Available online at www.sciencedirect.com

ScienceDirect

Agricultural and Forest Meteorology 137 (2006) 138–149

AGRICULTURAL AND FOREST METEOROLOGY

www.elsevier.com/locate/agrformet

CO_2 fluxes over an old, temperate mixed forest in northeastern China

De-Xin Guan [a,*], Jia-Bing Wu [a], Xiao-Song Zhao [a], Shi-Jie Han [a],
Gui-Rui Yu [b], Xiao-Min Sun [b], Chang-Jie Jin [a]

[a] Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, China
[b] Institute of Geographic Science and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China

Received 17 February 2004; received in revised form 24 May 2005; accepted 14 February 2006

Abstract

Eddy-covariance measurements of carbon dioxide exchange were made above a temperate mixed forest for 16 months in northeastern China. The stand is a natural grown, unmanaged mixture of deciduous broad-leaved and coniferous forest and the trees cover a wide range of age classes with a maximum about 450 years. The objective of this study was to test the traditional hypothesis that forests at a late stage of development are insignificant carbon sinks. CO_2 exchanges of the ecosystem were studied under conditions of adequate soil water supply. The main results are that:

(1) Ecosystem respiration and its components, including soil, stem and leaf respiration, all fit exponential correlations with soil or air temperature, but the ratios of these components to total ecosystem respiration varied during the year. When temperature rose, the ratio of soil respiration to total respiration was relatively stable, while that of leaf and stem respiration increased and decreased, respectively. Soil respiration was the biggest component (48% of the whole ecosystem respiration on average, without including the respiration of fallen trees and coarse woody debris). Leaf respiration was the second largest (22–40%) and stem respiration was the least (13–29%).

(2) The ecosystem has very large assimilation potential as environmental factors are adequate in growing season, but the actual gross ecosystem exchange (G_{ee}) was only about 45% of the potential due to the influence of water vapor pressure deficit (VPD). High VPD reduced the photosynthetic capacity and the highest relative reductions occurred in afternoon when VPD was higher, with relative reductions between 0.3 and 0.6 during this time. Bigger reduction occurred in May and July, corresponding the 2 months when VPD are higher.

(3) Respiration (R_e) and net ecosystem exchange (N_{ee}) were about 74% and 26% of actual G_{ee} during growing season. Net assimilation began in the middle of April and ended in early September. The largest uptake occurred in June, then July and August. Large net CO_2 losses occurred in late September and October because of relatively high temperature and leaf fall from most trees in the forest.

(4) This forest was a carbon sink of 169–187 g C m^{-2} yr^{-1} over a 12-month-period commencing August 2002. Application of the $u*$ correction decreased the annual uptake of carbon by 24.6 g C m^{-2} on average, corresponding to 13.5% of the corrected annual N_{ee}.

There are many uncertainties for determination of absolute values of long-term net carbon exchange even in sites with ideal topography using Eddy-covariance. More detailed experiments and related theoretical studies are needed in the future.

Keywords: Net ecosystem exchange; Carbon dioxide; Eddy-covariance; Old forest

---

[*] Corresponding author. Tel.: +86 24 83970336; fax: +86 24 83970200.
E-mail address: guan.dexin@hotmail.com (D.-X. Guan).

0168-1923/$ – see front matter © 2006 Elsevier B.V. All rights reserved.
doi:10.1016/j.agrformet.2006.02.003

1. Introduction

It is widely accepted that increasing atmospheric CO_2 is one of the most important factors leading to global warming. Forests are considered to be the terrestrial ecosystems that assimilate the largest amount of CO_2 and store it for a relatively long time, and hence estimating CO_2 sequestration by forests is particularly important in connection with global change studies and for the Kyoto protocol. Forests and other terrestrial ecosystems vary significantly and hence ecosystem scientists need tools to assess the flows of carbon, water and energy to and from the terrestrial biosphere across a wide spectrum of time- and space scales (Running et al., 1999; Canadell et al., 2000; Baldocchi et al., 2001). Recent developments in Eddy-covariance techniques have allowed long-term, continuous measurements of CO_2 and water vapor flux to be made routinely. On the basis of continuous measurements of carbon dioxide exchange at an increasing number of sites throughout the world since the mid-1990s (e.g. Wofsy et al., 1993; Valentini et al., 1996), regional flux networks such as CARBOEUROFLUX, AMERIFLUX, OzFlux or ASIAFLUX have created the global network FLUXNET (Baldocchi et al., 2001). Over 200 tower sites are registered on the international FLUXNET data archive, including 80 sites in forest (Baldocchi et al., 2001). Eddy-covariance techniques have become an essential feature of several international programs studying the role of the biosphere in the global carbon cycle.

China has a very large terrestrial and forest area, but it has remained a blank in measuring forest CO_2 fluxes by Eddy-covariance techniques before instruments were installed by the CHINAFLUX project in late summer, 2002. As a team responsible for one forest site of CHINAFLUX, we have measured CO_2, water vapor and energy fluxes by the Eddy-covariance technique in a mixed forest of Korean pine and broad-leaved species in the Changbai Mountains. Inclusion of the CHINAFLUX data set into the global FLUXNET database will aid research into the global carbon cycle.

Age or succession stage of a forest obviously affects the CO_2 flux. Theoretically, assimilation is thought to be balanced by respiration as a forest stand reaches an 'advanced' stage of development (Melillo et al., 1996). This hypothesis is based on studies showing a decline in net primary productivity with stand age (e.g. Yoder et al., 1994; Gower et al., 1996; Ryan et al., 1997; Knohl et al., 2003). Those findings are mostly derived from measurements in managed, even-aged, single-species forests, aged between 40 and 150 years in the temperate zone (Buchmann and Schulze, 1999). Little evidence exists that this hypothesis holds true for net ecosystem exchange of unmanaged forests that cover a wide range of age classes due to natural regeneration and which consist of a highly diverse canopy structure (Knohl et al., 2003). There is some information about the carbon dioxide exchange of forests at later stages of development (Buchmann and Schulze, 1999). Measurements have been reported for relatively old coniferous forests, including a 450-year-old Douglas fir/western hemlock site in Washington, USA (Falk et al., 2002), a 250-year-old Ponderosa pine site in Oregon, USA (Law et al., 2001) and a 300-year-old *Nothofagus* site in New Zealand (Hollinger et al., 1994). In each case, these forests have maintained the capability to sequester carbon. The latest measurement in Germany showed that a 250-year-old beech forest was a large carbon sink of 494 g C m^{-2} yr^{-1} (Knohl et al., 2003).

Our site is in the National Natural Conservation Park of Changbai Mountain, in Jilin province (northeastern China). The forest at the tower site is an unmanaged, uneven-aged mixture of broad-leaved deciduous and coniferous species, with the oldest tree reaching at least 450 years old according to tree-ring cores. The stand shows typical characteristics of a forest at a comparatively late successional stage, i.e. occurrence of natural regeneration, a wide tree age distribution, diverse canopy structure, and a lot of dead wood.

The objectives of this study were to test the hypothesis that forests at a comparatively late stage of development are insignificant as carbon sinks and to investigate the driving variables for the carbon dioxide exchange of the forest.

2. Materials and methods

2.1. Site description

The experimental site is located within the National Natural Conservation Park of Changbai Mountain, in eastern Jilin province in northeastern China. The measurement tower is situated at 42°24′09″N, 128°05′45″E at an elevation of 738 m. The National Natural Conservation Park was established in 1960, when it was taken out of management and developed without human disturbance to protect one of the largest typical temperate forests in East Asia. A homogeneous mixture of broad-leaved deciduous and coniferous forest extends more than 10 km in the south and west, respectively, and for nearly 3 and 0.5 km in the north and east, respectively. Secondary natural forests, about 80 years old, are distributed immediately in the east and extend far away. The closest change in land use is the Erdao Baihe town about 1 km northeast from the tower.

The forest surrounding the tower is dominated by Korean pine (*Pinus koriaensis*), Tuan linden (*Tilia amurensis*), Mono maple (*Acer mimo*), Manchurian ash (*Fraxinus mandshurica*), Mongolian oak (*Quercus mongolica*), elm (*Ulmus glabra*) and other deciduous species interspersed. The density of trees around the tower with stem diameters > 8 cm is about 560 trees ha^{-1}. The above-ground biomass storage is about 380 m^3 ha^{-1}. Maximum tree height varies between 23 and 28 m with a maximum leaf area index (L) of 5.8 m^2 m^{-2}. The stem densities of the four dominant tree species versus diameters of breast height (DBH) are shown in Fig. 1 (estimated from the figures of Sun and Zhao, 1995; Sun et al., 1997). It can be seen that the trees cover a wide range of age classes. To estimate the age of the forest, we took some tree-ring core samples of bigger trees around the tower and the results showed that, the oldest live trees of Korean pine, Tuan linden and Mono maple could reach 260–300 years, and the oldest specie was Manchurian ash with a maximum age about 450 years. By dry weight, the storage of fallen trees in the forest varies from several to 10 t ha^{-1}. The average annual input of fallen trees is 0.6 t ha^{-1} (Dai et al., 2002). Litter production is 3.8 t ha^{-1} yr^{-1}. Total litter cover is 14.7 t ha^{-1}, consisting of non-decomposed 5.8 t ha^{-1} and semi- and fully decomposed 8.9 t ha^{-1}, respectively. The soil is montane dark brown forest soil. It is considered that the forest ecosystem is at steady stage of climax community (Yang et al., 1985).

The site is located in the monsoon-influenced, temperate continental climate region. Meteorological records from a weather station about 1 km east of the tower for 1982–2003 show that annual mean air temperature is 3.6 °C and mean precipitation is 695 mm. The prevailing wind direction and the higher wind speeds are all southwestern (Fig. 2). Wind direction from the town occurred only 3% of the time during the 16 months of measurement. The results of footprint analysis according to Schuepp et al. (1990) shows that flux from the town area is less than 2% of the total flux during the measurement. So we neglected the town area in the calculation of daily, monthly and annual carbon flux.

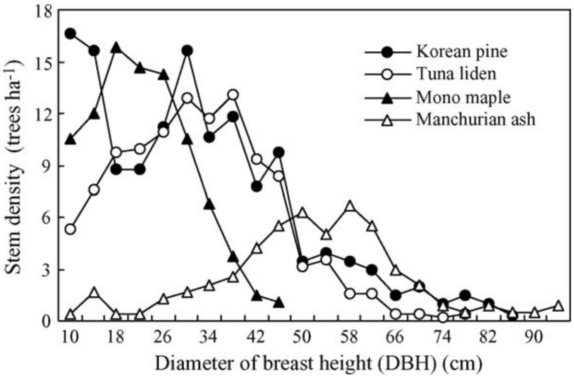

Fig. 1. Stem density of four dominant tree species around the tower.

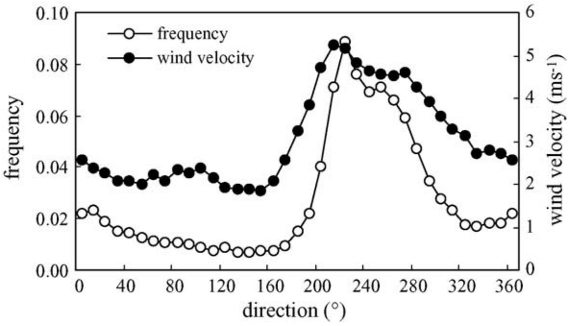

Fig. 2. The frequency of wind direction and corresponding wind velocities distribution.

2.2. Instrumentation

Nine platforms and instrument arms were mounted on a 62 m tall triangular meteorological tower, 0.80 m on each side. A small hut for the equipment is located 15 m northeast of the tower. The instruments at the site are divided into four categories: (1) Eddy-covariance system, (2) mean wind, temperature, humidity and CO_2 concentration profile measurement system, (3) soil temperature, moisture and heat flux measurement system, and (4) the routine meteorological system. The instruments have been in operation since 24 August 2002.

Fluxes of carbon dioxide, water vapor, heat and momentum were continuously measured at the 40 m level using the Eddy-covariance technique. The flux system consisted of a triaxial sonic anemometer (CAST3, Campbell Scientific, USA) and a fast response open-path CO_2/H_2O infrared gas analyzer (Li-7500, LiCor Inc., USA) mounted on an arm extending 3 m from the tower. Signals from both instruments were sampled at 10 Hz. The Li-7500 was calibrated 1 year later and showed no shift from original calibrations.

CO_2 concentration profiles were measured at seven heights (2.5, 8.0, 22.0, 26.0, 32.0, 50.0 and 61.8 m) using an infrared gas analyzer (Li-820, LiCor Inc., USA). Inlets with a 10 μm filter head were fixed on the arms and the pipes extended along the tower to an electromagnetic valve system connecting to the infrared gas analyzer. Air at the heights was pumped into the infrared gas analyzer and CO_2 concentrations were measured sequentially. The valve system regularly sampled the air lines from different heights and finished one cycle of the seven levels every 3 min. A standard CO_2 gas bottle was also connected to the valve system and calibrated the infrared gas analyzer every 3 h.

Air humidity and air temperature (HMP45C, Vaisala, Helsinki, Finland), wind speed (A100R, Vector Instruments, Denbighshire, UK) were measured at the heights same as carbon dioxide concentrations. Wind direction (W200P, Vector Instruments, Denbighshire, UK) and Precipitation (RainGauge 52203, Young, Traverse City, MI, USA) were collected at 61.8 m. Air pressure (CS105, Vaisala, Helsinki, Finland) was measured at 2 m.

Photosynthetically active radiation (PAR) at 32 m (LI-190Sb, LiCor Inc., USA), as well as at 2 m with five linear sensors (LQS70-10, APOGEE, USA) distributed randomly around the tower. Net radiation was calculated from down and upward, short- and long-wave radiations, i.e. the measurements of four-sensor combined radiation meter (CNR-1, Kipp & Zonen, Delft, The Netherlands). Short-wave downward radiation (CM11, Kipp & Zonen, Delft, The Netherlands) was measured at 32 m.

Soil moisture was measured in one vertical soil profile (5, 20, and 50 cm) with TDR (CS616_L, Compbell, USA). Soil temperature was measured in two vertical soil profiles (0, 5, 20, 50 and 100 cm) with two types of sensor, respectively (105T and 107L, Campbell, USA). Three soil heat flux plates (HFP01, HukseFlux, The Netherlands) at 2–3 cm soil depth were used to measure the average soil heat flux (G) near the tower. Canopy surface temperature was measured by an infrared thermometer (IRTS-P, APOGEE, USA).

Data loggers (CR23X and CR10X, Campbell Scientific, Logan, UT, USA) were used to collect and store all data every 10 s, well as the 30 min averages.

Leaf area index (L) was measured using a Plant Canopy Analyzer (Li 2000, LiCor Inc., Lincoln, NE, USA) along a 200 m transect in the southwest direction from the tower during late April to late October. Three repeated measurements were made using a 60° view cap. Leaf area index is calculated as the difference between the measurement on the floor and on the tower platform at 32 m.

2.3. Flux calculations and corrections

From the time series of vertical wind velocity and temperature, carbon dioxide density and water vapor density, the fluxes were calculated online after each 30 min interval using the calculation software designed by Campbell Scientific Inc. Turbulent carbon dioxide fluxes (F_c), latent heat flux (λE) and sensible heat flux (H) were determined as

$$F_c = \rho \overline{c'w'} \tag{1}$$

$$\lambda E = \lambda \rho \overline{w'q'} \tag{2}$$

$$H = \rho C_p \overline{T'w'} \tag{3}$$

where ρ is the density of dry air, w the vertical wind speed, c the mixing ratio of CO_2, λ the latent heat of vaporization, E the water vapor flux, q the specific humidity, C_p the specific heat capacity of dry air and T is the sonic temperature. Overbars denote time averages and primes denote the departures. Both the CO_2 flux (F_c) and latent flux (λE) were corrected for density effects using the method described by Webb et al. (1980).

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 CO_2 flux associated with storage of CO_2 below the measuring height of the Eddy-covariance system (F_s) was determined in two ways: (a) using the profile measurements to determine the rate of change of CO_2 stored in the air layer below the flux measurement height (40 m); (b) as the rate of change of the CO_2 concentration at 40 m (linear interpolation of the concentration of 32 and 50 m). When CO_2 concentration profile measurement system did not work, concentration measured by Li-7500 was used. As both storage fluxes had similar values, we used (b) for further calculations because it reflects better the same source area as the turbulent flux. Final CO_2 fluxes were calculated as the sum of the turbulent flux and the storage term:

$$N_{ee} = F_c + F_s \tag{4}$$

Fluxes into the ecosystem (e.g. assimilation) are noted with a negative sign, while fluxes from the ecosystem to the atmosphere (e.g. respiration) are given with a positive sign.

Available data covered 86.9% of the measurement during the period. Small gaps up to 2 h due to instrumental failure were filled using interpolation and larger gaps were filled with empirical regressions for respiration and assimilation derived for 10 days intervals. Only high quality data were accepted to formulate the regression relationships. Non-stationary data (Foken and Wichura, 1996), data with high variance $[CO_2] > 5$ ppm and nighttime data under conditions of $u^* < 0.2$ m s^{-1} were excluded from regression analysis. Gaps in daytime data (PAR > 1 μmol m^{-2} s^{-1}) were filled by a Michaelis–Menten equation (see Eqs. (5)–(8) in Section 3.1). The model has been shown to be a useful framework for the whole ecosystem CO_2 exchange (Wofsy et al., 1993; Hollinger et al., 1994; Goulden et al., 1997; Lindroth et al., 1998; Chen et al., 1999; Lee et al., 1999; Anthoni et al., 1999).

To fill the gaps in the dark periods an exponential expression was used (see Eq. (10) in Section 3.1). This expression was also used to substitute for the negative flux measurements at night ensure the data had ecological meaning.

It is recognized by the flux monitoring community that the EC technique is likely to underestimate Eddy fluxes under calm conditions at night, but there is no consensus as to how to best correct the problem (Lee et al., 1999). Most of the researchers screened the nighttime data on the basis of a friction velocity u^* threshold (Goulden et al., 1996; Black et al., 1996; Jarvis et al., 1997; Lindroth et al., 1998). We did see only a negligible trend of increasing N_{ee} with u^* (Fig. 3). However, in our later discussion of errors associated with carbon uptake estimates from the EC data we also calculate annual N_{ee} using a u^* threshold of 0.20 m s^{-1}.

An analytical footprint model by Schuepp et al. (1990) was used to estimate source areas for the measured fluxes. Under neutral atmospheric conditions, the source weight function peaked at approximately 90 m from the tower, 50% of the integrated source weight function was reached at 260 m, and 80% at 790 m.

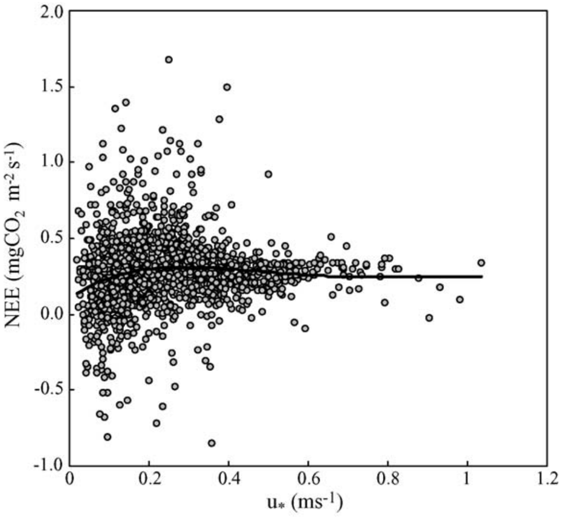

Fig. 3. Friction velocity u^* and N_{ee} in night (PAR < 1 μmol m^{-2} s^{-1}) during June to August.

3. Results and discussion

Meteorological conditions during the measurements are reported by Zhang et al. (2006). It seems that there was no water limitation during growing season since volumetric soil water content in 50 and 20 cm depth was larger than 30% and 18% during the early spring to late autumn, respectively.

3.1. Comprehensive expressions of CO_2 flux of the forest ecosystem

Net ecosystem exchange of CO_2 between the forest ecosystem and atmosphere is the sum of fluxes due to canopy photosynthesis and by respiration of the rhizosphere, leaves and stems. The magnitude of these processes varies with season due to variations in environments and plant characteristics, such as canopy development and photosynthetic properties. Net ecosystem exchange N_{ee} can be expressed as

$$N_{ee} = R_e + G_{ee} \tag{5}$$

$$G_{ee} = \frac{\alpha Q_{abs} P_{max}}{\alpha Q_{abs} + P_{max}} \tag{6}$$

where G_{ee} is gross ecosystem exchange, R_e is ecosystem respiration, and can be separated into autotrophic respiration, R_a, and heterotrophic respiration, R_h:

$$R_e = R_a + R_h \tag{7}$$

α is the quantum yield. Q_{abs} absorbed PAR is expressed as

$$Q_{abs} = kQ_0(1 - \rho_c)[1 - \exp(-kL)] \tag{8}$$

in which k is the absorption coefficient, Q_0 incident PAR above canopy, ρ_c the canopy reflectance and L is the leaf area index.

P_{max} is maximum photosynthetic capacity and it is depend on soil moisture availability and on atmospheric demand for water vapor. Because soil water was adequate, we may be able to capture this dependence by a hyperbolic function (Lohammer et al., 1980; Leuning, 1995):

$$P_{max} = \frac{P_{max0}}{1 + D/D_0} \tag{9}$$

where D and D_0 are the water vapor pressure deficit (VPD) and a parameter, respectively, and where P_{max0} is the value of P_{max} when there is no limitation to photosynthesis of VPD.

Expressions for R_{e} and R_{a} take the form:

$$R_{\mathrm{e}} = R_{\mathrm{e0}} \exp[a_{\mathrm{e}}(T_{\mathrm{soil}} - T_{\mathrm{soil0}})] \tag{10}$$

$$R_{\mathrm{a}} = R_{\mathrm{leaf}} + R_{\mathrm{stem}} \tag{11}$$

where

$$R_{\mathrm{leaf}} = R_{\mathrm{l0}} M_{\mathrm{leaf}} \exp[a_{\mathrm{leaf}}(T_{\mathrm{air}} - T_{\mathrm{air0}})] \tag{12}$$

$$R_{\mathrm{stem}} = R_{\mathrm{s0}} M_{\mathrm{stem}} \exp[a_{\mathrm{stem}}(T_{\mathrm{air}} - T_{\mathrm{air0}})] \tag{13}$$

and where M_{leaf} and M_{stem} are the mass of leaves and stems, T_{air} air temperature and T_{air0} a reference temperature, R_{e0}, R_{l0}, R_{s0}, a_{e}, a_{leaf} and a_{stem} are parameters. Similarly expression for R_{h} is

$$R_{\mathrm{h}} = R_{\mathrm{h0}} M_{\mathrm{leaf}} \exp[a_{\mathrm{h}}(T_{\mathrm{soil}} - T_{\mathrm{soil0}})] \tag{14}$$

where we substituted soil temperature for air temperature and included M_{l} to account for the supply of recent photosynthate to supply root and microbial respiration in the rhizosphere.

As soil moisture was relatively adequate during growing season, leaf area index (L) is mainly controlled by daily mean air temperature (T_{a}) and is well described by an exponential function:

$$L = 1.273 \exp(0.0801 T_{\mathrm{a}}), \qquad R^2 = 0.948 \tag{15}$$

Leaf mass during growing season is given by

$$M_{\mathrm{leaf}} = \frac{M_{\mathrm{max}}(L - L_0)}{L_{\mathrm{max}} - L} \tag{16}$$

where M_{max} is the maximum leaf mass at the peak of the growing season (kg ha^{-1}), $L_0 = 1.5$ is the estimation of L of stems, $L_{\mathrm{max}} = 5.8$ is the maximum value of L.

We assumed that soil water supply was not a limitation and thus the essential factors controlling the CO_2 flux of the forest ecosystem are air and soil temperature, PAR and VPD (Fig. 4).

This set of equations is used to describe the CO_2 exchanges of the system. Then, the parameters to be uncovered are α, P_{max0}, D_0, R_{e0}, R_{l0}, R_{s0}, R_{h0}, a_{e}, a_{leaf}, a_{stem} and a_{h}. These parameters were estimated according to the measurements and cited from the literature as follows:

(1) We set $k = 0.5$ in Eq. (8) estimated by PAR measurements above and under canopy. We then calculated Q_{abs} based on the 30 min measurements of incident PAR above canopy, Q_0, canopy reflectance ρ_{c} (estimated from short wave radiation measurement) and the leaf area index L measured in 5–10 days interval. Then, α and P_{max} were estimated in 10-day windows by an iterative method using the Eddy-covariance (EC) measurements and Q_{abs}.

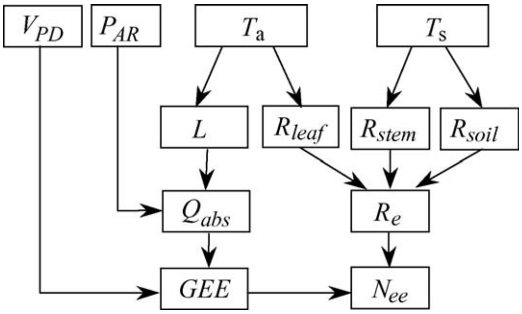

Fig. 4. Environmental controlling mechanisms of the CO_2 flux of the forest ecosystem under the sufficient soil water supply.

The parameter P_{max0} and D_0 were estimated in monthly window from April to September. At first, the measurement series of N_{ee} and Q_{abs} of each window were divided into eight VPD classes of 0.25 kPa each between 0 and 1.5 and one class for VPD > 1.5 kPa. We obtained eight sets of P_{max} and average Q_{abs} in each month by the same iterative method as above. These data were employed to estimate P_{max0} and D_0 by iterative method instead. The estimation gave $P_{\mathrm{max0}} = 0.51$, 1.81, 2.26, 2.15, 1.94, 1.37 mg CO_2 m^{-2} s^{-1}, $\alpha = 0.72$, 2.39, 3.76, 4.59, 4.73, 3.43×10^{-3} mg CO_2 μmol^{-1} and $D_0 =$ 1.49, 1.69, 1.16, 3.01, 5.87 kPa for April–September, respectively.

(2) R_{e} was estimated by night EC measurements and gave the coefficients $R_{\mathrm{e0}} = 0.0356$, $a_{\mathrm{e}} = 0.1296$ as $T_{\mathrm{soil0}} = 0$ °C with correlation $R^2 = 0.4650$.

(3) R_{s0}, R_{h0} were obtained from Wang et al. (2004, 2005). When $T_{\mathrm{airo}} = T_{\mathrm{soil0}} = 0$ °C, $R_{\mathrm{s0}} = 0.2080 \times 10^{-3}$ mg CO_2 kg^{-1} s^{-1}, $R_{\mathrm{h0}} = 0.0172$ mg CO_2 m^{-2} s^{-1}, $a_{\mathrm{stem}} = 0.0988$, $a_{\mathrm{h}} = 0.1268$.

R_{l0} and a_{leaf} were estimated by the results of subtracting R_{stem} and R_{h} from R_{e}. And gave $R_{\mathrm{l0}} =$ 0.0088, $a_{\mathrm{leaf}} = 0.1534$.

(4) Leaf mass during the growing season was estimated by Eq. (16), in which M_{max} was estimated from field litter samples. M_{stem} was calculated by forest investigation, and gave the value 380 t ha^{-1}.

3.2. *Daytime CO_2 assimilation of the forest ecosystem*

The forest ecosystem assimilates CO_2 by photosynthesis of the leaves. Gross assimilation, G_{ee}, is depended on leaf area index, L, Q_{abs} and VPD as described by Eqs. (6), (8) and (9). If $P_{\max0}$ is substituted for $P_{\max}$ in Eq. (6), we obtain the potential gross ecosystem assimilation, G_{ee0}, that is the estimation simply due to variation in leaf area index L, whereas G_{ee} estimated from EC measurements is the photosynthetic capacity influenced both by L and by VPD. Fig. 5 shows monthly averaged daytime variations in G_{ee} and G_{ee0} from April to September. It can be seen from the figure that the forest had a small capacity for CO_2 assimilation in April, and the averaged maximum of G_{ee0} was 0.27 mg CO_2 m^{-2} s^{-1}. G_{ee0} rose in May and averaged maximum increase to 1.04 mg CO_2 m^{-2} s^{-1}. It rose up to higher values in the fast growing season, June–August, with averaged maxima of 1.61, 1.43, 1.42 mg CO_2 m^{-2} s^{-1}, respectively.

Dryer air reduces the photosynthetic capacity, via decreasing $P_{\max}$ as expressed in Eqs. (6) and (9). The reductions can be seen from the departures of G_{ee} from G_{ee0} in Fig. 5. G_{ee} estimated from the EC measurements is lower than G_{ee0} during the growing season, and G_{ee} is asymmetrical around noon, with the maximum value generally appearing between 9:00 and 10:00 h. This characteristic is similar to leaf-scale measurements on crops (Henson et al., 1989; Leuning et al., 1995).

In order to see the magnitude and daytime variation of the reduction, diurnal dynamics of relative reduction of G_{ee} to G_{ee0}, $1 - G_{\mathrm{ee}}/G_{\mathrm{ee0}}$, and corresponding VPD are plotted in Fig. 6. It is also found that the reductions are asymmetrical during the daytime, smaller in the morning and bigger in the afternoon. Large reduction occurred during 13:00–17:00 h, corresponding the time when VPD is higher. The relative reduction during this time ranged between 0.3 and 0.6. Another large reduction happens at early morning and this may be due to dew on the leaves. The smallest reduction appears about at 7:30–8:00 h and the reason may be the evaporation of the dew and relatively lower VPD during the daytime.

The relative reductions are also different among the months. Biggest and second big reduction occurred in May and July, respectively, corresponding the 2 months when VPD are higher. The relative reductions in the 2 months could get up to 0.6 and 0.5, respectively. The values in April, August and September are approximately same in the afternoon.

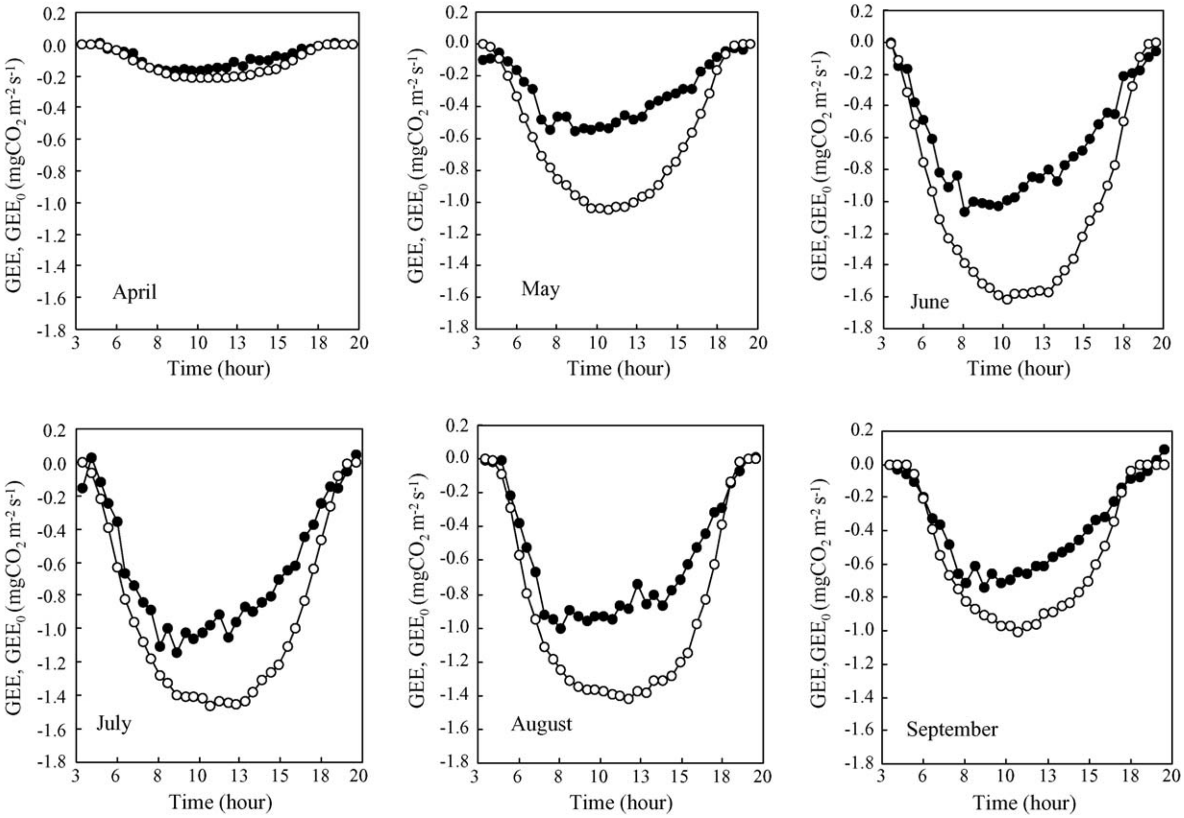

Fig. 5. Monthly averaged daytime variations in measured gross ecosystem exchange G_{ee} (●) and the potential values depended on leaf area index, G_{ee0} (○), from April to September.

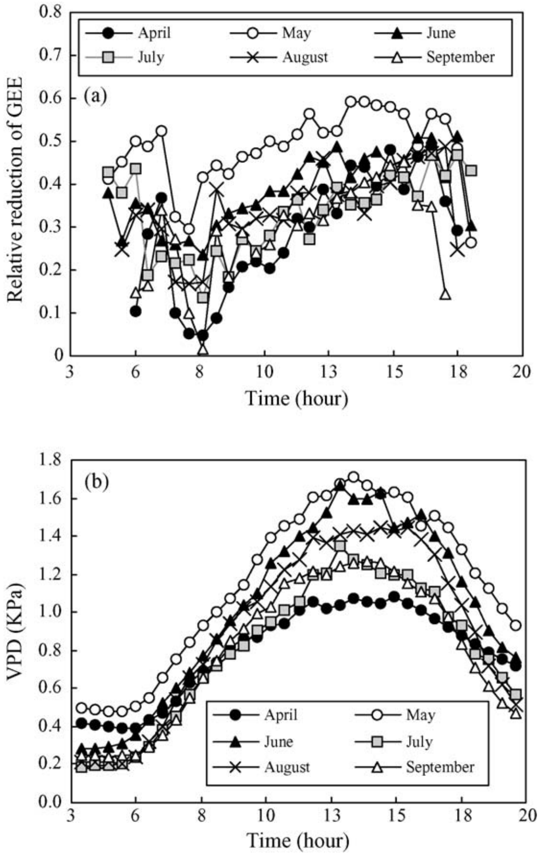

Fig. 6. Monthly averaged daytime variations of relative reduction of G_{ee} to G_{ee0}, $1 - G_{ee}/G_{ee0}$ (a), and corresponding VPD (b) from April to September.

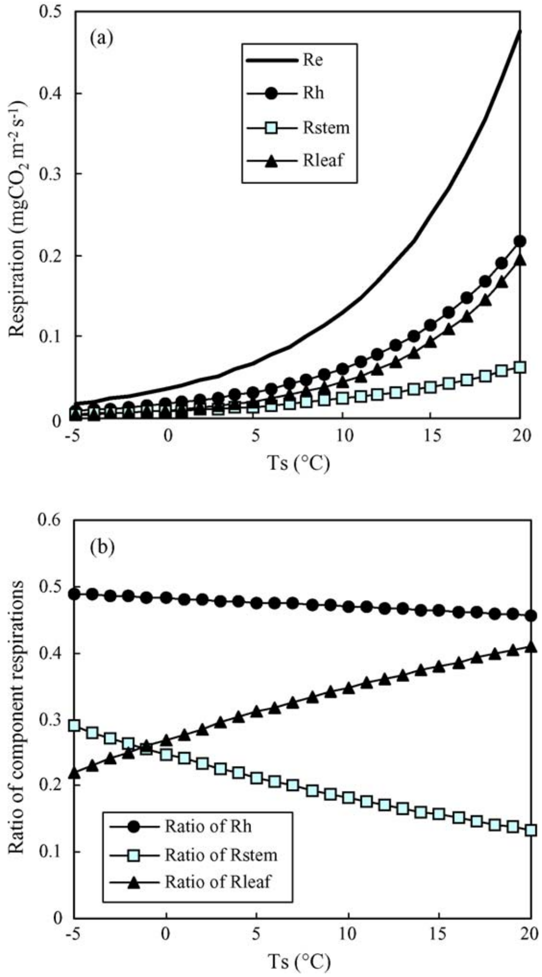

Fig. 7. Ecosystem respiration and its components (a) and ratios of these components (b) varying with soil temperature.

3.3. Respiration of the ecosystem components influenced by temperature

The respiration–soil temperature relationships of whole ecosystem (measurements by the EC technique), R_e and the components were shown in Fig. 7a. Ratios of respirations of the three components to that of whole ecosystem are plotted in Fig. 7b. It can be seen that soil respiration is the largest among the three components. It is about 46–49% of the total respiration and is relatively stable when temperature varies. If the respiration of fallen trees is taken into consideration, soil respiration may contribute >50% of whole ecosystem respiration. Raich and Schlesinger (1992) estimated that soil-surface CO_2 efflux was 48–71% of ecosystem respiration, and our result (49%) was within the lower part of this range.

Foliage respiration was the second in magnitude among the respiration fractions. Its ratio to the whole ecosystem respiration increased as temperature rises, from 22% at $T_s = -5$ °C to 40% at $T_s = 20$ °C. This is due to the synchronous seasonal variation of temperature and L. There was bigger area of leaves in the hotter season as well as greater respiration. The foliage respiration may be slightly overestimated because respiration of fallen trees and coarse woody debris is involved.

Stem respiration was lower than foliage respiration except during the cold season. The ratio of stem respiration to the whole ecosystem respiration decreases as temperature rose, from 29% at $T_s = -5$ °C to 13% at $T_s = 20$ °C.

Law et al. (1999) reported that, in a mixture of old-growth (250-year-old) and young (45-year-old) ponderosa pine trees in central Oregon, the contribution of soil-surface CO_2 efflux, stem respiration and leaf respiration to ecosystem respiration was 76.4, 6.0 and 17.6%, respectively. The corresponding values in a young (approximately 8 years old) ponderosa pine plantation in the Sierra Nevada Mountains were 64.8%, 9.5%, and 25.4%, respectively (Xu et al., 2001). The corresponding values at our site are 46.5%, 14.2%, and 39.3%, respectively. The lower percentage of leaf respiration at the Oregon and Nevada sites is primarily due to low *L* (1.5 and 4.5 at the two sites). The higher percentage of stem respiration at our site than at the two sites (14.2% versus 9.5% and 6%) is caused by the bigger biomass of our site (>280 m^3 ha^{-1} versus 129 and 7 m^3 ha^{-1}).

3.4. Seasonal variation of N_{ee} and the components of the ecosystem

Fig. 8 shows the seasonal patterns of daily net ecosystem exchange (N_{ee}). Characteristics of seasonal dynamic of N_{ee} are that there are small positive fluxes in winter, and negative fluxes in the growing season. N_{ee} began to rise to positive in early September and manifest large positive values in late September and October because relatively high temperature and defoliation of most trees of the forest. However, very large positive values of N_{ee} appeared occasionally in July or August, such as the circled points in Fig. 8. This always happened on overcast days (low PAR) when soil temperature was high. The largest assimilation of the forest is in June, due to less cloudiness and relatively high leaf area. The maximum daily uptake is also occurred in June, reaching -6.5 g C m^{-2} d^{-1}.

In order to show the assimilation and respiration process of the forest ecosystem, Fig. 9 shows the dynamics of daily values of net ecosystem exchange (N_{ee}), ecosystem respiration (R_e), gross ecosystem exchange (G_{ee}), potential gross ecosystem exchange (G_{ee0}) and net ecosystem exchange (N_{ee0}) depended on leaf area index, from April to September. The ecosystem has very large assimilation potential if the environmental controlling factors were adequate (mainly the demand for water by the atmosphere during the measurement). G_{ee0} could reach -26 g C m^{-2} d^{-1}. And (N_{ee0}) could get up to -18 g C m^{-2} d^{-1}. But under the suppression of photosynthesis by atmospheric water deficit, these exchange capacities were reduced significantly. G_{ee} and N_{ee} are down to under -12.1 g C m^{-2} $d^{-1}$and under -6.5 g C m^{-2} d^{-1}, respectively.

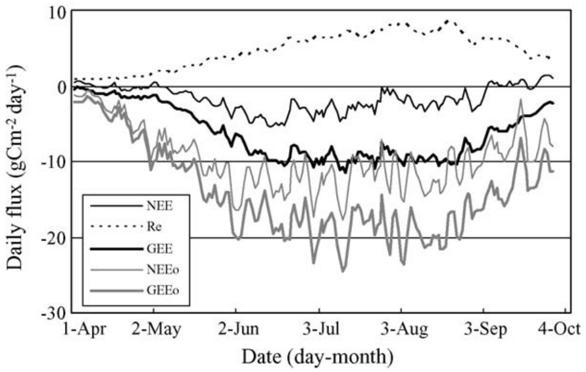

Fig. 9. Dynamics of measured and potential daily exchanges during growing season (3-day running averages).

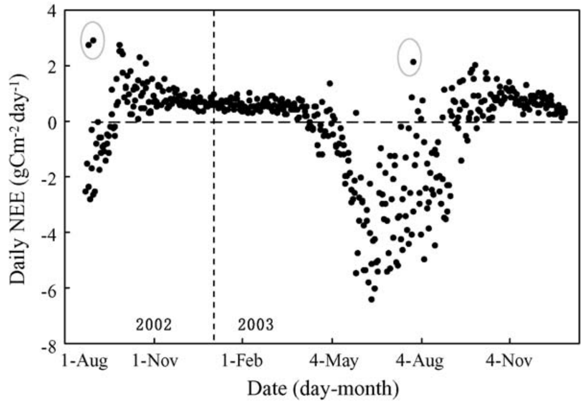

Fig. 8. Dynamics of daily N_{ee} during the measurements.

Accumulation result from April to September was that actual gross ecosystem exchange (G_{ee}) was only about 45% of the potential (G_{ee0}) due to the influence of VPD. Respiration (R_e) and net ecosystem exchange (N_{ee}) were about 74% and 26% of actual G_{ee} during growing season.

3.5. Annual N_{ee} and u correction*

Fig. 10 shows the variation of annual N_{ee} as a function of the commencement day for summation, with

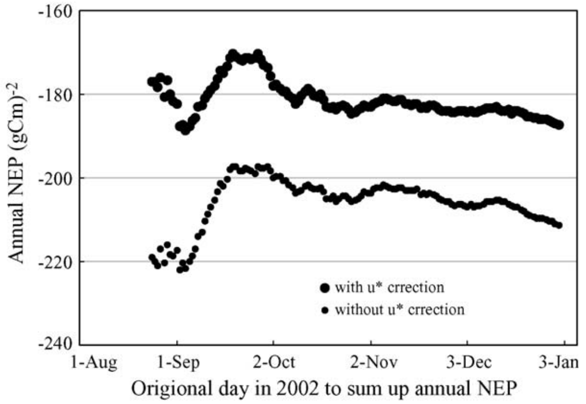

Fig. 10. Variation of cross annual NEP with the original day to commence, with and without u^* correction, respectively.

and without the u^* correction. Annual N_{ee} was varied between -169 and -187 g C m^{-2} after u^* correction, depending on the commencement day. It was lowest if commence from early September, and highest as commencing from late September. This means N_{ee} during early to middle September in 2002 and 2003 were obviously different. The measurements show that N_{ee} during 1–20 September in 2002 was -12.3 and -1.7 g C m^{-2} for the same period in 2003. The large difference was mainly due to different meteorological conditions for the 2 years. During the September 2002 there was a higher sum of PAR (606.5 MJ) compared to 572.7 MJ in 2003, while soil temperature at 5 cm was 13.5 °C in 2002 compared to14.7 °C in 2003. This resulted in greater photosynthesis and less respiration and hence more CO_2 uptake by the ecosystem in 2002. Annual N_{ee} was approximately constant when summation commenced from late October.

The u^* correction greatly affected estimates of the N_{ee}, either on daily or longer time scale (e.g. monthly, yearly). Fig. 10 gives the result that the correction decreases the annual uptake of carbon in the magnitude of 22.2–44.7 g C m^{-2} with an average 24.6 g C m^{-2}, corresponding to 12.3–25.6% with an average 13.5% of the corrected annual N_{ee}.

4. Concluding remarks

In the analysis of the mechanisms of the carbon process of the forest ecosystem, it was found that temperature and atmospheric water demand were the main controlling factors except for solar radiation, under the condition of soil water supply was adequate. Although the forest ecosystem has large CO_2 assimilation potential when the environmental controls were not limiting, VPD significantly reduced the assimilation capacity. Moreover, after the respiration, net ecosystem exchange of the ecosystem was only a small part of the assimilation potential.

In the CO_2 flux calculation, we found the threshold of friction velocity $u^* = 0.2$ m s^{-1} was appropriate for the correction of under-measurement of nighttime flux. This correction decreased by 13.5% the estimation of net carbon uptake of the forest ecosystem. Large uptake happen during fast growing season (June to August) and low release occurred in winter (November to March). Relatively large release took place in late September and October due to defoliation and relative high temperature.

Our results of annual N_{ee} are different from those of Zhang et al. (2006) (-308 ± 116 g C m^{-2}, from 24 August 2002 to 23 August 2003) though the original measurements were same. The discrepancy may due to different methods of flux calculation and correction, including that of threshold of u^* and winter flux calculation and so on. Winter flux correction was a big issue in the calculation because there was long winter duration in the site. Zhang et al. (2006) used a theoretical method in the correction, but they still had some negative daily N_{ee} during winter. Negative fluxes during winter nighttime, in our correction, were replaced by estimates using the exponential Eq. (10) to provide ecologically meaningful results. This resulted in a difference of 80.7 g C m^{-2} in N_{ee} from October 2002 to March 2003 between us. The u^* threshold significantly influences the accumulated N_{ee} (Goulden et al., 1996; Massman and Lee, 2002; Baldocchi, 2003). Little difference in u^* threshold between 0.17 (Zhang et al., 2006) and 0.2 m s^{-1} of our study resulted in difference of 15% of valid data number from June to September and explained the difference of 23 g C m^{-2} in N_{ee}. There are many uncertainties for determination of absolute values of long-term net carbon exchange even in sites with ideal topography using the Eddy-covariance method (Massman and Lee, 2002; Baldocchi, 2003). More detailed experiments and related theoretical studies are needed in the future.

Acknowledgements

We thank Dr. Ray Leuning for his substantial suggestions in manuscript revising, as well as another anonymous reviewer. We thank the Compbell Science Corporation and Beijing Tempro Corporation for their technical support of the flux measurement. Thanks are also due to Mr. Xu Hao and Dai Guanhua for their earnest routine maintenance of the instruments. The research was funded by Chinese Academy of Sciences (no. KZCX1-SW-01-01A), Ministry of Science and Technology (no. 2002CB412501), and National Natural Science Foundation of China (no. 30370293).

References

Anthoni, P.M., Law, B.E., Unsworth, M.H., 1999. Carbon and water vapor exchange of an open-canopied ponderosa pine ecosystem. Agric. For. Meteorol. 95, 115–168.

Baldocchi, D., Falge, E., Gu, L.H., Olson, R., Hollinger, D., Running, S., Anthoni, P., Bernhofer, C., Davis, K., Evans, R., Fuentes, J., Goldstein, A., Katul, G., Law, B., Lee, X.H., Malhi, Y., Meyers, T., Munger, W., Oechel, W., Paw U, K.T., Pilegaard, K., Schmid, H.P., Valentini, R., Verma, S., Vesala, T., Wilson, K., Wofsy, S., 2001. FLUXNET: a new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. Bull. Am. Meteorol. Soc. 82 (11), 2415–2434.

Baldocchi, D.D., 2003. Assessing ecosystem carbon balance: problems and prospects of the Eddy-covariance technique. Global Change Biol. 9, 478–492.

Black, T.A., den Hartog, G., Neumann, H.H., Blanken, P.D., Yang, P.C., Russell, C., Nesic, Z., Lee, X., Chen, S.G., Staebler, R., Novak, M.D., 1996. Annual cycles of water vapour and carbon dioxide fluxes in and above a boreal aspen forest. Global Change Biol. 2, 219–229.

Buchmann, N., Schulze, E.-D., 1999. Net CO_2 and H_2O fluxes of terrestrial ecosystems. Global Biogeochem. Cycles 13 (3), 751–760.

Canadell, J., Mooney, H., Baldocchi, D., Berry, J., Ehleringer, J., Field, C.B., Gower, T., Hollinger, D., Hunt, J., Jackson, R., Running, S., Shaver, G., Trumbore, S., Valentini, R., Yoder, B., 2000. Carbon metabolism of the terrestrial biosphere. Ecosystems 3, 115–130.

Chen, W.J., Black, T.A., Yang, P.C., Barr, A.G., Neumann, H.H., Nesic, Z., Blanken, P.D., Novak, M.D., Eley, J., Ketler, R.J., Cuenca, R., 1999. Effects of climatic variability on the annual carbon sequestration by a boreal aspen forest. Global Change Biol. 5, 41–53.

Dai, L., Chen, G., Deng, H., Xu, Z., Li, Y., Chen, H., 2002. Storage dynamics of fallen trees in a mixed broadleaved and Korean pine forest. J. For. Res. 13 (2), 107–110.

Falk, M., Paw, U.K.T., Schroeder, M., 2002. Interannual variability of carbon and energy fluxes for an old-growth rainforest. In: Proceedings of the 25th Conference on Agricultural and Forest Meteorology, AMS, Norfolk.

Foken, T., Wichura, B., 1996. Tools for quality assessment of surface-based flux measurements. Agric. For. Meteorol. 78, 83–105.

Gower, S.T., McMurtrie, R.E., Murty, D., 1996. Aboveground net primary production decline with stand age: potential causes. Trends Ecol. Evol. 11 (9), 378–382.

Goulden, M.L., Munger, J.W., Fan, S.M., Daube, B.C., Wofsy, S.C., 1996. Exchange of carbon dioxide by a deciduous forest: response to interannual climate variability. Science 271, 1576–1578.

Goulden, M.L., Daube, B.C., Fan, S.-M., Sutton, D.J., Bazzaz, A., Munger, J.W., Wofsy, S.C., 1997. Physiological responses of a black spruce forest to weather. J. Geophys. Res. 102, 28987–28996.

Henson, I.E., Jensen, C.R., Turner, N.C., 1989. Leaf gas exchange and water relations of lupins and wheat. I. Shoot respondses to soil water deficits. Aust. J. Plant Physiol. 16, 401–413.

Hollinger, D.Y., Kelliher, F.M., Byers, J.N., Hunt, J.E., McSeveny, T.M., Weir, P.L., 1994. Carbon dioxide exchange between an undisturbed old-growth temperate forest and the atmosphere. Ecology 75 (1), 143–150.

Jarvis, P.G., Massheder, J.M., Hale, S.E., Moncrieff, J.B., Rayment, M., Scott, S.L., 1997. Seasonal variation of carbon dioxide, water vapor, and energy exchanges of a boreal black spruce forest. J. Geophys. Res. 102, 28953–28966.

Knohl, A., Schulze, A., Kolle, O., Buchmann, N., 2003. Large carbon uptake by an unmanaged 250-year-old deciduous forest in Central Germany. Agric. For. Meteorol. 95, 115–168.

Law, B.E., Goldstein, A.H., Anthoni, P.M., Unsworth, M.H., Panek, J.A., Bauer, M.R., Fracheboud, J.M., Hultman, N., 2001. Carbon dioxide and water vapor exchange by young and old ponderosa pine ecosystems during a dry summer. Tree Physiol. 21 (5), 299–308.

Law, B.E., Ryan, M.G., Anthoni, P.M., 1999. Seasonal and annual respiration of a ponderosa pine ecosystem. Global Change Biol. 5, 169–182.

Lee, X., Fuentes, J.D., Staebler, R.M., Neumann, H.H., 1999. Long-term observation of the atmospheric exchange of CO_2 with a temperate deciduous forest in southern Ontario, Canada. J. Geophys. Res. 104, 15975–15984.

Leuning, R., 1995. A critical appraisal of a combined stomatalphotosynthesis model for C3 plants. Plant Cell Environ. 18, 339–355.

Leuning, R., Kelliher, F.M., DePury, D.G.G., Schulze, E.-D., 1995. Leaf nitrogen, photosynthesis, conductance and transpiration: scaling from leaf to canopies. Plant Cell Environ. 18, 1183–1200.

Lindroth, A.A., Grelle, A., Moren, A.S., 1998. Long-term measurements of boreal forest carbon balance reveal large temperature sensitivity. Global Change Biol. 4, 443–450.

Lohammer, T., Larsson, S., Linder, S., Falk, S.O., 1980. FAST simulation models of gaseous exchange in scots pine. Ecol. Bull. 32, 05–523.

Massman, W.J., Lee, X.H., 2002. Eddy-covariance flux corrections and uncertainties in long-term studies of carbon and energy exchanges. Agric. For. Meteorol. 113, 121–144.

McMillen, R.T., 1988. An Eddy correlation technique with extended applicability to non-simple terrain. Boundary-Layer Meteorol. 43, 231–245.

Melillo, J.M., Prentice, I.C., Farquhar, G.D., Schulze, E.-D., Sala, O.E., 1996. Terrestrial biotic responses to environmental change and feedbacks to climate. In: Houghton, J.T., Meira Filho, L.G., Callander, B.A., Harris, N., Kattenberg, A., Maskell, K. (Eds.), Climate Change 1995: The Science of Climate Change. Cambrigde University Press, New York, pp. 444–481.

Raich, J.W., Schlesinger, W.H., 1992. The global carbon dioxide flux in soil respiration and its relationship to climate. Tellus 44B, 81–99.

Ryan, M.G., Binkley, D., Fownes, J.H., 1997. Age-related decline in forest productivity: pattern and process. Adv. Ecol. Res. 27, 213–262.

Running, S.W., Baldocchi, D.D., Turner, D., Gower, S.T., Bakwin, P., Hibbard, K., 1999. A global terrestrial monitoring network, scaling tower fluxes with ecosystem modeling and EOS satellite data. Remote Sens. Environ. 70, 108–127.

Schuepp, P.H., Leclerc, M.Y., MacPherson, J.I., 1990. Footprint prediction of scalar fluxes from analytical solutions of the diffusion equation. Boundary-Layer Meteorol. 50, 355–374.

Sun, Z., Zhao, S., 1995. Community features Tilia Broadleaved Korean Pine Forest on northern slope of Changbai mountain. Chin. J. Ecol. 14 (5), 26–30 (in Chinese).

Sun, Z., Dai, L., Zhang, Y., 1997. Study of diameter breast high structure of the main trees in tilia broadleaved Korean pine forest. Chin. J. Ecol. 16 (1), 19–22 (in Chinese).

Valentini, R., De Angelis, P., Matteucci, G., Monaco, R., Dore, S., Scarascia Mugnozza, G.E., 1996. Seasonal net carbon dioxide exchange of a beech forest with the atmosphere. Global Change Biol. 2, 199–207.

Wang, M., Han, S., Wang, Y., 2004. Important factors controlling rate of soil respiration in forest soil. Chin. J. Ecol. 23 (5), 24–29 (in Chinese).

Wang, M., Ji, L., Li, Q., 2005. Stem respiration of *Pinus koraiensis* in Changbai mountain. Chin. J. Appl. Ecol. 16 (1), 7–13 (in Chinese).

Webb, E.K., Pearman, G.I., Leuning, R., 1980. Correction of flux measurements for density effects due to heat and water vapor transfer. Q. J. R. Meteorol. Soc. 106, 85–100.

Wilczak, J.M., Oncley, S.P., Stage, S.A., 2001. Sonic anemometer tilt correction algorithms. Boundary-Layer Meteorol. 99 (1), 127–150.

Wofsy, S.C., Goulden, M.L., Munger, J.W., Fan, S.M., Bakwin, P.S., Daube, B.C., Bassow, S.L., Bazzaz, F.A., 1993. Net exchange of CO_2 in a midlatitude forest. Science 260, 1314–1317.

Xu, M., Debiase, T.A., Qi, Y., Goldstein, A., Liu, Z., 2001. Respiration in a young ponderosa pine plantation in the Sierra Nevada mountains, California. Tree Physiol. 21, 309–318.

Yang, H., Wang, B., Han, J., 1985. Numerical classification of the Korean pine broad-leaved forest at Changbai mountain. In: Research Station of Changbai Mountain Forest Ecosystem, Chinese Academy of Sciences (Eds.), Research on Forest Ecosystem. Chinese Forestry Press, Beijing, pp. 15–32 (in Chinese).

Yoder, B.J., Ryan, M.G., Waring, R.H., Schoettle, A.W., Kaufmann, M.R., 1994. Evidence of reduced photosynthetic rates in old trees. For. Sci. 40 (3), 513–527.

Zhang, J., Han, S., Yu, G., 2006. Seasonal variation in carbon dioxide exchange over a 200-year-old Chinese broad-leaved Korean pine mixed forest. Agric. For. Meteorol. 137, 150–165.