c \) is the Michaelis-Menten constants for \( \text{CO}_2 \) (Pa), and \( K_o \) is the Michaelis-Menten constants for \( \text{O}_2 \) (Pa). Here, \( V_{\text{max}} \) varies with temperature and soil water as follows:

\[
V_{\text{max}} = V_{\text{max},25} a_{T_{25}}^{\frac{T_v - 25}{10}} f(N) \beta_i f(T_v) \tag{A6}
\]

where \( V_{\text{max},25} \) is the value at 25°C, \( a_{T_{25}} \) is a temperature sensitivity parameter for \( V_{\text{max}} \) (fixed at 2.4), \( T_v \) is leaf temperature, \( f(N) \) is an adjustment parameter for the rate of photosynthesis that accounts for the leaf nitrogen (N) content (\( f(N) = 1 \) in this study), \( \beta_i \) varies from 0 to 1 (depending on soil water conditions), and \( f(T_v) \) is a function that mimics the thermal breakdown of metabolic processes (Bonan 1996):

\[
f(T_v) = \left[1 + \exp \left(\frac{-220000 + 710 \cdot (T_v + 273.16)}{8.314 \cdot (T_v + 273.16)}\right)\right]^{-1} \tag{A7}
\]

The photosynthetic rate in the LSM is determined by iterative calculation of the model defined by equations A1 to A7 and a modified stomatal conductance model:

\[
g_{\text{sm}} = \frac{A e}{c_i e_j} P_{\text{atm}} + g_s \tag{A8}
\]

where \( g_{\text{sm}} \) is the stomatal conductance for water vapor (mol m\(^{-2}\) s\(^{-1}\)), \( m \) is an empirical regression parameter, \( A \) is the photosynthetic rate (\( \mu \text{mol} \text{CO}_2 \text{m}^{-2} \text{s}^{-1} \)), \( c_i \) is the \( \text{CO}_2 \) concentration at the leaf surface (Pa), \( e_j \) is the vapor pressure at the leaf surface (Pa), \( e_i \) is the saturation vapor pressure (Pa) inside the leaf at the vegetation temperature, and \( g_s \) is the minimum stomatal conductance (0.002 mol m\(^{-2}\) s\(^{-1}\)) when \( A = 0 \). These calculations are made for both sunlit and shaded parts of the canopy (\( A_{\text{sun}} \) and \( A_{\text{shade}} \)) and are summed for the entire canopy as \( \text{GPP} = [A_{\text{sun}} \cdot L_{\text{sun}} + A_{\text{shade}} \cdot L_{\text{shade}}] \).

Plant respiration is broken into maintenance and growth respiration. Total maintenance respiration in the LSM is determined by the sum of the foliar (\( R_m \)), stem (\( R_s \)), and root (\( R_r \)) respiration:

\[
R_{m} = R_{gm} + R_{m} + R_{sr} \tag{A9}
\]

\[
= \left[L \cdot R_{25} \cdot f(N) \cdot \beta_i + V_{bs} \cdot R_{25} + V_{sr} \cdot R_{25} \right] a_{\text{gm}}^{\frac{T_v - 25}{10}}
\]

where \( L \) is the leaf area index (m\(^2\) m\(^{-2}\)), \( R_{25} \) is foliar respiration at 25°C (\( \mu \text{mol} \text{CO}_2 \text{m}^{-2} \text{s}^{-1} \)), \( V_{bs} \) is stem biomass (kg m\(^{-2}\)), \( R_{25} \) is stem respiration at 25°C (\( \mu \text{mol} \text{CO}_2 \text{kg}^{-1} \text{s}^{-1} \)), \( V_{sr} \) is root biomass (kg m\(^{-2}\)), \( R_{25} \) is root respiration at 25°C (\( \mu \text{mol} \text{CO}_2 \text{kg}^{-1} \text{s}^{-1} \)), and \( a_{\text{gm}} \) is a temperature sensitivity parameter. Growth respiration (\( R_g \) in LSM) is proportional to GPP, as follows:

\[
R_g = a_{gr} \cdot \text{GPP} \tag{A10}
\]

where \( a_{gr} \) is a proportionality coefficient.

Heterotrophic respiration (\( R_h \)) is determined by the following equation:

\[
R_h = \theta a_1 + \theta a_2 + \theta S_c a_4^{\frac{T_s - 10}{10}} \tag{A11}
\]

where \( \theta \) is the volumetric soil water content a depth of 1 m (m\(^3\) m\(^{-3}\)), \( a_1 \) is half of field capacity, \( a_2 \) is half of the saturated capacity, \( S_c \) is soil carbon to a depth of 1 m (kg m\(^{-2}\)), \( a_3 \) is the respiration rate (\( \mu \text{mol} \text{CO}_2 \text{kg}^{-1} \text{s}^{-1} \)) at 10°C, \( a_4 \) is a temperature sensitivity parameter, and \( T_s \) is the temperature (°C) of the first soil layer.

Finally, NEP, NPP, \( R_{\text{base}} \), and \( R_{\text{soil}} \) were calculated using the following equations:

\[
\text{NEP} = \text{GPP} - \text{RE} \tag{A12}
\]
NPP = NEP + $R_h$  \hspace{1cm} \text{(A13)}

$R_{\text{root}} = R_{\text{mr}} + R_{\text{g}} \frac{V_{hr}}{V_{bs} + V_{hr}}$  \hspace{1cm} \text{(A14)}

$R_{\text{soil}} = R_{\text{root}} + R_h$  \hspace{1cm} \text{(A15)}

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