Comparison of eddy covariance and chamber-based methods for measuring CO₂ flux in a temperate mixed forest

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Summary Two methods, eddy covariance and chamber-based measurements, were employed to measure the net ecosystem CO₂ exchange in a mature temperate mixed forest in 2003. The eddy covariance system was used as a reference, which was compared with the chamber-based method. Based on chamber fluxes, the ecosystem had a gross primary production of 1490 g C m⁻² year⁻¹, 90% of which was released as efflux back into the air via respiration of the entire ecosystem. This was comprised of about 48% from soil surface CO₂ efflux, 31% from leaf respiration and 21% from stem and branch respiration. Net ecosystem exchange (NEE), estimated from the sum of daily component fluxes, was 146 g C m⁻² year⁻¹. Ecosystem respiration (ER), estimated from the sum of daily ecosystem respiration, was 1240 g C m⁻² year⁻¹. NEE was 9.8% of actual gross primary production (GPP). The eddy covariance estimates of NEE, ER and GPP were 188, 1030 and 1220 g C m⁻² year⁻¹, respectively. The eddy covariance estimation of NEE was higher than that of the chamber-based estimation by 22.5%. On a daily basis, NEE of the scaled chamber measurements was in acceptable agreement with eddy covariance measurement data with R² values of 0.71. The discrepancy between the measurement of the two methods was greater in the non-growing season primarily due to the lack of spatial variability in the scaled chamber estimates and weak atmosphere turbulence by eddy covariance measurements. There are many uncertainties for determination of absolute values of ecosystem component flux. More detailed experiments and related theoretical studies are needed in the future.

Keywords: chamber-based measurement, eddy covariance method, foliage respiration, net ecosystem exchange of CO₂, soil respiration, stem respiration.

Introduction

Forests contain 66–80% of all carbon stored in the world’s above-ground biomass. About 45% of this is found in below-ground terrestrial pools (Waring et al. 1998, Zha et al. 2007), constituting a significant contribution to the global carbon budget. Quantification of the annual carbon cycle in terrestrial ecosystems is crucial to understanding and managing the global carbon cycle (Frank and Dugas 2002). Global CO₂ exchange research is focused on the CO₂ exchange between forests and the atmosphere. Continuous measurements of CO₂ exchange have been taking place in various terrestrial ecosystems (Baldocchi et al. 2001) since the 1990s and they help to clarify the contributions of various ecosystems to the global carbon cycle (Law et al. 1999a, Baldocchi et al. 2002). Recently, a considerable amount of data has been acquired by measuring and modeling the carbon balance of temperate and northern boreal forest ecosystems (Houghton et al. 1999, Law et al. 1999a, Baldocchi et al. 2002, Bolstad et al. 2004, Guan et al. 2006). However, there is still much uncertainty about the strength of the carbon source/sink in these forests due to the discrepancies in estimation methods, the complexity of terrestrial ecosystems and the scarcity of research sites (Field and Fung 1999, Schimel et al. 2000).

Net ecosystem exchange (NEE) of carbon dioxide (CO₂) is determined by the balance of respiratory and assimilatory processes. It is dependent on the complex interaction of many factors including leaf area, CO₂ exchange capacity, photosynthetic (leaves) and non-photosynthetic (stems and roots) tissue activity, canopy structure, stand biomass of plant species and meteorological conditions including light, air temperature, air humidity, wind speed and atmospheric CO₂ concentration (Ehleringer and Field 1993, Baldocchi and Wilson 2001, Baldocchi et al. 2002). Hence, it is necessary to understand the biological and physical controls on photosynthesis and respiration in order to estimate how net ecosystem exchange of CO₂ will respond to environmental changes.

Recently, eddy covariance and chamber-based measurements have been used to estimate an ecosystem’s carbon exchange (Lavigne et al. 1997, Bolstad et al. 2004, Wu et al. 2006). Net CO₂ exchange in ecosystems, including respiration, has been measured successfully and reliably quantified by eddy covariance measurements (Baldocchi et al. 2002). In addition, the eddy covariance method has been applied in the ChinaFLUX project—an independent
CO2 concentration as well as pressure gradients, turbulent flows, and uncertainties associated with so-called chamber ecosystems (Baldocchi 1990). Chambers may disturb the environment and alter estimates of average respiration rates (Janssens and Ceulemans 1998, Janssens et al. 2001, Zha et al. 2007, Savage et al. 2008). At the same time, these samples are subject to methodological errors for interpretation (Tang et al. 2008), especially relative to measurements taken simultaneously at the same sites using eddy covariance and chamber-based methods presents problems for interpretation (Tang et al. 2008), especially relative to measurements taken simultaneously at the same sites using the two different methods.

In this study, chamber-based measurements were used to measure the CO2 fluxes in soil, woody tissues (stem and branch) and foliage during an entire year. Furthermore, the eddy covariance system was used as a reference system for comparison with the chamber system measurements to measure forest ecosystem flux. The objectives of our study were to:

1. Extrapolate the chamber-based measurements to an annual budget of stand-scale ecosystem using half-hourly measurements of soil, air and sapwood temperature;
2. Quantify seasonal and annual components of ecosystem CO2 exchange fluxes in a temperate mixed forest; and
3. Compare the eddy covariance technique with the chamber-based method for estimating ecosystem CO2 exchange fluxes.

**Methods**

**Site description**

The study area is located in the Changbai Mountain Natural Reserve, northeastern China. The natural reserve, which contains one of the largest protected temperate forests in the world, was established in 1960 (Shao et al. 1994, Stone 2006). The meteorological tower is situated at 42° 24’ 09” N, 128° 05’ 45” E at an elevation of 738 m. The forest at the tower site is unmanaged and contains trees of a variety of ages. The site is level (slope of 1–2°), which is ideal for this study; the overstory and understory of the forest are homogeneous.

The average tree canopy was ~26 cm in height. The mean age of the overstory trees was about 250 years old. The tree species in the canopy were dominated by Pinus koraiensis Sieb. et Zucc. (34% of the trees), Tilia amurensis Rupr. (42%), Quercus mongolica Fisch. ex Ledeb. (13%) and Fraxinus mandshurica Rupr. (10%). These four species comprised 62.6% of all individuals (Hao et al. 2007). Stand density was 1556 trees per hectare for all living trees. Basal area was 43.2 m² ha⁻¹ in 2003.

The understory mainly consisted of Actinidia kolomikta (Maxim. et Rupr.) Maxim., Filipendula palmata (Pall.) Maxim., Osmunda cinnamomea L., Meehania articifolia (Miq.) Makino and dwarf shrubs (Corylus heterophylla Maxim. et Rupr. ex Trautv. Acer barbinerve Maxim., Euonymus alatus (Thunb.) Sieb. and Ribes mandshuricum (Maxim.) Kom.

The area is in a temperate continental climatic zone, with an annual average precipitation and air temperature of 700 mm and 3.6 °C, respectively, a January mean temperature of −15.6 °C and a July mean temperature of 19.7 °C. These values were measured at a nearby weather station over a period from 1982 to 2003. Most precipitation in this area occurs from June to September (480–500 mm; Zhang et al. 2005).

The period of snow cover is from November to April, with a maximum depth of about 30 cm. Stand soil is classified as dark brown forest soil (Mollisols according to American Soil Taxonomy Series 1999). The soil has a pH of 5.8, with the top 30 cm containing an average of 13% organic carbon and 0.89% total nitrogen.

**Net ecosystem exchange**

Net ecosystem CO2 exchange in a mature temperate mixed forest was measured from the meteorological tower at 40 m above ground using the eddy covariance method (Guan et al. 2006). The tower was located at the center of the forest stand. High-frequency (10 Hz), three-dimensional wind speed was measured using a sonic anemometer (CAST3, Campbell Scientific, Logan, UT). CO2 and H2O mixing ratios at 10 Hz...
were measured using an infrared gas analyzer (Li-7500, Li-Cor Inc., USA). Data loggers (CR23X and CR10X, Campbell Scientific) were used to collect and store all data at 10-s intervals, as well as for the calculation of 30-min averages. The Li-7500 was calibrated 1 year later and showed no shift from the original calibrations.

CO₂ fluxes were calculated online using the eddy covariance method. A 2D coordinate rotation was applied according to McMillen (1988) to force the average vertical wind speed (w) to zero and to align the horizontal wind (u*) to mean wind direction. To investigate the influence of various coordinate rotations, we also applied a 3D rotation and a planar-fit rotation (Wilczak et al. 2001). However, differences in the annual carbon flux were small (0.5% for 3D and 2.3% for planar fit).

The CO₂ flux associated with storage of CO₂ below the measurement height of the eddy covariance system was determined using the changing rate of the CO₂ concentration measured by LI-7500 at 40 m. Final CO₂ fluxes were calculated as the sum of the turbulent flux and the storage term.

It is recognized by the flux monitoring community that the eddy covariance technique is likely to underestimate eddy fluxes under calm conditions at night, but there is no consensus as to how to best solve this problem (Lee et al. 1999) Most researchers screen night data based on a friction velocity u* threshold (Goulden et al. 1996, Black et al. 1996, Jarvis et al. 1997, Lindroth et al. 1998). Although we found only a negligible trend of increasing NEE with u*, we calculated an annual NEE using a u* threshold of 0.20 m s⁻¹.

Data was available for 86.9% of the measurement period. Small gaps of up to 2 h due to instrumental failure were filled via interpolation. Larger gaps were filled with empirical regressions for respiration and assimilation derived for 10-day intervals. Only high quality data were accepted to formulate the regression relationships. Non-stationary data (Foken and Wichura 1996), high variance CO₂ > 5 p.p.m. and night data with u* < 0.2 m s⁻¹ were excluded from the regression analysis.

To fill the gaps in the dark periods, an exponential expression was used:

\[
R_e = R_{e0} \exp(a_e(T_s - T_{s0}))
\]

(1)

where \(R_e\) is the ecosystem respiration, \(T_s\) is soil temperature, \(T_{s0}\) is the reference soil temperature and \(R_{e0}\) and \(a_e\) are parameters. \(R_{e0}\) was estimated via night eddy covariance (under the condition \(u^* > 0.2 \text{ m s}^{-1}\)) measurements and yielded the coefficients \(R_{e0} = 0.0356, a_e = 0.1296\) with \(T_s = 0 \text{ oC}\) and a correlation of \(R^2 = 0.465\).

Gaps in daytime data were filled by a Michaelis–Menten equation:

\[
\text{NEE} = \frac{a_2 P_{\text{max}}}{a_3 + P_{\text{max}}}
\]

(2)

where \(a_1\) is respiration in the dark, \(a_2\) is the maximum rate of photosynthesis and \(a_3\) is the Michaelis–Menten constant.

These parameters were derived from eddy covariance measurements for 10-day intervals (results not shown). GPP averaged in 30 min was estimated by the equation

\[
\text{GPP} = R_e - \text{NEE}
\]

(3)

NEE took the eddy C measurements as the values were reasonable and took the filled value (estimated by Eq. (2)) as the measurements were unreasonable. We estimated NEE from the eddy covariance measurements when the values were reasonable and gap-filled using Eq. (2) when they were not reasonable (including the measurements of 2 mg CO₂ m⁻² s⁻¹ < NEE < -2 mg CO₂ m⁻² s⁻¹ and under the condition \(u^* < 0.2 \text{ m s}^{-1}\)). \(R_e\) was estimated by Eq. (1). The daily GPP was integrated from 30-min interval values.

The local meteorological conditions were recorded continuously along with the eddy covariance data. These data were measured at 2 Hz and averaged over a 30-min period using a data logger (CR10X-TD, Campbell Inc., USA). Air temperature and relative humidity were measured using a ventilated psychrometer (HMP45C, Vaisala, Helsinki, Finland) mounted at heights of 2, 5, 8, 22, 26, 32 and 50 m above the ground. Continuous soil temperatures were measured using thermistor sensors at depths of 0, 5, 20, 50 and 100 cm. Soil moisture was measured in one vertical soil profile using time-domain reflectometers (CS616-L, Campbell Inc.). Photosynthetic active radiation (PAR) was measured using a net radiometer (LI-190SB, Li-Cor Inc., Lincoln, NE) at a height of 32 m and a net radiometer (LQS70-10, APOGEE, USA) at a height of 2 m above the ground. Soil heat flux (G) was determined using two soil heat flux plates (HFP01, HukseFlux, The Netherlands) installed in elevated and depressed micro-habitats near the tower at a depth of 2–3 cm.

Leaf area index (LAI) was measured at 5–10 day intervals using an LAI-2000 canopy analyzer (Li-Cor Inc., USA) along a 200-m transect in the southwest direction from the meteorological tower during the growing season. Leaf area index was calculated as the difference between the measurements on the floor and at a tower platform height of 32 m.

**Soil surface CO₂ efflux**

The CO₂ efflux of the soil surface was measured using static chamber and gas chromatography techniques (Wang and Wang 2003). Measurements were taken at approximately 4–8 day intervals from April to November and once every month during winter. Each chamber was made of stainless steel and consisted of two parts: a square box (without a top and bottom, length × width × height = 0.5 m × 0.5 m × 0.1 m) and a removable cover box (without a bottom, length × width × height = 0.5 m × 0.5 m × 0.5 m). In late March 2003, six square boxes were installed in areas that were believed to be representative of the average characteristics of the site. Each soil chamber was wrapped with a layer of white adiabatic covering to minimize temperature changes during the sampling period. A small fan was mounted on the upper topside of the chamber to provide a
small but adequate amount of mixing. All green vegetation present inside the soil collars was clipped to ground level beforehand to ensure that only soil respiration was measured. Soil respiration was sampled between 9:00 and 11:00 am for the daily mean to ensure that only soil respiration was measured.

Not only were periodic measurements of soil temperature and water content taken but also those for respiration. Soil temperature at a depth of 5 cm was simultaneously monitored in each chamber when the gas samples were collected using copper-constantan thermometers. Soil volumetric water content was measured by a portable time-domain reflectometer (TDR 100, Campbell Inc.).

**Stem respiration**

Stem respiration was measured at 3–7-day intervals from May to December for each tree species of *P. koraiensis*, *T. amurensis*, *Q. mongolica* and *F. mandshurica*. The methods have been described by Xu et al. (2000) and Wang et al. (2006). Tree samples ranged from 20 to 86 cm in diameter at breast height (DBH). A soil collar was fastened to a stem on the collar with 100-ml plastic syringes attached to a three-way stopcock at 0, 10, 20 and 30 min. Gas samples were sealed and measured using a gas chromatograph (HP 4890D; Agilent Technologies, Palo Alto, CA) within 12 h.

Continuous air temperature at 5 cm depth was simultaneously monitored by a portable soil temperature probe. Continuous air temperature was measured at a height of 2 m to estimate sapwood temperature. There was a high correlation between sapwood and air temperatures (Wang et al. 2008).

The trees were cored and sapwood thickness and wood mass density were measured to calculate sapwood volume for the four tree species. Stem respiration rates per unit area were converted to rates per unit of sapwood volume based on sapwood biomass and wood mass density. It was assumed that sapwood respiration per unit area during changes in stem temperature.

To raise the scale of chamber measurements of stem respiration to the stand level, respiration fluxes per unit of sapwood volume were calculated based on our field measurements, and the modeled relationship per hectare was used to estimate stem respiration per unit ground area. Stem sapwood biomass for each species was calculated based on sapwood thickness and regional allometric biomass equations (Table 1; Xu et al. 1985). It was assumed that all trees were the same shape.

**Calculation of photosynthesis and respiration**

To estimate mean daytime net CO$_2$ exchanges from the temperate mixed forest ecosystem, we developed nonlinear regression equations to predict net CO$_2$ exchange using continuous meteorological data. Following Hollinger et al. (1994), we fit a rectangular hyperbola to the relationship between PAR and $A_n$:

$$A_n = \frac{A_{\text{max}} \cdot \alpha \cdot \text{PAR}}{A_{\text{max}} + \alpha \cdot \text{PAR}} - R_{\text{day}}$$  (4)

where $A_{\text{max}}$ is the maximum photosynthetic rate, $\alpha$ is the initial slope of the light response curve, i.e. the apparent quantum yield, $R_{\text{day}}$ is the respiration during daytime and $A_n$ is the daytime net CO$_2$ exchange. For this analysis, it was assumed that carbon assimilation is driven only by light, and other limitations (temperature, vapor pressure deficit, drought stress etc.) were not considered.

The nighttime net CO$_2$ exchange was assumed to be determined by respiration. Half-hourly nighttime net CO$_2$ exchange rates were regressed on air or soil temperature using an exponential function via Eq. (5). Temperatures used in Eq. (5) were the air temperature in the canopy at a height of 2 m and soil temperature at 5 cm depth. SPSS 13.0 (SPSS Inc., Chicago, IL) was used to estimate parameters in Eqs. (4–5).

Leaf photosynthesis was measured from May to September at intervals of 3–4 weeks. In total, 150 samples at different positions in the forest canopy (low, mid and high) were taken. They were approximately evenly distributed across the four dominant tree species and were collected before dawn and measured during the period of full leaf expansion. Leaf photosynthesis rates were measured according to the protocols described in Bolstad et al. (2004). Branches were detached, immediately placed in a plastic bag with a moistened paper towel and transported in the dark to the laboratory. Branches
were cut again and base parts were placed under water in a dark room to be measured within 2 h. Measurement of the photosynthetic light response was conducted in the morning from 7:00 to 9:00 a.m. with an LI-6400 portable photosynthesis system (Li-Cor Inc.). The light level in the leaf chamber was incrementally reduced from a maximum of 1800 µmol m⁻² s⁻¹ while maintaining temperature and relative humidity at ambient conditions. Each tree species was measured three to four times.

After measurement of photosynthesis, foliage was sampled for dry weight and leaf area. Leaves were weighed after being dried at 85 °C for at least 2 days. Foliage respiration was measured monthly from May to September 2003 with an LI-6400 portable photosynthesis system at night (9:00–11:00 p.m.) on all dates. Temperatures were manipulated to +5 and −5 °C of the ambient temperature to determine the relationship between respiration and temperature. Respiration rates were measured at 5 and 30 °C with a controlled temperature LI-6400 gas exchange system in the growth season.

We compared measurements made on foliage in situs for P. koreana, Q. mongolica, T. amurensis and F. mandschurica with measurements made on the same foliage after the branches (at least 6 cm diameter of branch with foliage) had been excised and rehydrated (‘cut-hydro’). The results showed, that for a short time (90 min), photosynthesis parameters were not affected by detachment of the branch for all trees except F. mandschurica. Since for this species, at 20 min after detachment, the photosynthetic rate was reduced by 8.45%, measurements were taken immediately after branch detachment.

The leaf photosynthesis of herbaceous vegetation was measured biweekly using a closed chamber-based method during the growing season. Gas samples were collected and CO₂ concentration was analyzed as described above for soil respiration measurements. The light level inside the chamber was controlled in order to measure photosynthetic light response. Nocturnal leaf respiration was measured using the closed chamber at different temperatures. After measurement of photosynthesis, all plants inside the big chamber were cut for leaf area and dry weight analysis.

Equations (4–5) were used in scaling up from leaf photosynthesis to canopy level. We evaluated this integral under the following pair of assumptions: PAR within the canopy follows Beer’s law; light saturated photosynthetic rate \( A_{\text{max}} \) at any point in the canopy is proportional to the ratio of local PAR to full-sun PAR. Canopy temperature was approximated by air temperature in the canopy at a height of 2 m. The LAI of each tree species was estimated from the percentage of the total tree canopy LAI and the biomass of different species (Table 2). The LAI of each species was calculated by multiplying the leaf area percentage by total leaf area in different tree species. To find the LAI of needles, 50 fascicles of needles of various ages were fixed onto transparent adhesive tape, and the area of the needles was measured. Then, samples were dried at 85 °C for 2 days to obtain the dry biomass for the specific leaf area. Values for each specific leaf area were 1.68 m² g⁻¹ (new needle of Korean pine), 1.69 m² g⁻¹ (old needle of P. koreana), 1.97 m² g⁻¹ (T. amurensis), 1.22 m² g⁻¹ (F. mandschurica) and 1.72 m² g⁻¹ (Q. mongolica), respectively. We represented leaf growth dynamics by applying a time-dependent LAI (Figure 1A).

An exponential temperature response function was used to express soil, stem and foliage respiration:

\[
R = \beta_0 \cdot e^{\beta_1 \cdot T}
\]

where \( R \) is the respiration rate; \( T \) is the temperature of soil, stem and foliage; and \( \beta_0 \) and \( \beta_1 \) are fitted parameters. The respiration parameters were used for predicting CO₂ efflux every 30 min over the season based on continuous temperature measurements. The respiration parameter \( Q_{10} \) can be derived from \( Q_{10} = e^{10 \cdot \beta_1} \).

Statistical analysis

Data from the chamber-based method are presented as means and standard errors of the mean (SEM) for the six replicate chambers at each of the sampling times. The relationships between CO₂ flux and photosynthetic parameter variables were analyzed by regression analysis using SPSS 13.0 (SPSS Inc.). The Student’s \( t \) test was used to analyze the difference between the eddy covariance technique and chamber-based estimates. The significance was determined at \( \alpha = 0.05 \).

Results

Soil surface CO₂ efflux

Measurements of soil respiration indicated that seasonal variation ranged from 0.49 to 4.12 µmol m⁻² s⁻¹ in the mature temperate mixed forest (Figure 1B). The soil surface CO₂ efflux rates peaked in early August (Day 217) and late August (Day 234) and then declined thereafter. When the measurements were taken in 2003, the peak in soil respiration was consistent with soil temperature. Mean daily soil temperature at a depth of 10 cm peaked at 18.5 °C in August. Soil moisture did not appear to constrain soil respiration since precipitation was evenly distributed throughout the growing season. Mean daily soil volumetric moisture at 10 cm varied between 0.20 and 0.47 m³ m⁻³. It peaked in early May when snow melted and reached a minimum in late June and October.
\[ y = 2 \times 10^{-6}x^4 - 2 \times 10^{-5}x^3 + 0.0051x^2 - 0.4896x + 14.996 \]

\[ R^2 = 0.9685 \]
CO₂ FLUX OF A TEMPERATE MIXED FOREST

Table 3. Parameters in the temperature response function Eq. (5) for soil respiration (Rₘ, µmol m⁻² s⁻¹), stem respiration (Rₖ, µmol m⁻² s⁻¹) and foliage respiration (Rₐ, µmol m⁻² s⁻¹) from the four species.

<table>
<thead>
<tr>
<th>Model</th>
<th>R²</th>
<th>n</th>
<th>Q₁₀</th>
</tr>
</thead>
<tbody>
<tr>
<td>Korean pine</td>
<td>0.414</td>
<td>76</td>
<td>2.09</td>
</tr>
<tr>
<td>Tilia tuan</td>
<td>0.523</td>
<td>67</td>
<td>1.86</td>
</tr>
<tr>
<td>Mongolian oak</td>
<td>0.665</td>
<td>91</td>
<td>2.12</td>
</tr>
<tr>
<td>Manchurian ash</td>
<td>0.408</td>
<td>59</td>
<td>2.41</td>
</tr>
<tr>
<td>Soil</td>
<td>0.640</td>
<td>58</td>
<td>2.20</td>
</tr>
</tbody>
</table>

Here, R² is the coefficient of determination.

Soil respiration relative to average soil temperature showed a strong exponential relationship. The parameters in Eq. (5) for soil respiration are summarized in Table 3. Q₁₀ was derived as 2.2. The fitted lines indicate the temperature sensitivity in the mature temperate mixed forest stand (R² = 0.87). Cumulative soil respiration summed to 593 g C m⁻² year⁻¹ in 2003.

Stem respiration

Stem respiration as a function of sapwood temperature for the four tree species during 2003 is shown in Table 3. Sapwood temperature explains 83–95% of the variation in stem respiration. Growing under similar conditions, the four species exhibited different characteristics of respiration on a unit area basis. The Q₁₀ values (indicative of temperature sensitivity) also varied from 1.86 to 2.41 among the trees (Table 3). Stem respiration per unit ground area was calculated. The trends in respiration flux of stem and branch and that of temperature were consistent given that they were driven by air temperature. There was a strong seasonal variation in stem and branch respiration, ranging from 0.14 to 2.18 µmol m⁻² s⁻¹, peaking in mid-June (Day 173) to late August (Day 233). The branch respiration of shrubs showed a similar seasonal pattern, ranging from 0.07 to 0.62 µmol m⁻² s⁻¹. The minimum occurred in winter and the maximum in June and July. Short-term (1–2-week time scale) variation was also detected (Figure 2).

Foliage CO₂ exchange fluxes

Foliage CO₂ exchange was regressed against PAR for the period of the growing season. There was a good fit to Eq. (4) (R² > 0.73; Table 4). The nocturnal leaf respiration was driven primarily by air temperature. Additionally, LAI and foliage photosynthetic characteristics varied during the growing season. Foliage CO₂ exchange rates were distinctly bell-shaped (Figure 3). Leaf CO₂ exchange flux rate per unit ground area in trees was 2.30 µmol m⁻² s⁻¹ in late April; it increased to 14.6 µmol m⁻² s⁻¹ in early July, remained steady until early August and then quickly decreased to 2.10 µmol m⁻² s⁻¹ in late September. Leaf CO₂ exchange flux rates in the shrub and herbaceous understory were different from those in tree foliage. There were two peaks in CO₂ exchange flux in early May and in the middle of July, which were 0.62 and 0.51 µmol m⁻² s⁻¹ in shrubs and 1.94 and 2.64 µmol m⁻² s⁻¹ in herbaceous plants, respectively. Tree foliage is the major path for the assimilation of CO₂ from the atmosphere. The percentage of carbon assimilation by tree foliage was 90%, while shrubs accounted for 3% and herbaceous plants 7%.

Components of ecosystem CO₂ flux

Daily mean ecosystem respiration (ER) varied between 0.85 and 8.00 µmol m⁻² s⁻¹ in our study (Figure 4). Ecosystem respiration averaged 1.42 µmol m⁻² s⁻¹ in winter. It reached a minimum in January–March and rapidly increased after mid-April. It peaked in mid-July and maintained this peak for about 3 weeks. Then, ecosystem respiration dropped to low winter values in mid-November. The component respiration showed similar seasonal variations to the ecosystem respiration. Cumulative ecosystem respiration and its components are summarized in Table 5. Total ecosystem respiration was 1240 g C m⁻² year⁻¹ in 2003. Cumulative annual soil respiration, stem respiration and leaf respiration were 593, 385 and 264 g C m⁻² year⁻¹, respectively, accounting for 47.8, 31 and 21% of total ecosystem respiration. Above-ground autotrophic respiration (stem + foliage respiration) accounted for 52% of total respiration, with leaf respiration slightly higher than stem respiration in the mature temperate mixed forest stand. In summary, according to the results of the chamber measurements, the gross CO₂ assimilation of the ecosystem estimated from the sum of daily values was 1490 g C m⁻² year⁻¹ and the net ecosystem CO₂ flux was 146 g C m⁻² year⁻¹.

Comparison of chamber measurements with eddy covariance for NEE, ER and GPP

Figure 6 shows the seasonal patterns of daily mean NEE, ER and GPP using eddy covariance measurements from April to September. Seasonal changes in NEE were characterized by small positive fluxes in winter and negative fluxes in the growing season. NEEeddy began to rise to positive values in early September and reached large positive values in late September and October due to relatively high temperatures and defoliation of most of the trees in the forest. Values for GPPeddy and NEEeddy were below −12.1 and −6.50 g C m⁻² day⁻¹, respectively. The peaks in GPPeddy and NEEeddy fluxes occurred in the middle of July. The mean daily rates of GPPeddy and NEEeddy were 11.9 and 1.95 g C m⁻² day⁻¹ during the growing season (May–September), respectively. Accumulation results from May to September showed that net ecosystem exchanges (NEEeddy) were about 74% and 26% of actual GPPeddy during the growing season. The mean

Figure 1. Tree leaf area index development in 2003 (A). Measurements of soil respiration in the temperate mixed forest stand with daily mean soil temperature (B). Each datapoint of soil respiration is spatial average with error bars indicating standard errors (measured with chamber-based method). Daily average air temperature was measured at the height of 2 m, daily average soil temperature at 5 cm depth (C). Daily average soil moisture (volume of water/volume of 10–20 cm mean depth) was measured using time-domain reflectometer (D).

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daily rate of GPPchamber and NEEchamber were 14.5 and 2.60 g C m$^{-2}$ day$^{-1}$ during the growing season (May–September).

On an annual time scale, NEEchamber (146 g C m$^{-2}$ year$^{-1}$) was 22.5% lower than NEEeddy (188 g C m$^{-2}$ year$^{-1}$). Eddy covariance flux data generally followed similar seasonal variations to those produced by the summed chamber-based method, with lower CO2 exchange flux in the winter and greater flux in the summer. However, the increase in flux

![Figure 2](http://treephys.oxfordjournals.org/)

**Figure 2.** Seasonal trends in stem and branch respiration per unit ground area (measured with chamber-based method).

Table 4. Seasonal variations of photosynthetic parameters for foliage.

<table>
<thead>
<tr>
<th>Month</th>
<th>Parameters from light response curves</th>
<th>$a$</th>
<th>$b$</th>
<th>$R_d$</th>
<th>$A_{max}$</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Korean pine</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(new needle)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>May</td>
<td></td>
<td>0.014 ± 0.010</td>
<td>0.029 ± 0.019</td>
<td>0.698 ± 0.114$^b$</td>
<td>2.220 ± 0.197$^c$</td>
<td>0.960 ± 0.008</td>
</tr>
<tr>
<td>June</td>
<td></td>
<td>0.006 ± 0.009</td>
<td>0.018 ± 0.022</td>
<td>0.710 ± 0.690$^b$</td>
<td>6.934 ± 5.133$^c$</td>
<td>0.967 ± 0.015</td>
</tr>
<tr>
<td>July</td>
<td></td>
<td>0.029 ± 0.003</td>
<td>0.118 ± 0.013</td>
<td>0.993 ± 0.206$^b$</td>
<td>4.055 ± 0.827$^b$</td>
<td>0.984 ± 0.011</td>
</tr>
<tr>
<td>August</td>
<td></td>
<td>0.016 ± 0.015</td>
<td>0.089 ± 0.051</td>
<td>0.754 ± 0.502$^b$</td>
<td>6.372 ± 1.855$^c$</td>
<td>0.941 ± 0.028</td>
</tr>
<tr>
<td>September</td>
<td></td>
<td>0.017 ± 0.006</td>
<td>0.121 ± 0.004</td>
<td>1.231 ± 0.352$^a$</td>
<td>6.982 ± 1.532$^a$</td>
<td>0.932 ± 0.081</td>
</tr>
<tr>
<td>Korean pine</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(old needle)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>May</td>
<td></td>
<td>0.004 ± 0.003</td>
<td>0.012 ± 0.007</td>
<td>0.750 ± 0.101$^a$</td>
<td>3.287 ± 0.733$^c$</td>
<td>0.936 ± 0.033</td>
</tr>
<tr>
<td>June</td>
<td></td>
<td>0.009 ± 0.004</td>
<td>0.027 ± 0.014</td>
<td>0.647 ± 0.269$^b$</td>
<td>3.103 ± 0.180$^c$</td>
<td>0.972 ± 0.031</td>
</tr>
<tr>
<td>July</td>
<td></td>
<td>0.009 ± 0.008</td>
<td>0.027 ± 0.018</td>
<td>0.358 ± 0.195$^c$</td>
<td>3.311 ± 0.974$^a$</td>
<td>0.881 ± 0.139</td>
</tr>
<tr>
<td>August</td>
<td></td>
<td>0.016 ± 0.002</td>
<td>0.033 ± 0.002</td>
<td>0.520 ± 0.009$^b$</td>
<td>2.064 ± 0.099$^b$</td>
<td>0.971 ± 0.003</td>
</tr>
<tr>
<td>September</td>
<td></td>
<td>0.016 ± 0.003</td>
<td>0.029 ± 0.002</td>
<td>0.740 ± 0.051$^a$</td>
<td>1.83 ± 0.124$^c$</td>
<td>0.812 ± 0.044</td>
</tr>
<tr>
<td>Tilia tuan</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>May</td>
<td></td>
<td>0.018 ± 0.002</td>
<td>0.066 ± 0.015</td>
<td>1.652 ± 0.484$^a$</td>
<td>3.734 ± 0.465$^b$</td>
<td>0.964 ± 0.021</td>
</tr>
<tr>
<td>June</td>
<td></td>
<td>0.004 ± 0.002</td>
<td>0.020 ± 0.012</td>
<td>1.105 ± 0.170$^b$</td>
<td>5.360 ± 1.276$^c$</td>
<td>0.957 ± 0.030</td>
</tr>
<tr>
<td>July</td>
<td></td>
<td>0.021 ± 0.007</td>
<td>0.089 ± 0.008</td>
<td>0.692 ± 0.059$^c$</td>
<td>4.461 ± 1.310$^b$</td>
<td>0.979 ± 0.013</td>
</tr>
<tr>
<td>August</td>
<td></td>
<td>0.019 ± 0.004</td>
<td>0.087 ± 0.012</td>
<td>1.161 ± 0.169$^b$</td>
<td>4.587 ± 0.664$^b$</td>
<td>0.955 ± 0.036</td>
</tr>
<tr>
<td>September</td>
<td></td>
<td>0.008 ± 0.002</td>
<td>0.030 ± 0.014</td>
<td>1.180 ± 0.153$^b$</td>
<td>3.674 ± 0.456$^b$</td>
<td>0.894 ± 0.044</td>
</tr>
<tr>
<td>Mongolian oak</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>May</td>
<td></td>
<td>0.012 ± 0.002</td>
<td>0.246 ± 0.337</td>
<td>1.530 ± 0.208$^a$</td>
<td>19.503 ± 6.389$^a$</td>
<td>0.988 ± 0.007</td>
</tr>
<tr>
<td>June</td>
<td></td>
<td>0.007 ± 0.006</td>
<td>0.023 ± 0.018</td>
<td>0.639 ± 0.513$^b$</td>
<td>11.387 ± 4.538$^a$</td>
<td>0.960 ± 0.048</td>
</tr>
<tr>
<td>July</td>
<td></td>
<td>0.007 ± 0.006</td>
<td>0.047 ± 0.039</td>
<td>0.744 ± 0.381$^b$</td>
<td>7.744 ± 3.174$^c$</td>
<td>0.971 ± 0.029</td>
</tr>
<tr>
<td>August</td>
<td></td>
<td>0.018 ± 0.004</td>
<td>0.087 ± 0.025</td>
<td>0.799 ± 0.193$^b$</td>
<td>4.765 ± 0.205$^b$</td>
<td>0.977 ± 0.001</td>
</tr>
<tr>
<td>September</td>
<td></td>
<td>0.007 ± 0.005</td>
<td>0.027 ± 0.015</td>
<td>1.234 ± 0.211$^b$</td>
<td>4.054 ± 0.213$^b$</td>
<td>0.903 ± 0.004</td>
</tr>
<tr>
<td>Manchurian ash</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>May</td>
<td></td>
<td>0.012 ± 0.005</td>
<td>0.103 ± 0.021</td>
<td>1.175 ± 0.119$^a$</td>
<td>8.817 ± 2.020$^b$</td>
<td>0.983 ± 0.012</td>
</tr>
<tr>
<td>June</td>
<td></td>
<td>0.017 ± 0.007</td>
<td>0.103 ± 0.016</td>
<td>1.138 ± 0.238$^a$</td>
<td>7.404 ± 3.380$^b$</td>
<td>0.855 ± 0.178</td>
</tr>
<tr>
<td>July</td>
<td></td>
<td>0.005 ± 0.002</td>
<td>0.028 ± 0.014</td>
<td>0.608 ± 0.056$^b$</td>
<td>6.043 ± 1.263$^b$</td>
<td>0.978 ± 0.126</td>
</tr>
<tr>
<td>August</td>
<td></td>
<td>0.032 ± 0.002</td>
<td>0.511 ± 0.545</td>
<td>0.376 ± 0.379$^b$</td>
<td>16.577 ± 8.102$^a$</td>
<td>0.730 ± 0.310</td>
</tr>
<tr>
<td>September</td>
<td></td>
<td>0.067 ± 0.002</td>
<td>0.342 ± 0.165</td>
<td>1.231 ± 0.242$^a$</td>
<td>5.0430 ± 1.454$^b$</td>
<td>0.863 ± 0.124</td>
</tr>
</tbody>
</table>

Data of $R_d$ and $A_{max}$ were presented as mean ± SEM. Differences between averages followed by a different letter or letters were statistically significant at $P < 0.05$. 

**TABLE 4**
as the season developed was much greater for the chamber estimate than the eddy covariance estimate. There was a significant correlation between the chamber and eddy covariance flux estimates (P < 0.001). According to the average half-hourly data, in the growing season, chamber estimate fluxes had values 22% higher than estimates obtained from the eddy covariance method, while in winter chamber estimates were 57% lower.

Discussion

Effect of temperature and soil water content on respiration

Temperature is the primary control on respiration in the northern forests (Tang et al. 2006), and an exponential response function might explain most of the observed temporal variation (Table 3). Soil CO2 efflux measurements using the chamber-based method indicate that diurnal fluctuations were very small in our experiment (data not shown). Our results were consistent with other studies (Kursar 1989, Janssens et al. 1998) and were probably due to the small changes in soil temperature under the forest canopies. On this annual time scale, the model fit the chamber data very well and explained 80% of the temporal variation in soil CO2 efflux (Figure 1B). Temperature alone explained over 87% of the temporal variation (Table 3). Annual variation in soil CO2 efflux was large and closely linked to the temporal pattern of soil temperature.

It is generally believed that uncertainty in the results from chamber-based methods results primarily from microenviron-
mental changes inside the chamber, including air temperature, humidity, pressure and the mixture of air components (Lavigne et al. 1997). In our study, the temperature difference between the inside and outside of the chamber was very small. The average difference was 0.1 °C, with a maximum of 1.1 and a minimum of −1.2 °C. Thus, the data from the chamber-based method showed that there was little impact from the microenvironment. During the course of soil CO2 efflux measurements, the fluctuations in chamber headspace CO2 concentrations (maximum headspace CO2 concentrations 1050 µmol mol$^{-1}$) were about two times larger than those of the chamber-based space concentrations in the warmer season. The inside CO2 concentration and pressure gradients could be altered by means of closing the chambers, which could probably be explained by the biases in soil respiration towards underestimation in the growth season.

The fixed $Q_{10}$ values over the season provided useful estimates for component and summed total ecosystem CO2 flux at our site. Soil temperature did not vary with soil moisture in the Changbai temperate mixed forest, and high moisture occurred simultaneously with high temperature in the growing season (Figure 1C and D). Numerous studies indicate that soil moisture is an important factor limiting soil respiration, particularly in arid or semi-arid ecosystems (Xu and Qi 2001). However, soil respiration did not vary with soil moisture in our study (data not shown). Therefore, we used an exponential $T$ model to estimate CO2 flux (Xu and Qi 2001, Tang et al. 2006, Li et al. 2008). Average soil volumetric moisture of 0.20 m$^3$ m$^{-3}$ at a depth of 10 cm appears to be sufficient to maintain microbial activity and plant physiology in the forests in northeastern China (Guan et al. 2006). An adequate soil moisture level may explain the insignificant influence of soil moisture on soil respiration in our results. Therefore, we suggest that soil temperature is the primary determinant of soil respiration.

The potential controlling factors for stem respiration include temperature and other factors (e.g. soil water, tree species and old age; Xu et al. 2000). We found different responses of stem respiration in the four tree species and at different ages (Wang et al. 2008). Therefore, we constructed stem respiration exponential $T$ models for the different tree species (Table 3). Stem respiration functions are sensitive to temperature (Table 3). However, we did not distinguish the stem location or tree age in our study. As a result, our results averaged measurements from trees of different ages to analyze the correlation between stem respiration and temperature over the season. This method may have introduced some errors into our total respiration estimates. However, such errors were likely small because whole stem respiration only constituted about 10% of the total ecosystem respiration. The study site is typically snow covered for ~5–6 months each year. Soil temperature measurements showed that soil temperatures at a depth of 10 cm were never below 0 °C, even in winter, due to insulation from the snow pack. Thus, the small amount of soil respiration under the snow could be from microbial decomposition in unfrozen soils and from root maintenance respiration occurring in soil. CO2 efflux under snow could diffuse to the snow surface (McDowell et al. 2000, Panikov and Dedysh 2000). Stems and needles also release CO2 in the winter as respiration maintenance (Ryan et al. 2000). The soil temperature was never below freezing, but we did not measure the snow temperature. We therefore assumed that the small amount of soil respiration under the snow was due to snowpack insulation and not due to soil temperatures being below freezing. We also assumed that the respiration rates measured in the chamber were representative of the respiration rates occurring under the snow. Therefore, the soil respiration rates measured in the chamber were not underestimated when averaged over the season.

![Figure 5. Eddy covariance fluxes versus chamber estimates of ecosystem C exchange flux for daily average per unit ground area in the temperate mixed forest in 2003. A net uptake of carbon from the atmosphere is positive.](http://treephys.oxfordjournals.org/)

**Table 5. Estimated annual respiration fluxes for whole ecosystems and their components in 2003.**

<table>
<thead>
<tr>
<th>Component</th>
<th>Respiration CO2 fluxes (g C m$^{-2}$ year$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soil respiration</td>
<td>593</td>
</tr>
<tr>
<td>Stem respiration</td>
<td>385</td>
</tr>
<tr>
<td>Leaf respiration</td>
<td>264</td>
</tr>
<tr>
<td>ER$_{chamber}$</td>
<td>1240</td>
</tr>
<tr>
<td>NEE$_{chamber}$</td>
<td>146</td>
</tr>
<tr>
<td>GPP$_{chamber}$</td>
<td>1490</td>
</tr>
<tr>
<td>ER$_{eddy}$</td>
<td>1030</td>
</tr>
<tr>
<td>NEE$_{eddy}$</td>
<td>188</td>
</tr>
<tr>
<td>GPP$_{eddy}$</td>
<td>1220</td>
</tr>
</tbody>
</table>

**Figure 5.** Eddy covariance fluxes versus chamber estimates of ecosystem C exchange flux for daily average per unit ground area in the temperate mixed forest in 2003. A net uptake of carbon from the atmosphere is positive.
1990, Ryan et al. 1995). We used a fixed $Q_{10}$ function to estimate soil, stem and needle respiration for the whole year, which tends to overestimate respiration in the winter.

Components of respiration in the ecosystem

Our soil surface CO$_2$ efflux results were similar to data from Thieron and Laudelout (1996), who found that mean daily CO$_2$ efflux varied from 3.2 to 10.7 µmol m$^{-2}$ s$^{-1}$ in a deciduous forest in France. Our results were higher than the previous results of 0.5–3.7 µmol m$^{-2}$ s$^{-1}$ found for a ponderosa pine forest in Oregon, North America (Law et al. 1999a) as well as results of 0.4–4.0 µmol m$^{-2}$ s$^{-1}$ for a beech forest in France (Epron et al. 1999) and 2.5–5.4 µmol m$^{-2}$ s$^{-1}$ in summer for a young ponderosa pine forest in Nevada (Xu et al. 2001). Figure 1B indicates that the forest floor was always a net source of CO$_2$. When the forest floor began to thaw ($T_c > 0 \, ^\circ C$), soil respiration showed a remarkable increase in the magnitude of CO$_2$ emission. The increase of mean daily soil temperature (from −0.2 to 2.0 °C) resulted in an increase in CO$_2$ emissions in April (from 0.8 to 1.3 µmol m$^{-2}$ s$^{-1}$). The soil respiration typically ranged from 1.3 to 4.1 µmol m$^{-2}$ s$^{-1}$ in the growing season. Such an increase in air temperature (from 5.4 to 20.7 °C) during this period led to a burst in soil biome CO$_2$ release (Wu et al. 2006). This is primarily because our study took place in a 250-year-old forest with a great amount of living root biomass present (Janssens et al. 2001). Autotrophic respiration depends strongly on the amount of living root biomass, whereas heterotrophic respiration depends on the quantity of dead roots and organic matter in the soil (Rustad et al. 2000).

Foliage respiration was second in magnitude among the respiration fractions (Figure 4). This result is consistent with those of others (Guan et al. 2006). Our results show that the highest rates of foliage respiration were in June and July. This is when new foliage has completely expanded and developed, and the respiration rates of old needles increase for transporta-

Figure 6. Eddy and chamber-based fluxes of NEE, ER and GPP during growing season in 2003. This figure appears in color in the online version of Tree Physiology.
small source of ER (Figure 4). Overall, stem, foliage and soil respiration accounted for 21, 31 and 48% of the total ER, respectively. Soil surface CO₂ efflux has been found to be 30–90% of total ecosystem respiration in temperate forests (Bowden et al. 1993, Epron et al. 1999, Valentini et al. 2000), and our result was in the middle of that range. This was because there was a large amount of coarse woody debris (10 t ha⁻¹) in this forest (Dai et al. 2002). Our result of soil surface CO₂ efflux did not include coarse woody debris respiration. In young and old coniferous boreal forests, soil has been found to contribute 48–71% to whole ecosystem respiration, with foliage and stems contributing 25–43% and 5–15%, respectively (Lavigne et al. 1997). The corresponding values in a young (~8 years old) ponderosa pine plantation in the Sierra Nevada Mountains were 64.8, 9.5 and 25.4%, respectively (Xu et al. 2001). They were 48, 21 and 31% in our study. The higher percentage of stem respiration was primarily due to the large stem volume in the 250-year-old forest in our study. The lower percentage of leaf respiration at the Oregon and Nevada sites was due to low LAI (1.5 and 4.5 at two sites). The ratio varied with the seasons. Soil was the main source of CO₂ release in our study, especially in the growing season. Contributions of foliage and stem respiration to whole ecosystem respiration became dominant in winter (Figure 4).

The seasonal pattern of net ecosystem exchange in Figure 5 is similar to that of the temperate forests in southern Ontario, Canada (Arain and Natalia 2005). The maximum uptake rate was 7.0 g C m⁻² day⁻¹ at the end of June and July in a pine forest in Canada. Net ecosystem exchange at our study site was slightly smaller than that of young temperate forests based on eddy covariance measurements (Zha et al. 2007). Net ecosystem exchange of CO₂ fluxes ranged from −2.60 to 9.90 g C m⁻² day⁻¹ in our study site. A reasonable positive CO₂ uptake in the growing season and a small carbon source in the non-growing season were observed in the mature temperate mixed forest. The ER and NEE were 90.2 and 9.8% of gross carbon assimilation, respectively. Net ecosystem exchange of CO₂ in the ecosystem was only a small part of assimilation potential. It induced an annual net carbon gain of 146 g C m⁻² year⁻¹ in the mature temperate mixed forest. Gross primary production was 1490 g C m⁻² year⁻¹. Thus, the mature mixed forests in the Changbai Mountains are a carbon sink during the whole year.

Comparison between chamber and eddy covariance measurements

Figure 5 shows CO₂ flux of chamber estimates versus the eddy covariance method for daily average per unit ground area. Based on chamber-based measurements, annual NEE was estimated at 146 g C m⁻² year⁻¹, which was 22.5% less than eddy covariance measurements. In winter, daily estimates of NEE flux data from the eddy covariance system were about 50% lower than those from the chamber measurements, while in summer chamber measurements were 24.6% higher than eddy covariance measurements (Figure 5). This is consistent with other studies (Lavigne et al. 1997, Bolstad et al. 2004). Several possible mechanisms could be responsible for this result, including weak turbulence and drainage in the forest leading to underestimation of respiration by eddy covariance measurements in winter.

Daily estimates of NEE, ER and GPP fluxes generated by these two methods are shown in Figure 6. The two methods were in better agreement after adjusting CO₂ flux in the mature mixed forest using the equation NEEₚₑddy = 0.63 × NEE_chamber + 0.26, R² = 0.71 (Figure 7A). The estimates of ER and GPP using the two methods correspond well: ERₚₑddy = 1.23 × ER_chamber − 1.69, R² = 0.93 (Figure 7B); GPPₚₑddy = 0.79 × GPP_chamber + 0.59, R² = 0.80 (Figure 7C). The comparison between chamber and eddy covariance ecosystem respiration measurements showed a greater degree of agreement than did several other studies (Law et al. 1999b, Lavigne et al. 1997) and was consistent with Tang et al. (2008). The negative intercept in this equation indicates that ER_chamber estimates shift to a CO₂ source at 1.69 μmol m⁻² s⁻¹, as compared with ERₑddy. Our results show that ER_chamber was larger than ERₑddy, because the eddy covariance technique obtained samples from larger forest patches in multiple directions and the chamber-based method measured exactly the same plot throughout the measuring day (Lavigne et al. 1997, Law et al. 1999b, Zha et al. 2004). It should be noted that the presence of vegetation under the tree canopy and the low wind speed, especially at night, significantly affected vertical exchange of air and drainage (Lavigne et al. 1997, Law et al. 1999b, Zha et al. 2004). Lei and Koike (1998) have suggested that understory plants display the greatest carbon gain during early spring and late autumn under a leafless forest canopy compared with that of late spring and early summer. Compared with evergreen pine forests, the mature temperate mixed forest in this study site has an abundant number of respirators in its understory plants, including the shrub layer and herbaceous vegetation. The LAI of understory plants was about 1.5. Therefore, the presence of photosynthesizing understory vegetation between the soil surface and the lower forest canopy is very important for the ecosystem. There are only a small number of understory plants in evergreen pine forests (Law et al. 1999b, 2000). ER fluxes were a main source of uncertainty in the mature temperate mixed forest, and these results are consistent with Zamolodchikov et al. (2003). The scaling up of chamber data in the study area may cause errors and is undoubtedly a complicated exercise.

A variation in the GPP resulted from PAR and differences in the development state of the assimilation organs of vascular plants. The latter significantly affected GPP variations and was affected by temperature and changes in demand for water vapor owing to the local weather conditions during the measurement period. Despite this, the temperature and water vapor pressure deficits were not considered when estimating GPP using the chamber method. It is difficult to quantify the uncertainty due to methods of photosynthesis. GPP in our study forest is believed to be driven mostly by local hydrology (soil moisture and water vapor pressure deficit).
However, GPP\textsubscript{chamber} estimates may have been underestimated because of limited carbon uptake due to stomata closure after branches were chopped down.

The errors from this adjusted chamber flux resulted from variations in component fluxes, soil and stem respiration, LAI measurement and leaf photosynthesis measurements.

The comparison of the two methods in this study demonstrated that uncertainty ratios were about 22 and 21\% for ER and GPP, respectively. The relative standard error for large chamber respiration measurements was similar to that of the LI-6400 measurements (Stephen 2003) and it was about 15\% for the larger soil chamber in our study. The uncertainty in NEE was considered to be 20–40\%. The results of ecosystem CO\textsubscript{2} flux using the two methods indicated that a 0.63 adjustment factor was required to bring all the data into reasonable agreement. The uncertainty of the adjustment factor was about 40\% and the uncertainty of the eddy covariance system itself was around 10–20\% (Verma 1990). Therefore, the results of ecosystem CO\textsubscript{2} exchange from the chamber-based method are acceptable at the scale of a year, considering that the uncertainties associated with a below-canopy eddy covariance method are always large (Lavigne et al. 1997, Law et al. 1999b, Zha et al. 2004).

Eddy covariance is a micro-meteorological technique that allows non-invasive measurement of CO\textsubscript{2} exchange between the atmosphere and terrestrial ecosystems (Baldocchi et al. 1988). Recent technical advances have made long-term eddy covariance measurements practical, which could overcome the errors in summing component measurements using a chamber-based method. However, there is always lack of agreement between scaled-up chamber measurements and estimates of NEE (Lavigne et al. 1997, Law et al. 1999b). The aim of our study was to provide a cross validation of CO\textsubscript{2} exchange measured via chambers and eddy covariance. Even though the chamber and eddy covariance methods agreed well in the mature temperate mixed forest, chamber measurements of NEE, ER and GPP were larger than the eddy covariance measurements. Due to the discrepancy between the measurement theories of the two methods, complex error sources are not well understood and are subject to further investigation. The complex footprint covered by the eddy covariance measurements in the mature temperate mixed forest and the spatial heterogeneity for the scaling up of chamber measurements may be the major reasons.

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References


