Tellus (1999), 51B, 402–413
Printed in UK – all rights reserved

TELLUS
ISSN 0280–6495

Seasonal and inter-annual variation of CO_2 flux between a temperate forest and the atmosphere in Japan

By SUSUMU YAMAMOTO*, SHOHEI MURAYAMA, NOBUKO SAIGUSA and HIROAKI KONDO, *Environmental Assessment Department, National Institute for Resources and Environment, AIST, MITI, Onogawa 16–3, Tsukuba, Ibaraki 305-8569, Japan*

(Manuscript received 19 December 1997; in final form 9 November 1998)

ABSTRACT

The objective of this research is to elucidate the seasonal and inter-annual variations of CO_2 exchanges between the atmosphere and a temperate deciduous forest in Japan and to elucidate their relation to meteorological conditions. The uptake rates of CO_2 from October 1993 to December 1996 were estimated from field measurements of CO_2 concentrations and meteorological conditions using a tower. Net of uptake rate of CO_2 was positive (uptake by forest ecosystems) from June to September and negative (release to the air) from October to April. Averages of integrated uptake rates of CO_2 were 840, −450 and 390 gCO_2/m^2/year (2.3, −1.2 and 1.1 tC/ha/year) for daytime, night and whole day (net), but they had notable inter-annual variation due to the differences of averaged insolation and temperature each summer of 1994 to 1996. The errors of CO_2 flux due to topographical conditions were investigated through comparison with heat budgets. CO_2 uptake rate estimated by tower measurement might be underestimation of 40%, therefore, above net-uptake value, 1.1 tC/ha/year became 1.8. This value of uptake rate was smaller than the results obtained in other temperate deciduous forests. The causes of this are partially in the difference of the height of the site and the short active period of the present forest. According to the CO_2 flux measurements in several forests including the present one, the forest ecosystems could be a large sink of CO_2, however, more data of the CO_2 flux is needed at the various forests and latitudes to reduce the uncertainty of estimation of CO_2 uptake on a global scale.

1. Introduction

Carbon dioxide, a very important greenhouse gas, is contributing approximately 55% to global warming. Our knowledge of the sources and sinks of carbon on a global scale is not sufficient. The biosphere, in particular, forest ecosystems may be major sinks of carbon dioxide. However, recent estimations of carbon flux in the terrestrial biosphere have a high degree of uncertainty in magnitude (Keeling et al. (1992), Dixon et al. (1994), IPCC (1995)).

* Corresponding author.
E-mail: yamas@nire.go.jp

CO_2 uptake was estimated by Wofsy et al. (1993) using continuous measurements of CO_2 flux longer than one year in a deciduous forest in central Massachusetts, USA. After this, the seasonal variations of flux and uptake of CO_2 in various forests at the different latitudes were investigated, e.g., by Greco et al. (1996), Valentini et al. (1996), Grace et al. (1996), Black et al. (1996) and Malhi et al. (1997). According to their results, the uptake rates of CO_2 by the forests had large variety. Therefore, we need more investigation on CO_2 uptake to consider the rôle of the forests in CO_2 budgets on a global scale. Baldocchi et al. (1996) proposed strategies for measuring and modeling of CO_2 and H_2O fluxes over forests, and the establishment of a network of the long-term measurements of fluxes using towers.

The objective of the present research is to elucidate the seasonal and inter-annual variations in CO_2 exchange between the atmosphere and a temperate deciduous forest in Japan and to investigate their relationship to meteorological conditions. The uptake rates of CO_2 from October 1993 to December 1996 were estimated from field measurements of the gradient of CO_2 concentrations and meteorological conditions at a tower set up in a temperate deciduous forest in Japan.

2. Site and measurements

The measurements of the atmospheric concentration of CO_2 and meteorological conditions using a tower (height = 27 m) in a temperate forest were started in October 1993. The tower was set in the middle of Japan (36 08′ N, 137 25′ E) as shown in Fig. 1a. The tower was situated on one of the hills about 15 km east from Takayama City and the elevation of the site was about 1420 m above sea level. Fig. 1b shows the topographical condition of the surrounding of the tower. The undulation of the surrounding area in a radius of 500 m is about 100 m. The inclinations of the slopes are about 1/10 (6°) and 1/5 (12°) for the prevailing wind directions; SW and NE, respectively. The topographical effects of wind should be considered in the estimation of the flux. The fetch length of this deciduous forest varies from 500 m to 1 km with wind direction. The dotted lines in the Fig. 1b indicate roads near the site. The traffic amount was small and negligible.

The annual mean temperature was about 7.3°C and the monthly averaged temperature reached 20°C in August and −4.8°C in January. The ground surface was covered with snow from December to April (maximum snow depth was from 1.5 to 2 m). Most prevailing wind directions were west to south-west in the daytime and east to north-east in the night, during May to November, and north to west during December to April. In the daytime during summer, upward wind from the valley to the mountain developed.

The main species of trees in the site were deciduous broad-leaf trees such as birch (*Betula ermanii, Betula platyphylla*) and oak (*Quercus mongolica*), and the average height of the trees (canopy height) was about 17 m. This is a protected forest, therefore human disturbances should be few during the past 40 years. This site was covered by snow from December to April, and the beginning of June was the budding time and the beginning of October was the deciduous period of leaves. The seasonal variation of leaf and stem area index (LAI) measured by canopy analyzer (LI-COR) is shown in Fig. 2. The ground surface was covered by short bamboo grass. LAI of this forest was about 3.5 from the end of June to the end of September.

The observational items of routine and long-term are listed in Table 1. Mean values of CO_2 concentration at 4 different heights of the tower as shown in Table 1 were measured by an NDIR gas analyzer (Beckman Model 880). The CO_2 analyzer was calibrated by introducing 4 standard gases of 320 to 430 ppmv in dry air, and water vapor in sample air was removed before analysis. The estimated precision of this system was better than 0.1 ppmv. Assuming the typical difference of wind speed between 26 m and 10 m, 2 m/s and difference of CO_2 concentration between 18 and 27 m, 0.1 ppmv, the CO_2 flux estimated by the gradient method is 0.072 $gCO_2/m^2/h$ (0.45 $\mu mol/m^2/s$). This precision of the CO_2 measurement is sufficient for the present calculation of CO_2 flux. In addition to the routine observation, in intensive observation periods, fluctuations of CO_2 concentration and temperature, and turbulence of vertical wind were measured by high-response CO_2 sensors (Advanet Co., type: E009A) and sonic anemometer and thermometer (KAIJO Co., type: DAT-600).

Overall, 87% of the total days from October 1993 to December 1996 were available to calculate the daily average of CO_2 flux, but available days were less than 20 days in each month of March, May, July, October in 1994 and August in 1995.

3. Analytical method for CO_2 flux

The CO_2 flux was calculated by the eddy correlation and aerodynamic methods. In eddy correlation method, CO_2 flux (Fc) is computed directly from the equation, $Fc = w'c'$ using CO_2 fluctuation (c') data and turbulence of vertical wind (w') in the intense observation periods. The sampling duration and frequency for the calcula-

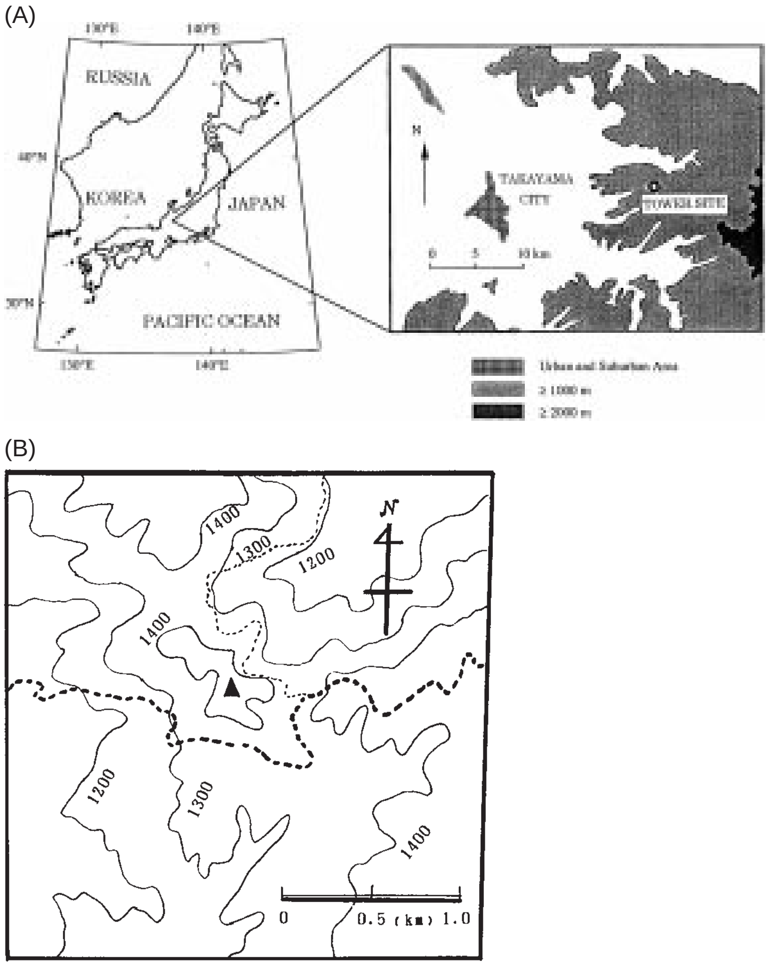

Fig. 1. (a) Map of the observation site. (b) Topographical map of the surrounding area of the tower (triangle), where the solid lines represent contours of elevation (m above sea-level) and dotted lines indicate the roads.

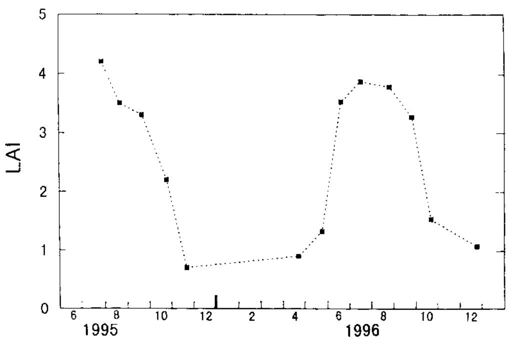

Fig. 2. Seasonal variation of leaf and stem area index (LAI).

tion of CO_2 flux were taken at 20 min and 2 Hz, respectively. The CO_2 flux obtained with the eddy correlation was applied to the density fluctuation correction of Webb et al. (1980). In this method, there is no need for hypothetical parameters, but measurement of c' through a whole year is required. In the aerodynamic method, CO_2 flux was determined, based on the vertical gradient of the CO_2 concentration and diffusion coefficient (K), $Fc = K\,dC/dz$. The value of K was calculated from mixing length theory, $K = l^2|du/dz|$, with reference to Watanabe et al. (1990), where l is the mixing length and du/dz is the gradient of the mean wind speed. The value, l, was determined in this research for the value of deciduous forests

Table 1. *Observational items and heights*

Period	Observation items	Observation heights	Instruments
routine measurement (whole year)	CO_2 (mean value)	27, 18, 8.8, 5.8 m	non-dispersive infrared gas analyzer
	insolation	25.5 m	pyranometer
	wind speed and direction (mean)	26, 9.5 m	combined wind vane and fan anemometer
	temperature and humidity (mean)	25.5, 9 m	platinum resistance thermometer and Humicap hygrometer
intensive periods	CO_2 and H_2O fluctuations	24.5, 11 m	ultrasonic anemometer and thermometer
	wind and temperature fluctuations	25, 10 m	open-path CO_2/H_2O infrared analyzer

from a comparison with the flux calculated by the eddy correlation method using the data obtained in the several intensive observation periods in July, August and November. In Table 2, values of mixing length are shown for the atmospheric stability category classified by wind speed and insolation. As shown in this table, the dependence of l on the atmospheric stability in daytime was small; then, the values, $l = 2.69$ m in daytime and $l = 2.28$ m at night were used for the calculation of the daily average of CO_2 flux. It should be noted that this value of l is useful only for the analyses of the fluxes at this tower and in the outer part of the roughness sub-layer. The merit of this method is that the flux of CO_2 throughout the whole year can be calculated from the mean values of CO_2 concentrations and wind speed. In present study, the CO_2 flux throughout the whole year was calculated using the aerodynamic method. The CO_2 flux in gaps of data were estimated from the data of insolation and CO_2 flux of same month in other years.

Fig. 3 is an example of the time variation of CO_2 fluxes calculated by the eddy correlation (FCO_2EC) and aerodynamic (FCO_2AD) methods on 29 and 30 July 1994. The fitting of fluxes by two methods was good during the daytime, and the flux had positive (uptake of CO_2 by vegetation) values. In contrast, the flux had negative (release of CO_2 to the air) and small values during the night, but the fitting of the two methods was poor. Fig. 4 shows the relation between eddy correlation and the aerodynamic methods. The correlation coefficient for them is 0.91. From these results, the aerodynamic method was more suitable for the averages of flux during longer periods than one day. Furthermore, the storage-rate of CO_2 in the canopy layer was calculated using the hourly change of vertical profile of CO_2 concentration. The typical value of the storage-rate was less than 0.5 $gCO_2/m^2/h$ (3.2 $\mu mol/m^2/s$) in the summer season. The storage-rate of CO_2 is important for the analyses of CO_2 budgets within a day, but is negligible for the seasonal and inter-annual variation of CO_2 budgets.

4. Results and discussions

4.1. *Seasonal and inter-annual variations of the CO_2 concentration and uptake rates*

Fig. 5 shows the inter-annual variation of daily average CO_2 measured at a height of 27 m on the tower from October 1993 to March 1997. Though the data were scattered, the concentration of CO_2 took the maximum values (367 to 371 ppmv) in April and the minimum values (355 to 359 ppmv) in September. The amplitude of seasonal variation

Table 2. *Value of mixing length for each atmospheric stability category*

Insolation (Is, kW/m^2) / Wind speed (U, m/s)	$Is > 0.5$ (daytime)	$0.5 \geq Is > 0.02$ (daytime)	$Is \leq 0.02$ (night)
$0 < U < 3$	3.0 m (9 h)	2.8 m (14 h)	2.3 m (42h)
$U > 3$	2.6 m (11 h)	2.7 m (10 h)	2.8 m (7 h)

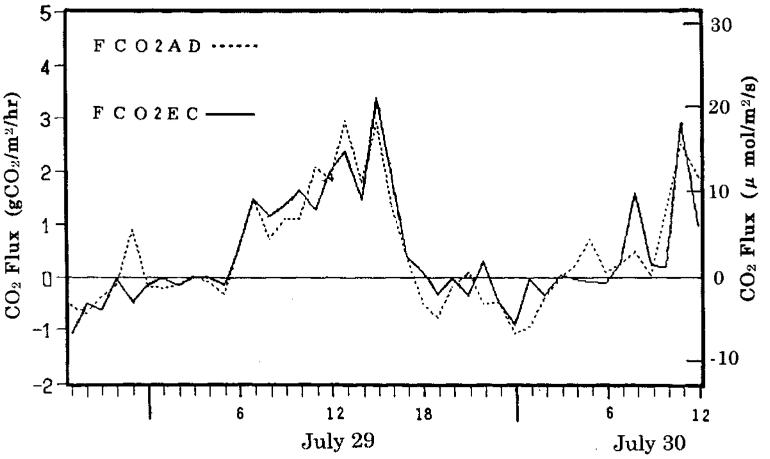

Fig. 3. An example of the time variation of CO_2 fluxes according to eddy correlation (FCO_2EC) and aerodynamic (FCO_2AD) methods.

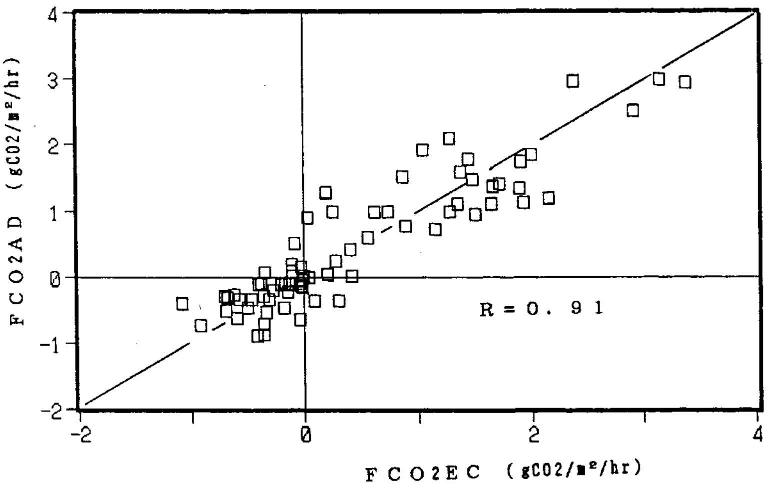

Fig. 4. Comparison of the eddy correlation (FCO_2EC) and aerodynamic (FCO_2AD) methods.

was about 12 ppmv and the yearly increase rate was about 1.7 ppmv/year.

Fig. 6 shows the relationship between CO_2 flux obtained by the eddy correlation method (FCO_2EC) and insolation during the active season of the forest. The hourly values of CO_2 flux on fine days were scattered from 0.5 to 4 $gCO_2/m^2/h$ (3.2 to 25 $\mu mol/m^2/s$), and the average value of these is about 2.03 $gCO_2/m^2/h$ (12.8 $\mu mol/m^2/s$) at $Is = 0.5$ kW/m^2 during the summer. This value is a little smaller than the value of 2.41 $gCO_2/m^2/h$ (15.2 $\mu mol/m^2/s$) in the tropical forest in the Amazon (Fan et al., 1990) and 2.44 (15.4) in the subtropical forest in Iriomote, Japan (Yamamoto et al., 1996). Furthermore, this value is comparable to the flux measured at temperate forests in Massachusetts, USA (Wofsy et al., 1993).

Fig. 7 shows the seasonal and inter-annual variations of the integrated uptake rate of CO_2 for daytime, night and whole days for each month from October 1993 to December 1996. This site is covered by snow from December to April, and the

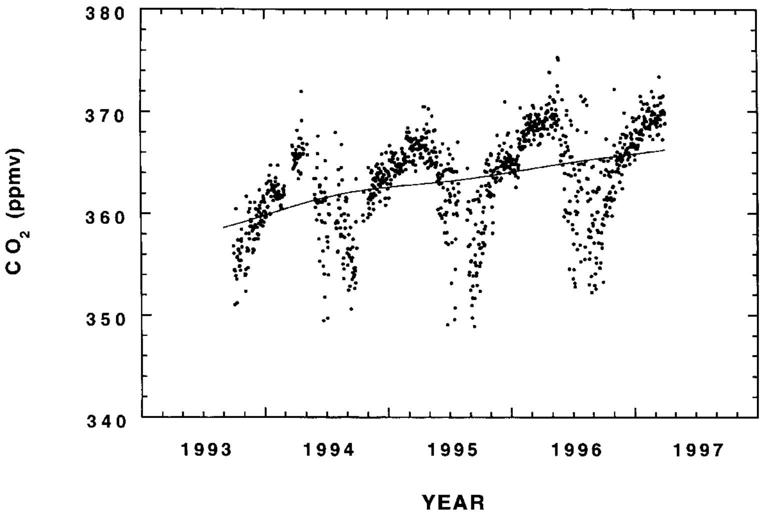

Fig. 5. Inter-annual variation of CO_2 concentration at the height of 27 m.

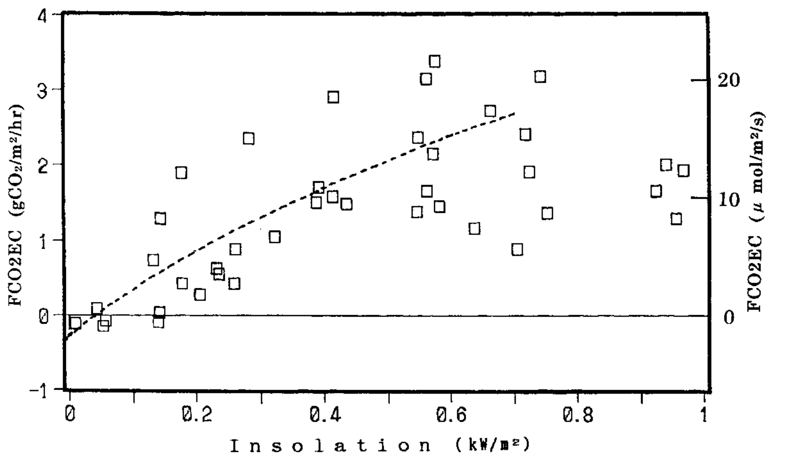

Fig. 6. Relationship between CO_2 flux using the eddy correlation method (FCO_2EC) and insolation during the active season of this forest. Though the data scatter is large, it can be approximated in the lower insolation range to 0.6 kW/m^2, using the following equation; $FCO_2EC = 6.2\ Is/(1 + 0.8Is) - 0.28$, where FCO_2EC is the flux of CO_2 ($gCO_2/m^2/h$) and Is is insolation (kW/m^2).

beginning of June is the budding time and the beginning of October is the deciduous period of leaves. The net uptake rate of CO_2 is positive (uptake by vegetation) from June to September and negative (release to the air) from October to April. At this site, the most active photosynthesis season is from the end of June to the beginning of September. On the other hand, the release rate of CO_2 from soil in summer and autumn is larger than the other seasons due to high temperature. It is notable that CO_2 is released from the ground under snow accumulation during the winter season. The absolute value of the outgoing CO_2 is small, but the accumulated value during the long winter is not negligible.

The integrated uptake amounts of CO_2 for daytime, night and whole days in 1994, 1995 and 1996 are shown in Table 3. Annual net uptakes of CO_2 including the effects of photosynthesis and respiration were 420, 240 and 500 gCO_2/m^2 in

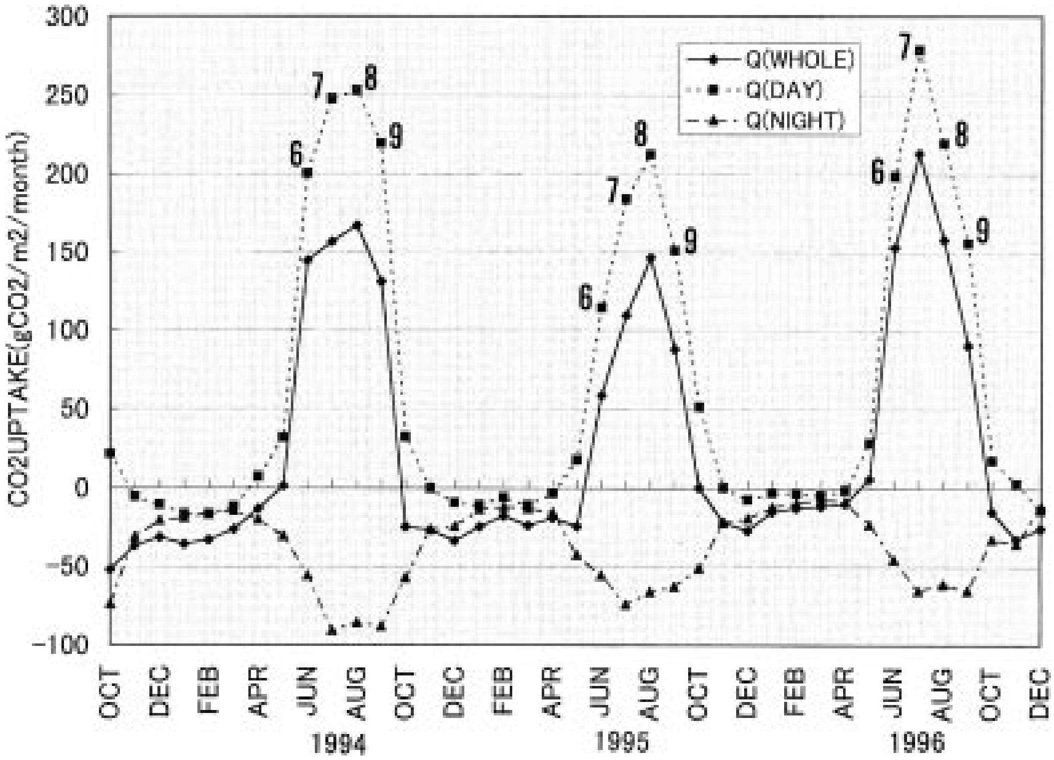

Fig. 7. Seasonal and inter-annual variation of integrated uptake rate of CO_2 for daytime, night and whole days, in each month from October 1993 to December 1996.

Table 3. *Integrated uptake rate of CO_2 ($gCO_2/m^2/year$) for daytime, night and whole days in 1994, 1995 and 1996*

Year	*Q* (whole)	*Q* (day)	*Q* (night)
1994	420	940	−520
1995	240	690	−450
1996	500	880	−380
mean	390	840	−450

1994, 1995 and 1996, respectively. These differences between the 3 years may be explained by the differences of insolation and air temperature during the summer for the 3 years. Fig. 8 shows the seasonal and inter-annual variation of mean insolation for daytime and mean air-temperature in each month from October 1993 to December 1996. Fig. 9 shows the variation of uptake rate of CO_2 and insolation (monthly mean of insolation during the daytime) from June to September in 1994, 1996 and 1996. From these results, the insolation in June and July 1995 was less than the other years and the temperature in June 1995 was lower than 1994 by 2.5°C. These months are very important for the forest activity such as leaf development and photosynthesis; then the weather conditions in this period had a large influence on the CO_2 budgets; for example, the uptake rate of CO_2 in June–July 1995 was 63% of the value in June–July 1994 and the change correlated with that of insolation.

4.2. *Errors of the uptake of CO_2 due to topographical effects*

In the calculation of CO_2 flux, the flatness and homogeneity of the site are assumed, but the topographical conditions of this site are not so ideal. Therefore, the errors in the estimation of CO_2 uptake rates due to the undulation and short fetch relative to the tower height above ground should be given consideration. Fig. 10 shows the relation between the wind direction and the ratio

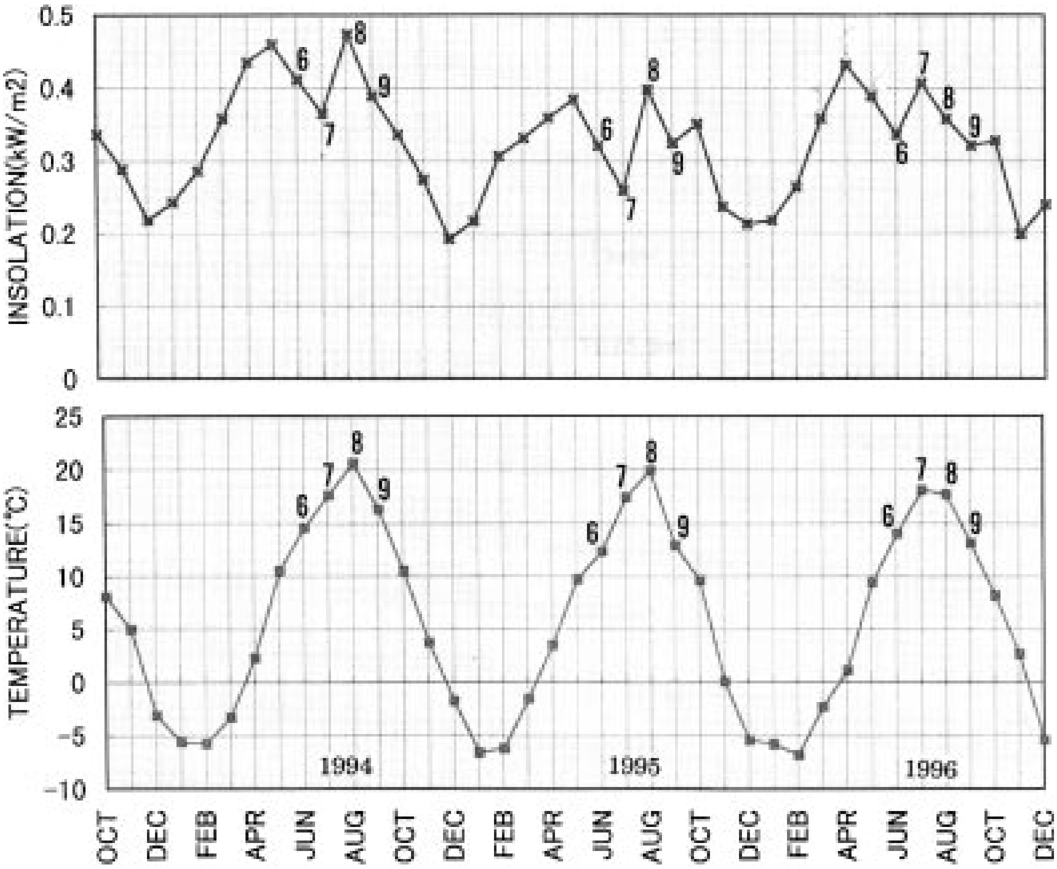

Fig. 8. The seasonal and inter-annual variation of mean insolation for daytime and mean air-temperature for each month from October 1993 to December 1996.

of vertical wind speed and total wind speed (w/U) in half-hourly averages during July to August in 1995. The ratio, w/U scatters from -0.1 to 0.3 depending on the wind direction. The tilt error for scalar fluxes is about 3% per degree of tilt with the micrometeorological rule-of-thumb (Moncrieff et al., 1996). Using this rule, the tilt errors in the present result are 18% (6°) for SW (prevail wind diretion in daytime from May to November) and 36% (12°) for NE (prevail wind direction in night from May to November). The ratio, w/U is sometimes larger than 0.3 (17°) for the wind direction W to NW as shown in Fig. 10. In these wind directions, flow separation could be occurred, but the influence to the flux measurement was not considered in this analysis.

Two causes of the errors were qualitatively considered here. One cause is the transfer of low CO_2 air by the vertical mean wind due to the inclination of the site, this error can be large during the daytime under fair weather conditions in summer. Wind directions of SW to W prevail at this site due to the development of the valley to hill wind system during the daytime in summer. This upward wind brings the air of low CO_2 concentration into the upper layer through the edge of the canopy on the lee side. The uptake rate of CO_2 during the daytime should be increased through the correction of this error.

The other cause is the flow of high CO_2 air from the edge of the forest during the night. Under stable and low wind conditions at night, the vertical exchange of CO_2 between canopy and the atmosphere should be small; then, the CO_2 emitted

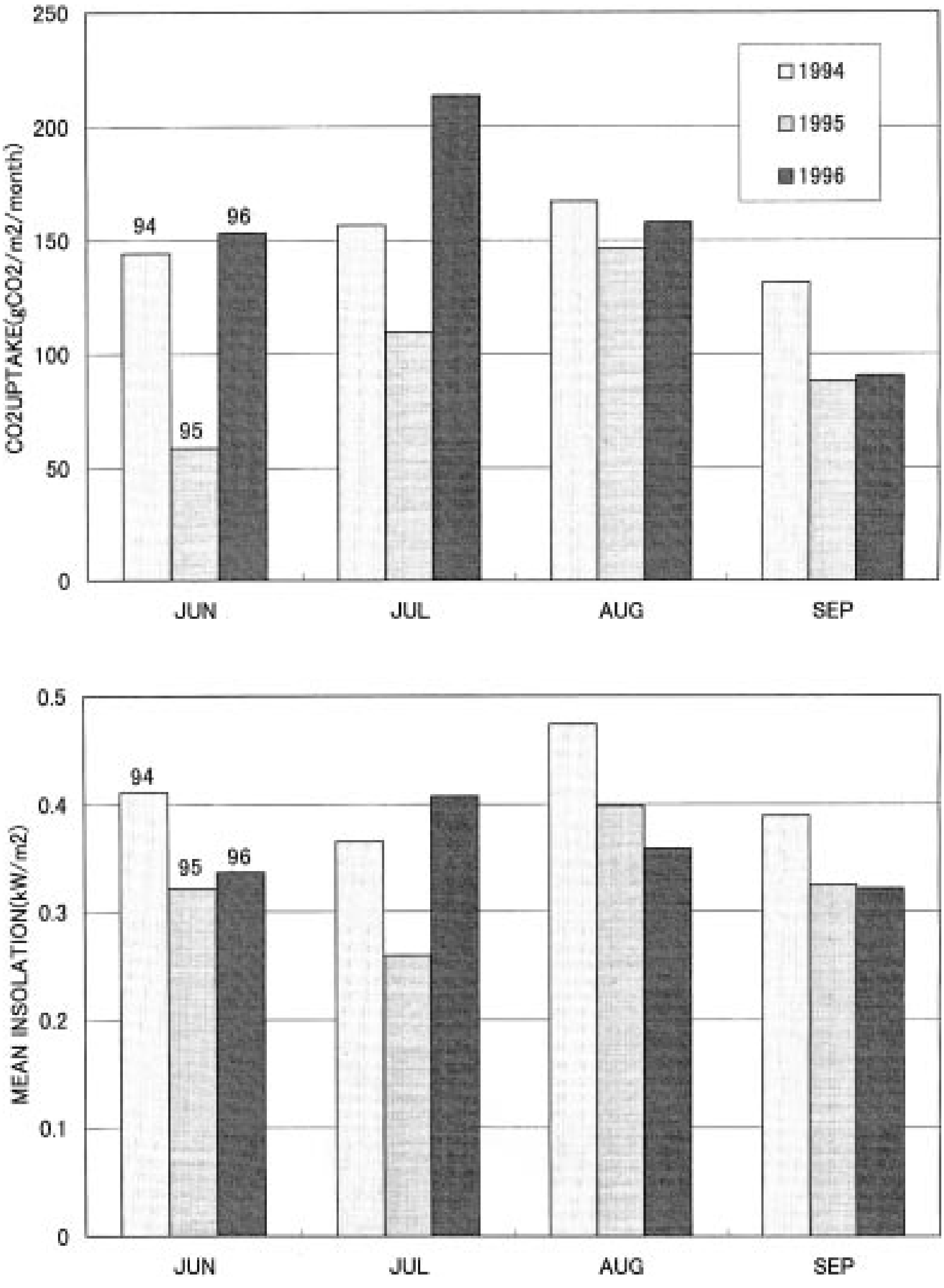

Fig. 9. Integrated uptake rate of CO_2 and insolation for daytime for each month from June to September in 1994, 1995, 1996.

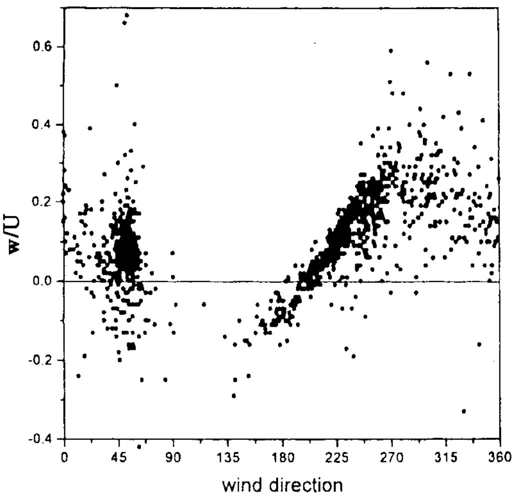

Fig. 10. Relation between wind direction and the ratio of the vertical and total wind-speeds, w/U in half-hourly averages during July to August, 1995.

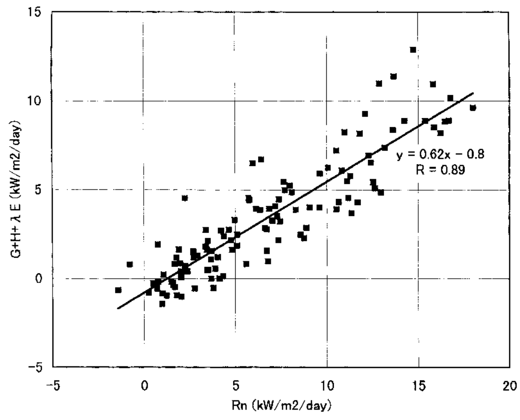

Fig. 11. Relation between daily integrated net radiation (Rn) and summation of heat conduction to the ground (G), sensitive heat flux (H) and latent heat flux (λE).

from the ground is stagnant in the canopy, and the air mass of high CO_2 is formed and brought out of the forest by the horizontal wind. A rough estimation of this error is possible from the analyses of CO_2 storage in the canopy layer and comparison with the respiration value. The storage-rate of CO_2 in the canopy was less than 0.5 $gCO_2/m^2/h$ (3.2 $\mu mol/m^2/s$) on summer nights, and this rate was of same order as the night flux of CO_2 between the forest and the atmosphere. Furthermore, the soil respiration was between 0.3 and 0.5 $gCO_2/m^2/h$ (1.9 and 3.2 $\mu mol/m^2/s$). From these results, the instantaneous rate of CO_2 flow may be small. However, such stable and high CO_2 conditions during the night occur frequently through the whole year except for winter, and the integrated amount of CO_2 flowage can be large. The uptake rate of CO_2 during the night should become negative with larger absolute value, through the correction of this error. These errors due to two causes have opposite directions; then, the errors might be cancelled partly in the estimation of net CO_2 uptake.

We can investigate the total amount of error of CO_2 flux by considering the heat budgets measured at the same site under a similarity hypothesis between heat and CO_2 fluxes. Fig. 11 shows the relation between net radiation (Rn) and summation of heat conduction to the ground (G), sensitive heat flux (H) and latent heat flux (λE) in daily integrated values during July to December 1997. If the heat storage in the canopy layer including biome, and the heat flow from the canopy due to the topographical conditions could be neglected, the value, $Ht = G + H + \lambda E$ should be balanced against the value, Rn. However, the value of Ht is smaller than Rn by 40% as shown in Fig. 11. Under the hypothesis of similarity between heat and CO_2 fluxes, CO_2 uptakes can be corrected using this result; the values in Table 3 should then be multiplied by 1.7.

The errors of the CO_2 uptake due to topographical conditions were considered here roughly, but more quantitative analyses of these errors using a numerical simulation model of flow and flux are needed for utilization of the results of the tower measurements under complex topographical conditions in Japan.

4.3. *The rôle of the forest ecosystem in the carbon budgets*

As mentioned in the *Introduction*, the long-term measurements are carried out in various types of forests and latitudes throughout the world. Table 4 sums up the several results of CO_2 uptakes from the continuous measurements. As shown in Table 4, the amount of carbon uptake by forests had large differences due to their types and locations. Therefore, it requires more data of long-term measurements of CO_2 flux to estimate the

Table 4. *List of the carbon balance measurements over the forests in the world (unit: in tonC/ha/year)*

Site (ref.)	Carbon uptake	Ecosystem respiration	Gross production	Remarks
Massachusetts, USA	3.7 (1991)	7.4	11.1	7.5°C — mm
(Wofsy et al., 1993)	deciduous forest (oak, maple, pine)			340 m
(Goulden et al., 1996)	2.1 (1994)	—	—	—
Oak Ridge, TN, USA	5.3	—	—	13.9°C 1350 mm
(Greco et al., 1996)	deciduous forest (oak, hickory, maple), LAI = 4.9			365 m
Central Italy	4.7	5.4	10.1	7.2°C 1100 mm
(Valentini et al., 1996)	deciduous forest (almost pure beech), LAI = 4.6			1564 m
Rondonia, Brazil	1.0	23.4	24.4	
(Grace et al., 1996)	tropical rain forest (palm rich), LAI = 4			120 m
Manaus, Brazil	5.9	24.5	30.4	2200 mm
(Malhi et al., 1997)	tropical rain forest, LAI = 5.6			90 m
Saskatchewan, Canada	1.3	8.9	10.2	458 mm
(Black et al., 1996)	boreal forest (aspen, jack pine, hazelnut), LAI = 3.3			1564 m
Takayama, Japan	1.8 (1994)	6.2	8.0	7.3°C 2382 mm
(Yamamoto et al., 1998)	deciduous forest (birch, oak), LAI = 3.5			1420 m

N.B. Air temperature, precipitation of annual mean and height of the site above sea level.

global uptake of CO_2 by forest ecosystems. However, all the data in Table 4 indicate the uptake of CO_2 by forest ecosystems, and their possible crucial role in the CO_2 global budgets.

Next, we would like to compare the present result of CO_2 uptake with the forest–ecological parameters measured by Nishimura and co-workers, of Gifu University at the same site. According to their results in 1994, the respiration rate of soil and roots was 2280 gCO_2/m^2/year (6.2 tC/ha/year) and the litter fall amount was 850 gCO_2/m^2/year (2.3 tC/ha/year). From these results and Table 3, the gross production of this forest was 2690 gCO_2/m^2/year (7.3 tC/ha/year) for 1994. The uptake rate of CO_2 has considerable inter-annual change, therefore, an analysis of the carbon balance in other years is needed. After correcting the underestimation of 40% inferred from the analysis of heat budgets, the carbon uptake and gross production become 1.8 and 8.0 tC/ha/year, respectively as shown in Table 4.

Furthermore, these results should be compared with the ecological survey, such as the growing rate of the biomass estimated from the measurements of the diameters and heights of the trees. The tree-biomass including root measured by Gifu University in this site was 67.6 tC/ha. For the preliminary result, carbon uptake rate is 1.7 tC/ha/year under the assumption of 40 years of mean tree-age and ignorance of carbon sequestration in the soil. This value is comparable with the carbon uptake rate, 1.8 tC/ha/year estimated from the tower measurement.

5. Conclusions

Seasonal and inter-annual variations of CO_2 exchanges between the atmosphere and a temperate forest in Japan were investigated through tower measurements from October 1994 to September 1996. The net uptake rate of CO_2 was positive (uptake by forest ecosystems) from June to September and negative (release to the air) from October to April. Averages of integrated uptake rates of CO_2 were 840, −450 and 390 gCO_2/m^2/year (2.3, −1.2 and 1.1 tC/ha/year) for the daytime, night and whole (net) days, respectively, but they had notable inter-annual variation due to the differences of insolation and temperature during each summer from 1994 to 1996. The errors of CO_2 flux due to topographical conditions were investigated through comparison with heat budgets. The CO_2 uptake rate estimated by tower measurement might be underestimated by 40%, therefore, the above value, 1.1 tC/ha/year became

1.8. This value of the uptake rate was smaller than the results obtained in other temperate deciduous forests. The causes of this are partially the difference of the height of the site and the short active period of the present forest. At the same time, a more quantitative investigation of the errors due to the topographical effects is required.

According to present study, the forest ecosystems can be a large sink of CO_2, but this needs more data of CO_2 flux in the forests of various types and latitudes to reduce the uncertainty of CO_2 uptake estimation on a the global scale. Moreover, the present results should be compared carefully with the ecological direct-survey of photosynthesis, respiration, growing rate and litter fall of the forest ecosystem.

6. Acknowledgments

The authors would like to express their appreciation to Prof. N. Nishimura and all the members of Institute for Basin Ecosystem Studies, Gifu University for their cooperation and useful comments. This study was supported by the global environment research program of the Environment Agency of Japan.

REFERENCES

Baldocchi, D., Valentini, R., Running, S., Oechels, W. and Dahlman. R. 1996. Strategies for measuring and modeling carbon dioxide and water vapor fluxes over terrestrial ecosystems. *Global Change Biology* **2**, 159–168.

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

Dixon, R. K., Brown, S., Houghton, R. A. et al. 1994. Carbon pools and flux of global forest ecosystems. *Science* **263**, 185–190.

Fan, S.-M., Wofsy, S. C., Bakwin, P. S., Jacob. D. J. and Fitzjarrald, D. R. 1990. Atmospheric–biosphere exchange of CO_2 and O_3 in the Central Amazon forest. *J. Geophys. Res.* **95**, 16,851–16,864.

Goulden, M. L., Munger, J. W., Fan, S.-M., Daube, B. C. and Wofsy, S. C. 1996. Measurements of carbon sequestration by long-term eddy covariance methods and a critical evaluation of accuracy. *Global Change Biology* **2**, 169–182.

Grace, J., Malhi, Y., Lloyd, J., McIntyre, J., Miranda, A. C., Meir, P. and Miranda, H. S. 1996. The use of eddy covariance to infer the net carbon dioxide uptake of Brazilian rain forest. *Global Change Biology* **2**, 209–217.

Greco, S. and Baldocchi, D. 1996. Seasonal variations of CO_2 and water vapor exchange rates over a temperate deciduous forest. *Global Change Biology* **2**, 183–197.

IPCC. 1995. *Climate change 1995: The Science of climate change.*

Keeling, R. F. and Shertz, S. R. 1992. Seasonal and inter-annual variations in atmospheric oxygen and implications for the global carbon cycle. *Nature* **358**, 723–727.

Malhi, Y., Higuchi, N., Nobre, A. D., Grace, J., Pereira, M. G. P. and Ribeiro, R. J. 1997. Direct measurement of a carbon sink in an area of tropical rain forest. *Proc. Fifth International Carbon dioxide conference, 1979.*

Moncrieff, J. B., Malhi, Y. and Leuning, R. 1996. The propagation of errors in long-term measurements of land–atmosphere fluxes of carbon and water. *Global Change Biology* **2**, 231–240.

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

Webbs, E. K, Pearman, G. J. and Leuning, R. 1980. Correction of flux measurements for density effects due to heat and water vapor transfer. *Quart. J. R. Met. Soc.* **106**, 85–100.

Watanabe, T. and Kondo, J. 1990. The influence of canopy structure and density upon the mixing length within and above vegetation. *J. Meteor. Soc. Japan* **68**, 227–235.

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

Yamamoto, S., Kondo, H., Gamo, M., Murayama, S. et al. 1996. Airplane measurements of carbon dioxide distribution on Iriomote island in Japan. *Atmospheric Environment* **30**, 1091–1097.