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Estimate of productivity in ecosystem of the broad-leaved Korean pine mixed forest in Changbai Mountain

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Abstract We measured soil, stem and branch respiration of trees and shrubs, foliage photosynthesis and respiration in ecosystem of the needle and broad-leaved Korean pine forest in Changbai Mountain by LI-6400 CO_2 analysis system. Measurement of forest microclimate was conducted simultaneously and a model was found for the relationship of soil, stem, leaf and climate factors. CO_2 flux of different components in ecosystem of the broad-leaved Korean pine forest was estimated based on vegetation characteristics. The net ecosystem exchange was measured by eddy covariance technique. And we studied the effect of temperature and photosynthetic active radiation on ecosystem CO_2 flux. Through analysis we found that the net ecosystem exchange was affected mainly by soil respiration and leaf photosynthesis. Annual net ecosystem exchange ranged from a minimum of about $-4.671\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ to a maximum of $13.80\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, mean net ecosystem exchange of CO_2 flux was $-2.0\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and $3.9\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in winter and summer respectively (mean value during 24 h). Primary productivity of tree, shrub and herbage contributed about 89.7%, 3.5% and 6.8% to the gross primary productivity of the broad-leaved Korean pine forest respectively. Soil respiration contributed about 69.7% CO_2 to the broad-leaved Korean pine forest ecosystem, comprising about 15.2% from tree leaves and 15.1% from branches. The net ecosystem exchange in growing season and non-growing season contributed 56.8% and 43.2% to the annual CO_2 efflux respectively. The ratio of autotrophic respiration to gross primary productivity (R_a:GPP) was 0.52 (NPP:GPP=0.48). Annual carbon accumulation underground accounted for 52% of the gross primary productivity, and soil respiration contributed 60% to gross primary productivity. The NPP of the needle and broad-leaved Korean pine forest was 769.3 $\text{gC}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$. The net ecosystem exchange of this forest ecosystem (NEE) was 229.51 $\text{gC}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$. The NEE of this forest ecosystem acquired by eddy covariance technique was lower than chamber estimates by 19.8%.

Keywords: carbon balance, eddy covariance technique, primary productivity, net ecosystem exchange of CO_2 flux, the broad-leaved Korean pine forest.

Change in atmospheric CO_2 mostly depends on exchange of carbon fluxes among carbon pools in carbon cycling. Forest is dominant in terrestrial ecosystems, which absorbs a large amount of CO_2 during growth and stores it for a long time. 80% of the carbon stored in terrestrial vegetation is forest biomass[1]. Tree respiration consumed more than 50% of the carbon fixed in photosynthesis[2]. Therefore, forests are important pools in the global carbon cycling[3]. However, there is considerable uncertainty regarding the impact of forests on global carbon budgets[4], because net ecosystem exchange of CO_2 in forest ecosystems depends on the balance of photosynthesis and respiration. Forest ecosystems absorb CO_2 from the atmosphere through photosynthesis and release CO_2 back to the atmosphere through respiration. The net ecosystem exchange of carbon (NEE) is much smaller than photosynthesis or respiration[5]. The change of balance may be due to the climate alteration, since the respiration variation responding to the temperature is an order of magnitude more than photosynthesis in forest ecosystems[6]. Carbon budgets in the forest ecosystems of temperate zone are very important for global carbon cycle. Forest C storage may change into net C source with global warming in the forest ecosystems of temperate zone[7]. However, the change of carbon balance of forest ecosystems is a complicated biological process and affected not only by microclimate factors (such as temperature, moisture and atmospheric CO_2) and soil nutrients, but also by the age of trees, diameter of breast height (DBH) and tree species[8−11].

Currently, microclimate and chamber measurements are used in CO_2 fluxes in forest ecosystems, particularly the eddy covariance method. The eddy covariance method and static chamber-gas chromatography method are applied to the network measurements of CO_2 fluxes in terrestrial ecosystems in China (ChinaFLUX). The eddy covariance method based on the principles of micro-meteorology is used to directly determine the exchanges of substances (such as CO_2 and water vapor) and energy between the land and atmosphere by measuring the change of wind velocity and gas density above land vegetations. It is characterized as rapid responses, unimpairing plant community and continuous measurement of CO_2 fluxes. This technique requires enough large forest floor and certain turbulent conditions, which is impossibly found in forest ecosystems. The absence of strong turbulence and topography-induced air drainage during the night are the two main factors that affect the accuracy of eddy covariance measurements[12,13]. Forest vegetation is a giant heterogenic system, every plant and the organ of them have different ratio of photosynthesis and respiration. The exchange of carbon between forest vegetation carbon pool and forest soil through the withering and decay of leaves shoots roots and fruits etc. The forest soil carbon pool exchanges carbon with the atmosphere through the respiration of soil microbes and the decomposition of soil organic matter. Therefore, it is important to estimate the contribution of different ecosystem components to forest ecosystem carbon exchange. However, integrative studies of CO_2 fluxes of different forest ecosystem components have rarely been reported[11]. Broad-leaved Korean pine forest in Changbai Mountain is a typical temperate vegetation type in north China, which lies in the east tip of northeast forest belt. And the region is sensitive to climate changes[14]. Therefore, monitoring the flux of the needle and broad-leaved Korean pine forest in Changbai Mountain for long time, and estimating the ecosystem carbon storage and exchange accurately may provide basis for the study of carbon revenue and expenditure in forest. And it may be of great importance to the evaluation of carbon balance in globe.

In this study, we used chamber techniques to measure soil-surface CO_2 flux (including root and heterotrophic respiration), stem respiration, CO_2 flux of foliage photosynthesis and respiration. We also quantified the net ecosystem exchange and the contribution of CO_2 flux of each component to the whole ecosystem. The NEE obtained by the eddy covariance method was compared with those observed with chamber measurements.

1 Materials and methods

1.1 Site description

Measurement site was located at the north slope of Changbai Mountain in State Natural Reserve (Antu County, Jilin Province; 42°24′N, 28°06′E) at an altitude of 736 m. The terrain of the site has a slope between 2% and 5%. The mean annual temperature varied between 3.3 and 7.3℃ with July mean temperature ranging from 3.3 to 19.3℃, and January mean temperature from −23.3 to −16.6℃. The site is characterized by a mountain climate with a cool and long winter and a short and rainy summer. The mean annual precipitation is 600—900 mm, 85% of which falling between June and September. Snowfall accounts for 10% of the annual precipitation with snow coverage time 130—150 d. The soil is brown forestry clay-loam soil with pH of 5.3—5.6 (0—10 cm)[15, 16].

The broad-leaved Korean pine forest extends at least 10 km. The stand age was approximately 180 years. The major species include Korean pine (*Pnius koraiensis*), Mongolian Oak (*Quercus mongolica*), Mono maple (*Acer mimo*), Amur linden (*Tilia amurensis*), Mongolian elm (*Ulmus mongolica*), Manshurian ash (*Fraxinus mandshurica*) and Manchurian walnut (*Juglans mandschurica*). This forest is a combination of a variety of species forming the forest shrub layer, which mainly includes sessile-flower acanthopanax (*Acanthopanax sessiliflorus*), many-prickle acanthopanax (*Acanthopanax senticosus*), and the shrub layer coverage was 40%. In this forest Korean pine (*Pnius koraiensis*) is the dominant species and the average diameter at breast height of which was 28.9 cm and the average tree height was 25 m. There are 560 stems per hectare with canopy coverage over 80% in this forest. The shrubs in this study site include Amur Deutzia (*Deutzia amurensis*), Manchurian hazelnut (*Corylus mandshurica*), Amur Honeysuckle (*Lonicera maackii*), Many-prickle Acanthopanax (*Acanthopanax senticosus*), Manchurian Currant (*Ribes mandshuricum*), Ural false spiraea (*Sorbaria sorbifolia*), etc. And the grasses include Sedge (*Carex* spp), brachybotrys (*Brachybotrys paridiformis*), Nettleleaf Meehania (*Meehania urticaefolia*) and bryophytes[17, 18].

1.2 Stand structure

We established two 20 m×20 m sampling plots with 60 m between the plots. A traditional forest inventory was applied to over and under story trees by measuring tree height, diameter at breast height (DBH) for each tree in the plot. And the average DBH of each tree species was calculated based on the inventory. We calculated forest timber volume and leaf mass using the models reported by Xu *et al.*[18]. We randomly selected ten 5 m×5 m subplots (for detailed sampling refer to ref. [18]). As for shrubs, we cut them from the roots and picked branches and leaves and then measured their fresh weights. Then we calculated the biomass of shrubs overground by measuring their water content. To measure herbage biomass, we randomly selected six 2 m × 2 m plots, and the sampling method was the same as for shrubs. Briefly, we cut the herbage from the roots and measured their fresh weight respectively. And then some samples were oven-dried to obtain their water content and the biomass of the herbage per hectare was calculated.

1.3 Leaf area index measurement

We acquired the forest ecosystem leaf area index (LAI) with two methods. We measured every sampling site in cloudy morning every 7 to 15 days from April 1 to October 30 with a LAI-2000 analyzer (Li-Cor, Inc., USA). In the two plots, we set 20 sampling sites every 2 m in southward, and the measurements were all done in the same 20 plots. In another way, we acquired leaf biomass of various trees in forestry ecosystem using the acquired model between DBH and leaf biomass. And using the leaf growth dynamic changing process we calculated the dynamic changes of LAI.

1.4 Microclimate and whole-system CO_2 flux measurements

There was forest meteorologic tower of 62 m height near the sampling plots, microclimate and whole-system CO_2 excahng were measured at the tower. Turbulence and fluctuations of CO_2 were measured at 40 m height with a tri-axial sonic anemometer (model CAST3, Campbell, USA) and a fast response open-path CO_2/H_2O infrared gas analyzer (Li7500, Li-Cor Inc., Lincoln, USA). The initial sampling frequency was 10 Hz and data was transmitted to the data collector (CR10X, Campbell Scientific, USA) to memorize, and 30 min throughput calculation was processed and memorized. In addition, air temperature was measured at seven heights (2.5, 8.0, 22.0, 26.0, 32.0, 50.0 and 60.0 m) with an analyzer (HMP45C, Vaisala, Helsinki, Finland). Photosynthetic active radiation (PAR) was measured at 32 m height with the instrument (LI-190Sb, Li-Cor Inc., USA), and soil temperature was measured in one vertical soil profile (0, 5, 10, 20, 50 and 100 cm) with an apparatus (105T, Campbell, USA). Soil moisture was measured at depth of 5, 20, and 50 cm with TDR probe (CS616_L, Compbell, USA). The initial sampling frequency of all the factors was 2 Hz and the data was collected through a data collector (CR23X and CR10X, Campbell Scientific, USA) and stored the mean every 30 min.

1.5 Soil-surface CO_2 efflux measurements

We selected 10 plots in the two sampling sites randomly. Soil-surface CO_2 efflux was measured with a LI-6400-9 soil chamber. 10-cm diameter PVC collars were inserted into the soil surface to measure soil respiration. The collars were inserted about 2 cm into the soil and kept fixed to avoid disturbance to soil and root respiration during measurements. Fixed collars were left in place for at least 24 h before the first measurement. The data were collected and stored by a Li-Cor-6400 (Li-Cor, Inc., USA) portable photosynthesis system. Soil temperature was measured at a depth of 0, 5, 10 cm with an attached temperature probe. We decreased the chamber CO_2 concentration to under the atmosphere. Five observations were recorded per measurement. Soil surface CO_2 efflux was measured from January 2003 to December 2003, and it took 7 to 10 days to complete one measurement.

1.6 Foliage respiration and photosynthesis measurement

Foliage respiration and photosynthesis rates were measured from May through September at each plot. Branches were collected from low, mid and high positions in the canopy at predawn. The branches were wrapped with a moistened towel and transported to a laboratory immediately. The branches were inserted into a barrel and placed in the dark. All measurements were made within 6 h of branch harvest. Foliage respiration was measured at a controlled temperature (5℃－25℃) and with a LI-6400 CO_2 analysis system. And a model between foliage respiration and temperature was established. The herbage leaf photosynthesis rates were measured using the static chamber-gas chromatography method. The chambers of 50 cm×50 cm in basal area and 50 cm in height were covered on the plots randomly, six repeats were made. Light intensity in chamber was controlled by different towels and the rate of foliage respiration and photosynthesis were measured. All living plants inside big chamber were cut to obtain herbage fresh weight. Leaves were dried at 85℃ for 48 h. Unit area herbage leaf CO_2 efflux was calculated based on water content.

1.7 Stem respiration measurement

At the beginning of March 2003, stem CO_2 efflux was measured with a LI-6400-09 soil respiration chamber[19]. Soil respiration chamber was attached to the surface of stem through a polyvinyl chloride (PVC, 10.1 cm internal diameter) collar. PVC collar was fixed to the stem at 1.3 m height using 100% silicone sealant. A short PVC pipe of 10.1 cm diameter was cut perpendicularly to make a PVC connect collar and fix on the surface of stem. The PVC collar matched the curvature of the stem on the one end and the pipe was cut flat on the other end. Both ends of the PVC pipe should be very smooth. After 24 h fastening to the stem, soil chamber was mounted horizontally to couple with the collar and the system was used to measure stem respiration. In order to reduce the edge effects we used thin PVC pipe (<3 mm) and less sealant. Measurement was performed every 7 to 11 days from March to November 2003.

In order to measure soil respiration rate with a LI-6400-09 soil respiration chamber, the distance between the far front of the chamber and soil surface, and soil surface area should be measured. The effective insertion depth was calculated according to the volume of the stem-mounted collars and the surface area for the stem within the PVC collar. The area of stem inside PVC collar was soil respiration area. The area of stem inside PVC collar was curved into trunk shape, and then it was marked and cut. The area was measured by a Li-Cor 3000 leaf area measurement (Li-Cor, Inc., USA). The volume of collar was measured by sealing the mouth of PVC collar with wrap and filling the chamber with water through a hole (sealed after test) on the top of the collar using a graduated cylinder. The volume of water input was the volume of PVC collar. The effective distance from soil respiration chamber to the stem (effective insertion depth during measurement of soil respiration).

$$h= (V-(D/2)^2\pi d)/(D/2)^2\pi, \qquad (1)$$

where h is the effective insertion depth, V is the volume of PVC collar, D is the diameter of PVC collar, d is the depth of respiration chamber inserted into PVC collar. We drilled a hole at about 5 cm below the collar to a depth corresponding to 1cm into the sapwood past cambium. This opening allowed insertion of a soil temperature probe to measure the temperature of the stem.

1.8 Biomass analysis

According to the relation of DBH and stem and foliage biomass of the major tree species in the broad-leaved Korean pine forest in Changbai Mountain reported by Xu *et al.*[18] (Table 1), the timber volume of the stand woods was calculated by using factorial method and the weight was calculated by volume density method. As for branch and foliage biomass, they estimated branch, leaf biomass-diameter at base curves, and calculated the total above-ground biomass of each tree species.

1.9 Estimate of productivity of forest ecosystem

The net primary productivity (NPP, also called net primacy production) at cellular level means the carbon fixed by photosynthesis (gross primary productivity, GPP) subtracts carbon released by plant respiration (R_a) (NPP = GPP−R_a). It was expressed as the energy or dry substances accumulated by plants in unit area and unit time. Net carbon exchange of ecosystem (NEE) refers to that net primary production subtracts loss of carbon by heterotrophic respiration (R_h). Net carbon exchange of ecosystem (NEE) can be used to depict gas exchange at different scales. In system undisturbed by nature or human, NBE=NEE. The relation of each organ of main tree species in broad-leaved Korea pine forest and tree DBHs was cited from the data Xu *et al.*[18] reported (Table 1). An empirical equation was used to calculate the aboveground biomass of each tree species. Net increment of forest biomass was the sum of stem, branch, root and foliage biomass. The former year DBH value was calculated according to the growth ring data, and then the former annual biomass was calculated using the empirical equation. The net increment of biomass was the difference of the two years, and the aboveground net primary production was obtained by calculating carbon density (0.5 tC/t)[20]. The underground biomass was calculated according to the ratio of aboveground and underground biomasses reported by Xu *et al.*[18]. The production of fallen leaves, underground and understory trees as well as herbage was cited from the data previously reported [18].

2 Results

2.1 Environmental factors

Fig. 1(a) showed the change of forest atmosphere and soil (10 cm) temperature. Although the atmosphere temperature change was drastic, the atmosphere and soil temperature alteration was similar. This was due to the higher heat capacity of the soil [13]. Fig. 1(b) showed the annual variation of the photosynthetic active radiation. The annual photosynthetic active radiation was symmetric bell-shaped. The photosynthetic active radiation increased gradually from winter, and it began to decrease from late April until late July. It was rainy in May, June and July in Changbai Mountain and the photosynthetic active radiation was low.

2.2 Soil respiration

The relation of soil CO_2 efflux and soil temperature at 10 cm of depth was obtained by LI 6400-9 soil respiration chamber and was shown in Fig. 2, and annual trends of soil CO_2 efflux was shown in Fig. 3. Soil surface CO_2 efflux includes soil heterotrophic respiration, root respiration and fallen leaves respira-

Table 1 The relation of DBH and different organ biomasses in broad-leaved Korean pine forest[18]

Tree species	Stem biomass	Branch biomass	The former year branch	Foliage biomass	The former year foliage biomass
Korean pine *Pinus koriaensis*	W=0.0417DBH$^{2.579}$	W=0.0178DBH$^{2.417}$		W=3.7×10^{-3} DBH$^{2.282}$	W=3.7×10^{-3} DBH$^{2.207}$
Mongolian Oak *Quercus mongolic*	W=0.0179DBH$^{2.857}$	W=1.97×10^{-3} DBH$^{4.292}$	W=1.34 ×10^{-6}DBH$^{4.08}$		W=3.66×10^{-5}DBH$^{3.49}$
Manshurian ash *Fraxinus mandshurica*	W=1.416DBH$^{1.71}$	W=1.154SDBH$^{1.549}$	W=1.4×10^{-5}DBH$^{3.547}$		W=0.7655DBH$^{0.886}$
Amur Linden *Tilia amurensis*	W=0.098DBH$^{2.353}$	W=2.87×10^{-3} DBH$^{2.99}$	W=9.23×10^{-5}DBH$^{2.88}$		W=0.469DBH$^{0.714}$

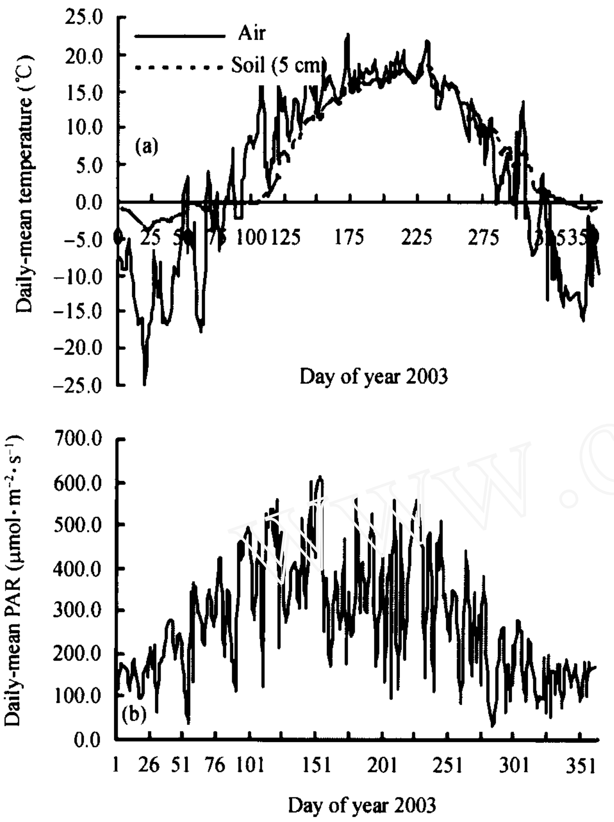

Fig. 1. Changes of soil (10 cm) temperature, atmosphere temperature (1.5 m) (a), and average daily photosynthetic active radiation in the broad-leaved Korean pine forest (b).

tion, and the ratio of root respiration to soil respiration (40%) was cited from Liu's[21]. Fallen leaves respiration contributes 28% to soil surface CO_2 efflux[22]. Our study showed that soil CO_2 efflux in the needle- and broad-leaved Korean pine forest had obvious seasonal variation (Fig. 3). Soil CO_2 efflux had only one peak and varied from 0.6 $\mu mol\cdot m^{-2}\cdot s^{-1}$ to 6.5 $\mu mol\cdot m^{-2}\cdot s^{-1}$. Soil CO_2 efflux was the lowest in January and February, and the change was not significant. The peak value appeared around day 210—234 in summer, and then declined rapidly. There was little variation after the first ten days of November. The phenomenon appeared because during winter the forest in Changbai Mountain was in dormancy. The soil temperature changed unobvious below ground (at 10 cm) and hardly below 0℃, though the air temperature in forest varied dramatically[23]. After the snow melted in early spring. soil temperature went up rapidly and soil CO_2 efflux rate varied greatly[22].

2.3 Stem respiration

The stem and branch respiration rates per hectare was calculated by using the relation of stem respiration and temperature for the main tree species in the needle and broad-leaved Korean pine forest (Fig. 4). Fig. 5 showed seasonal variation of stem and shrub branch respiration rates of the forest ecosystem. The variation trends of stem and branch respiration rates were significantly ranging from 0.15 to 1.4 $\mu mol\cdot m^{-2}\cdot s^{-1}$, which were consistent with those in shrub branch. During the whole year of 2003, shrub branch respiration ranged from 0.02 to 0.22 $\mu mol\cdot m^{-2}\cdot s^{-1}$. The annual variation of stem respiration was symmetric, the minimum occurred in January and February and the maximum in July and August. The stem respiration rate increased rapidly in early April, peaked in July and declined in mid-September, which varied similarly with soil respiration, for both of them changed with air temperature.

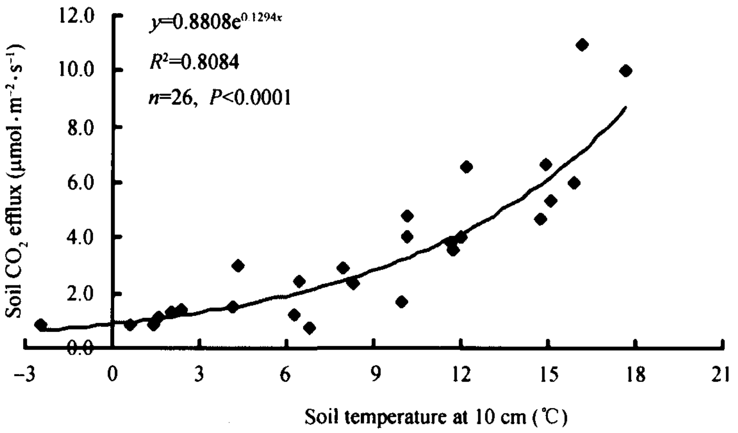

Fig. 2. Relationship between soil respiration CO_2 efflux and soil (10 cm) temperature in broad-leaved Korean pine forest ecosystem.

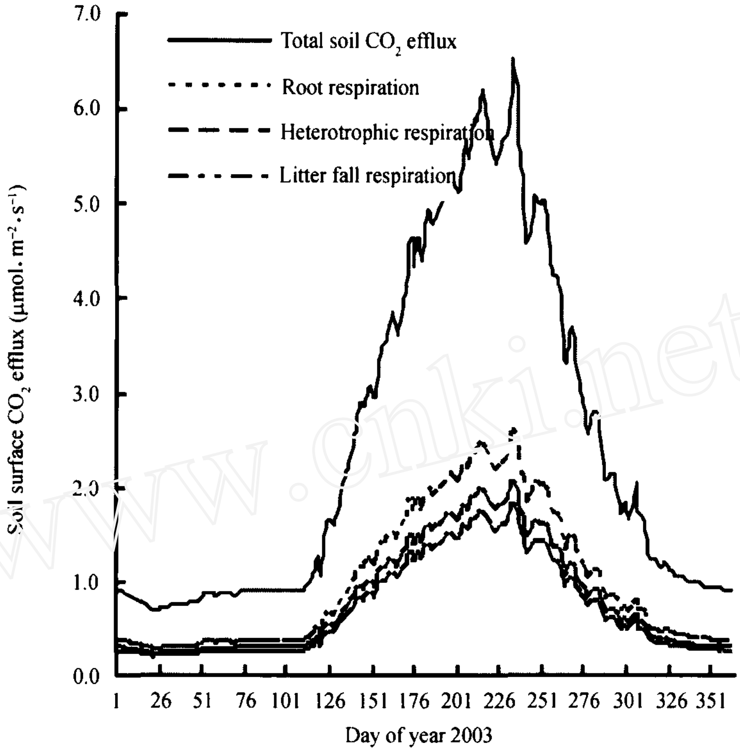

Fig. 3. Seasonal changes of soil surface CO_2 efflux, root and soil heterogenic respiration in broad-leaved Korean pine forest.

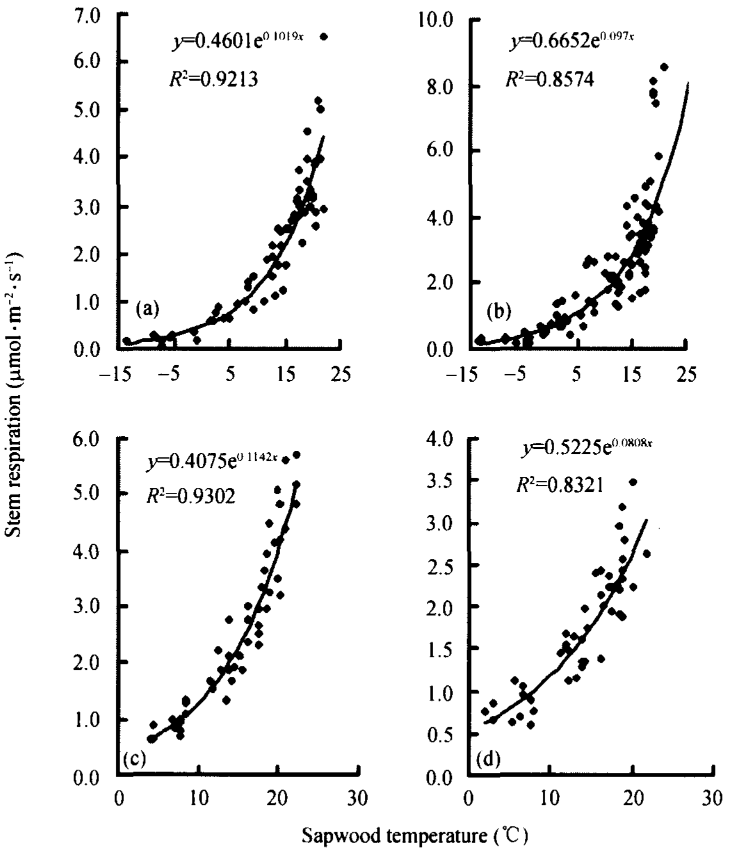

Fig. 4. The relation of temperature and the major tree species stem respiration in broad-leaved Korean pine forest. (a) Korea pine; (b) Mongolian Oak; (c) Manshurian ash; (d) Amur linden.

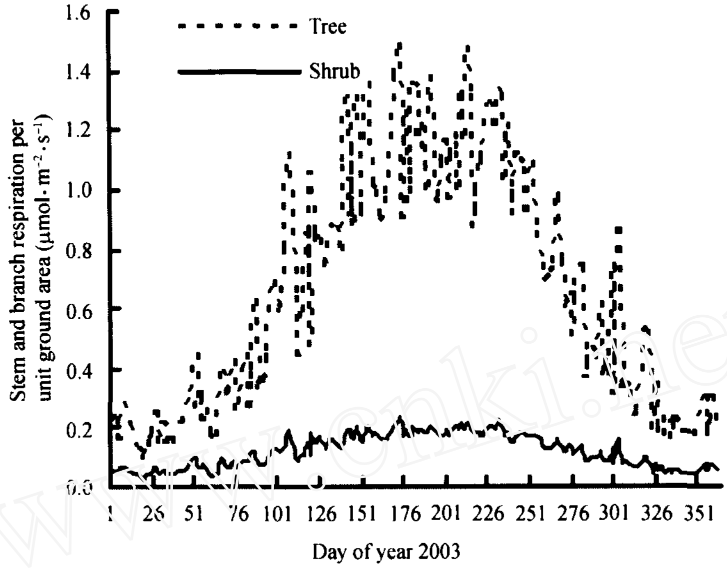

Fig. 5. Seasonal variation of wood and shrub stem respiration per area in broad-leaved Korean pine forest.

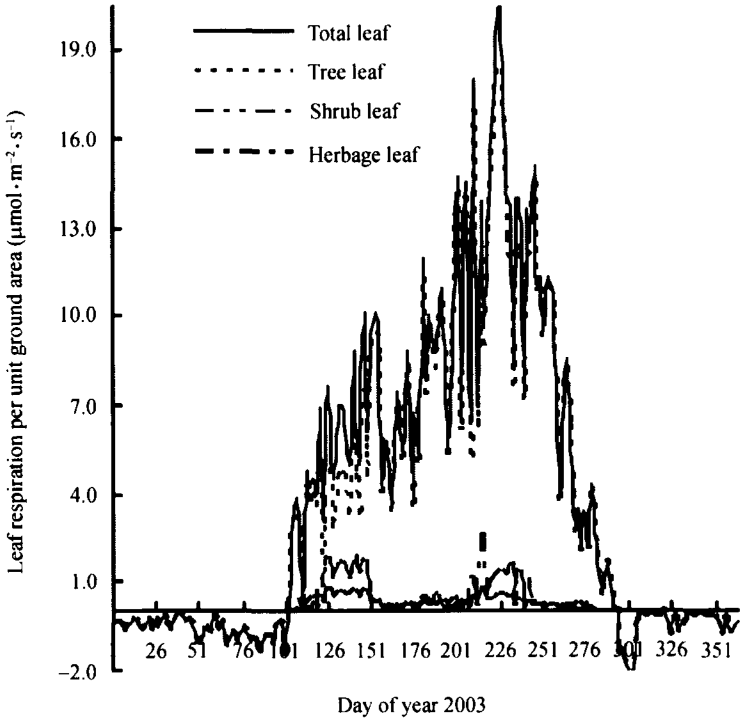

Fig. 6. Seasonal trend in foliage CO_2 exchange per unit ground area in the broad-leaved Korean pine forest ecosystem (wood, shrub and herbage).

2.4 *Leaf respiration and photosynthesis*

Fig. 6 presented mean foliage photosynthetic rate in 24 hours in tree, shrub and herbage in the forest in 2003. Although leaf photosynthesis was driven by effective radiation of photosynthesis inside forests during the growing season, the nocturnal foliage respiration was mainly driven by air temperature[19]. Additionally, leaf area index varied during the growing season and leaf photosynthetic rate was in asymmetric bell-shape. Leaf photosynthetic rate in trees was 0.7 μmol·m^{-2}·s^{-1} in early May and increased to 18.4 μmol·m^{-2}·s^{-1}in mid-August, followed by a rapid decrease to 7.1 μmol·m^{-2}·s^{-1} in late August. Needle respiration rates in Korean pine were from −0.1 to 1.51 μmol·m^{-2}·s^{-1} in winter.

Leaf photosynthetic rates in shrub and herbage were different from those in trees. There were two peaks in May and early August. This phenomenon has close relation to the climate. Shrub and herbage leaf expanding was earlier than tree leaf expanding, and understory photosynthetic radiation was sufficient in early May, thus the photosynthesis of understory shrub and herbage was strong. It is rainy and with low photosynthetic active radiation in June and July in Changbai Mountain (Fig. 1) and CO_2 absorbance was low[24], which was the reason for two peaks of foliage photosynthesis in shrub and herbage (Fig. 6). The two peaks were 0.88 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and 0.87 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in shrub and 1.90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and 2.64 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in herbage, respectively. The total foliage photosynthesis in the forest comprised those in trees, shrubs and herbage and its maximum was 20.4 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in middle August. The annual mean foliage respiration in trees, shrubs and herbage accounted for 89.9%, 3.4% and 6.7% of total foliage photosynthesis in the forest ecosystem.

CO_2 efflux in the needle and broad-leaved Korean pine forest ecosystem includes soil respiration, stem respiration and foliage respiration and photosynthesis in the ecosystem. Fig.7 demonstrated the seasonal variation of ecosystem CO_2 efflux in 2003, which was asymmetric with two peaks. The two peaks of 6.3 $\mu mol \cdot m^{-2} \cdot s^{-1}$and 13.8 $\mu mol \cdot m^{-2} \cdot s^{-1}$ occurring on day 147 and day 227 were due to rainy June and July. Annually it ranged from –4.671 to 13.80 $\mu mol \cdot m^{-2} \cdot s^{-1}$. During winter and summer the average ecosystem CO_2 efflux was –2.0 and 3.9 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively.

Fig. 8 showed the relative contribution of woody tissue (stem and branch), foliage and soil CO_2 efflux to the total ecosystem CO_2 efflux. The net CO_2 exchange of growth and non-growth seasons accounted for 56.8% and 43.2% of annual CO_2 efflux. Soil respiration was dominant in forest ecosystem, which accounted for 69.7% of the total ecosystem CO_2 efflux. Foliage and branch respiration accounted for 15.2% and 15.1% of the total ecosystem respiration, respectively.

2.5 *Ecosystem CO_2 efflux estimate*

The amount of carbon accumulated underground in the needle and broad-leaved Korean pine forest ecosystem was soil respiration from which falling leaves were subtracted[25], and the value was 841.98 $gC \cdot m^{-2} \cdot a^{-1}$ (Table 2). The underground biomass accounted for 0.87 of soil respiration in the whole year. Assume that plant roots consumed 50% of the carbon accumulated underground during growth, then the root respiration CO_2 efflux was 424.2 $gC \cdot m^{-2} \cdot a^{-1}$ which contributed 44% of soil respiration[21], and accounted for 31% of ecosystem CO_2 efflux.

The gross primary production (GPP) of the needle and broad-leaved Korean pine forest was the total sum of system photosynthesis (1612.74 $gC \cdot m^{-2} \cdot a^{-1}$) (Table 2). The annual primary production of trees, shrubs and herbage accounted for 89.7%, 3.5% and 6.8% of the gross primary production of the needle- and broad-leaved Korean pine forest. The sum of system autotrophic respiration (foliage respiration, branch respiration and root respiration) was 843.4 $gC \cdot m^{-2} \cdot a^{-1}$ (Table 2), and the ratio of autotrophic respiration to gross primary production (R_a:GPP) was 0.52 (NPP:GPP=0.48). The amount of annual accumulation of carbon underground accounted for 0.52 of gross primary production, and the ratio of soil respiration to gross primary production was 0.60. Annual carbon accumulation of the needle and broad-leaved Korean pine forest ecosystem was 856.2 $gC \cdot m^{-2} \cdot a^{-1}$ and the NEE was 229.51 $gC \cdot m^{-2} \cdot a^{-1}$ (Table 2).

2.6 *Chamber-eddy flux comparison*

Fig.9 depicted eddy covariance flux versus chamber-based estimates of seasonal variation of net ecosystem CO_2 exchange in the needle and broad-leaved Korean pine forest. The peak of net ecosystem exchange in summer was 5.48 $\mu mol \cdot m^{-2} \cdot s^{-1}$ from day 181 to day 193 and in winter it was the lowest ranging from 0.35 to 1.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ from eddy covariance measurements. Chamber-based estimates of the net ecosystem exchange were significantly higher than eddy covariance flux estimates. During growing season it was averagely 2.4 $\mu mol \cdot m^{-2} \cdot s^{-1}$ from eddy covariance measurements and 3.8 $\mu mol \cdot m^{-2} \cdot s^{-1}$ from chamber-based estimates of the net ecosystem exchange. The seasonal variation trends were consistent, the maximum of the net ecosystem exchange was in summer, absorbing atmospheric CO_2 and the minimum appeared in winter. But the change in flux with

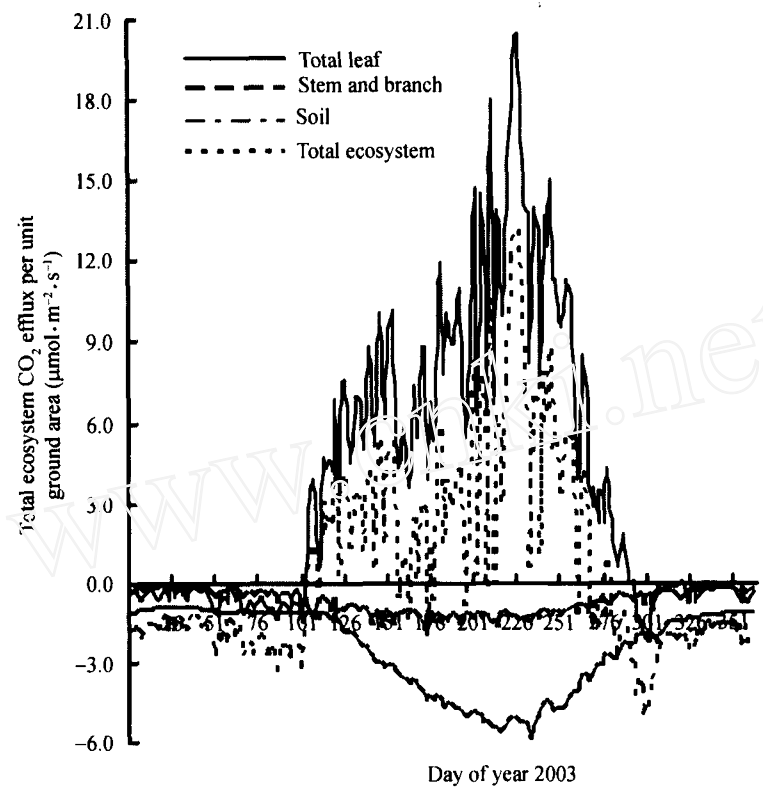

Fig. 7. Seasonal change of different components CO$_2$ efflux in the broad-leaved Korean pine forest ecosystem.

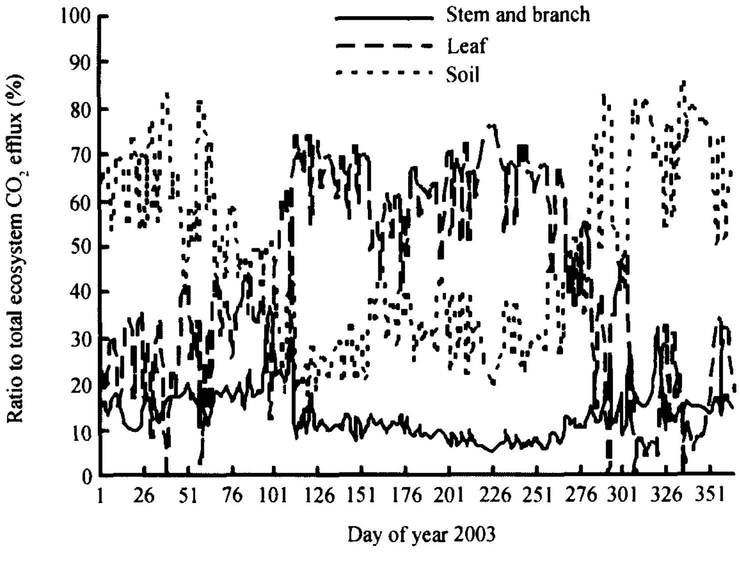

Fig. 8. The influence of different components on system CO$_2$ efflux in the broad-leaved Korean pine forest ecosystem.

season was much greater for the chamber-based estimates than eddy covariance measurements. A linear regression analysis between the chamber-based and eddy covariance measurements was significant ($P<$ 0.01 *t*-test). The sum of daily NEE was the net ecosystem exchange of CO$_2$. The total NEE for whole year from chamber-based estimates (229.51 gC·m^{-2}·a^{-1}) was 19.8% higher than that from eddy covariance measurements (184 gC·m^{-2}·a^{-1}). The NEE for growing season from chamber-based estimates was 48% higher than that from eddy covariance measurements. The ecosystem CO$_2$ efflux for whole year from chamber-based estimates was 58% higher than that from eddy covariance measurements.

Table 2 Different components biomass (gC·m^{-2}), respiration (gC·m^{-2}) and net primary production (NPP, gC·m^{-2}·a^{-1}) in the broad-leaved Korean pine forest ecosystem

Component	gC·m^{-2}
Biomass:	
Foliage biomass	417
Branch biomass	15696
Gross biomass aboveground	16113
Annual fallen leaves	122
Respiration:	
Annual leaf respiration	210.41
Annual stem respiration	208.84
Annual soil respiration	963.98
Annual ecosystem respiration	1383.23
Growth:	
Annual leaf growth	225.99
Annual aboveground growth	513.32
Annual net primary production ANPP	541.31
Annual underground carbon accumulation (soil respiration and fallen leaves)	841.98
Annual underground carbon accumulation: GPP	0.52
Annual underground carbon accumulation: soil respiration	0.87
Underground NPP: NPP	0.33
NPP:GPP	0.48
NEE	229.51
NEE[26]	184
NPP	769.3
NPP[27]	945.13

3 Discussion

In our study, it is considered that chamber-based estimates of component CO_2 efflux in forest ecosystem and measurements of related environmental factors and biological elements may be used in the estimates of net CO_2 exchange in forest ecosystem-atmosphere, which based on understanding of CO_2 exchange process and estimates of CO_2 fluxes in forest ecosystems in Changbai Mountain as well as comparison of chamber-eddy covariance flux.

We observed the significant differences in component CO_2 efflux in the needle and broad-leaved Korean pine forest (tree, shrub, herbage and soil) that may occur in space and time. Our results indicated that soil respiration was dominant in CO_2 efflux of forest ecosystem, which accounted for 69.7% of the total ecosystem CO_2 efflux and foliage CO_2 efflux and branch CO_2 efflux accounted for 15.2% and 15.1% of the total ecosystem CO_2 efflux, respectively. It was consistent with the results from Xu *et al.*[13] and Bolstad *et al.*[11] in the northern hard broad-leaved forest and was lower than those previously reported by Law *et al.*[25] in temperate ponderosa pine (76%). The stem respiration rates in our study were higher than those from Law *et al.* [25] and Xu *et al.* [13] in ponderosa pine forest, which was due to the high stem volume (478 m^3/ha) of needle- and broad-leaved Korean pine forest in Changbai Mountain. Lavigne *et al.* [28] reported that different age needle and broad-leaved forest soil respiration accounted for 48%—71% of ecosystem CO_2 efflux, and foliage respiration and stem respiration accounted for 25%—43% and 5%—5% of ecosystem CO_2 efflux, respectively. Soil respiration accounted for 68% of the total ecosystem respiration in North American hard broad-leaved forest, and foliage respiration and stem respiration accounted for 27% and 5%, respectively [29]. Our data were near those reported by them. The foliage respiration was higher than branch respiration, which indicated that the plants used up large amounts of fixed organic carbon from photosynthesis to maintain growth and development [30]. CO_2 fixed by photosynthesis and those decomposed through respiration in the ecosystem of needle and broad-leaved Korean pine forest accounted for 53.8% and 46.2% of total ecosystem CO_2 efflux in the whole year. The autotrophic respiration in the needle and broad-leaved Korean pine forest ecosystem accounted for 39.4% of primary production.

NPP:GPP reflected the efficiency of carbon fixed by ecosystem photosynthesis transformed to plant tissues. The NPP:GPP value of the broad-leaved Korean pine forest was in the range of NPP: GPP value of the needle-leaved pine forest (0.4—0.5) reported by Williams *et al.*[31]. But it was higher than the value of needle- and broad-leaved forest (0.23—0.36) reported by Ryan *et al.*[32]. As for the temperate forest ecosystem the NPP/GPP value ranged from 0.3 to 0.7[25,32,33].

Soil-surface CO_2 efflux was derived from metabolic activities of plant roots and microbial activity, and organic carbon and soil carbon determined the amount of respiration substrate. And soil physiochemical and meteorogical factors affect soil respiration process[34]. In the broad-leaved Korean pine forest, soil-surface CO_2 efflux ranged from 0.9 to 5.9 μmol·m^{-2}·s^{-1}, which was high compared with 0.5—3.7 μmol·m^{-2}·s^{-1} for Oregon forest soil respiration in North America[25] and

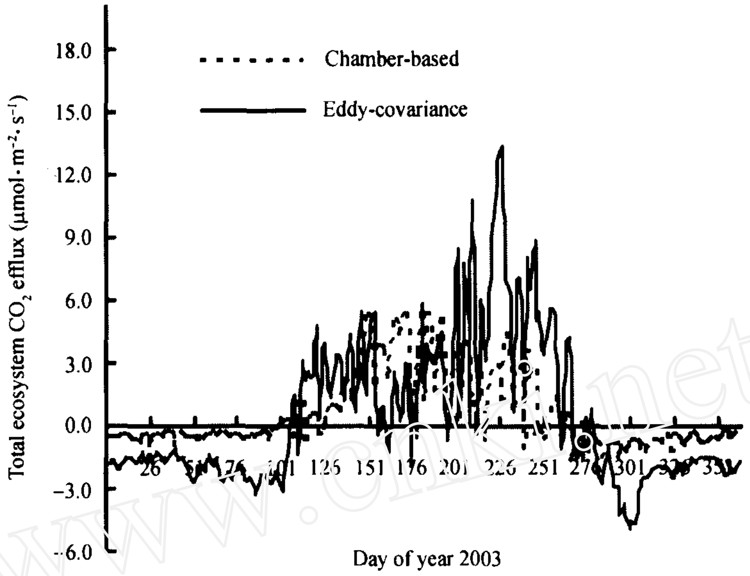

Fig. 9. Eddy covariance flux versus chamber-based estimates of NEE in the broad-leaved Korean pine forest ecosystem.

0.4—4.0 μmol·m^{-2}·s^{-1} for beech forest in France[35], since soil carbon and nitrogen content was higher in the broad-leaved Korean pine mixed forest than the above-mentioned two forests. Soil respiration in our study was consistent with those (2.5 — 5.4 μmol·m^{-2}·s^{-1}) previously reported for summer ponderosa pine forest by Xu *et al.* [13]. And the needle- and broad-leaved Korean pine forest soil respiration (963.98 gC·m^{-2}·a^{-1}) was low compared with the temperate broad-leaved forest in Korea (1070—1246 gC·m^{-2}·a^{-1})[36]. Our estimates of soil-surface CO_2 efflux was in the range of those for northern deciduous forests[11] and for ponderosa pine[5].

Exponential curve fitting between soil respiration and soil temperature was shown in Fig. 1, which was similar to those reported by other studies[37]. A linear relationship between soil respiration and soil temperature in Wiscosin hard broad-leaved forests was found by Bolstad *et al.* [11]. This may be due to that the alteration of soil temperature was consistent with the alteration of water content in Wiscosin hard broad-leaved forests, but it was opposite in most temperate forests[37], for example soil respiration was controlled by low water content other than soil temperature in early summer and late autumn in Changbai Mountain[38]. In addition, the linear response of soil respiration to soil temperature can be affected by sampling size and quantity. The sensitivity of soil respiration to soil temperature may be decreased with larger sampling size or more sampling sites[39], particular when using the small-area Li-Cor 6400-9 soil chamber.

Globally, soil respiration was 1.24 times of the net primary production of different plant species[40]. In our result, soil respiration was 1.25 times of the net primary production of the needle- and broad-leaved Korean pine forest. Our data were obviously lower than Law *et al* reported (1.65)[25]. The reason was that the broad leaved-Korean pine mixed forest in Changbai Mountain was mature forest and there were many fallen woods in it. The fallen woods respiration was neglected in our research. Therefore, in our future research we should investigate the contribution of roots and fallen woods to soil respiration.

We used soil chamber of Li-Cor 6400-9 to measure wood respiration and calculated stem respiration per unit area forest from timber volume and surface area. Stem respiration acquired by this method may be underestimated because DBHs were over 15 cm and branch respiration was higher in the small branches than those in the bigger ones[13, 19]. Therefore, stem respiration in the needle- and broad-leaved Korean pine forest may be underestimated. On the other hand, scaling up based on place and direction will estimate different surface CO_2 efflux. It was higher in the south than in the north[19, 22], and higher on the top than on the bottom[41]. We measured stem respiration at different DBHs on the side of north-south. And these caused the uncertainty of estimate of stem respiration in forest ecosystem. Stem respiration was different among different forest species and ages as well site conditions[42]. We acknowledge that in our studies and we measured stem surface respiration of different DBH only, and differences of tree species and proportional change on surface have not been investigated in details, which may has a little influence on the estimates of total forest ecosystem net CO_2 exchange since stem respiration was a small component of total ecosystem respiration. Future studies are required to develop a more accurate stem respiration measurement method.

The primary production of the needle- and broad-leaved Korean pine forest in Changbai Mountain was 1612.7 $gC\cdot m^{-2}\cdot a^{-1}$. Law *et al.*[25] reported that the primary production of the North American needle-leaved forest was 901 $gC\cdot m^{-2}\cdot a^{-1}$. Ryan *et al.*[32] investigated the primary production of the needle-leaved forest in 4 different sites, and their primary production was 772—1090 $gC\cdot m^{-2}\cdot a^{-1}$, respectively. The primary production of the needle- and broad-leaved Korean pine forest was higher than theirs, because the accumulation of the needle- and broad-leaved Korean pine forest in Changbai Mountain was large, and foliage biomass was much larger than the previously reported. The main uncertainty in our results resulted in the value of NPP∶GPP and Ra∶GPP, because the root biomass and respiration in forest ecosystem were uncertain. Law *et al.*[25] reported that NPP∶GPP of the needle-leaved forest was 0.45. Ryan *et al.*[32] reported NPP∶GPP of several needle- and broad-leaved forests was smaller than 0.5. Ours was 0.48.

The net ecosystem exchange in the needle and broad-leaved Korean pine forest was consistent with other respiration data obtained by chamber and eddy covariance measurements. And the estimates of chamber-based flux exceeded eddy covariance measurements[11, 29, 42]. The summed component CO_2 efflux estimating the net ecosystem exchange using chamber-based flux was often more than eddy covariance measurements[29]. Eddy covariance measurement is the method to obtain turbulence flux by calculating the covariance of pulsing and wind velocity. The measured turbulent flux density is not equal to the net ecosystem exchange if loss of horizontal advection or storage under the height of eddy covariance sensor occurred in the forest[43]. This error will happen especially in night when air cannot be fully mixed by turbulence, storage of CO_2 in air layer and soil cannot be correctly measured, and loss of CO_2 caused by drainage[29], which led to systemic bias of nocturnal CO_2 flux[44], and summed component CO_2 efflux using chamber-based flux was at abnormal level. The corrected eddy flux (including corrections of tilt, frequency response and horizon advection) was still 58% less than the accumulated NEE measured with chamber method. which was consistent with those for ponderosa pine forest (50%) of Law *et al.*[25] and was lower than those of Goulden *et al.*[29] and Lavigne *et al.*[28] (20%—40%). The lower net ecosystem exchange obtained by eddy covariance measurements compared to chamber-based ecosystem CO_2 flux maybe came from ecosystem soil respiration[11] which accounted for about 70% of total ecosystem CO_2 exchange. The shortage of spatial variation in sampling and uncertainties in chamber effect were questionable[45]. Using the chamber incorrectly may disturb soil environment, change the microclimate in study site and affect soil respiration flux[44—46]. Further studies in soil respiration with an increasing sampling size and quantity and eddy covariance measurements for soil respiration are required.

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