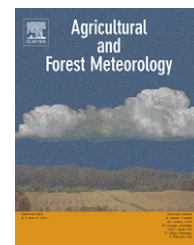


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## Spatial distribution of carbon balance in forest ecosystems across East Asia

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### ABSTRACT

The objective of this paper is to clarify what kind of environmental factors that regulate net ecosystem production (NEP), gross primary production (GPP), and ecosystem respiration (RE) in forest ecosystems across East Asia. Study sites were widely distributed and included diverse ecosystems, such as evergreen and deciduous, coniferous and broadleaf, planted and natural forests, from subarctic to tropical zones. We measured NEP using the eddy covariance technique at 13 forest sites in East Asia.

Annual values of GPP and RE are simply regulated by annual mean air temperature across East Asia. There is a clear linear relationship between annual GPP and annual mean air temperature because the air temperature influences both growing period length and the seasonal variation of the maximum photosynthetic capacity, which, together, regulate the annual GPP. On the other hand, there is a strong exponential relationship between annual RE and annual mean air temperature on an East Asia scale, which is quite similar to the relation obtained on a canopy scale. The dependency of annual RE on air temperature on the East Asia scale was similar to that of monthly RE on air temperature on an individual site scale excepting for temperate larch and mixed forests in northern Japan.

The reason why the relation is simple is that severe stress, which affects GPP or RE, is small in East Asia. The present study suggests that RE is sensitive to non-climate environmental factors when compared to GPP, thus the annual RE–air temperature relationship is more scattered than the annual GPP–air temperature relationship. The NEP is small at high latitude, relatively large at mid-latitude, and scattered at low latitude. As a whole, the NEP is more influenced by RE than GPP in East Asia. Compared to North America and Europe, the

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increase in the ratio of GPP to air temperature is slightly higher in East Asia. One of the possible reasons for this is that GPP in East Asia is not exposed to severe environmental stresses, such as summer drought.

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## 1. Introduction

The Kyoto protocol, which accounts for offsetting reduced targets of CO<sub>2</sub> emission by carbon sequestration in forests through forest management, became effective in February 2005. The rules, which were determined at COP6 and COP7 (Schulze et al., 2002), have focused attention on the role of the terrestrial biosphere in global scale carbon cycles. Therefore, accurate data are required for net ecosystem production (NEP) over various terrestrial ecosystems. However, uncertainty remains about the change in carbon stock from forest management and the response of the ecosystem CO<sub>2</sub> exchange to climate change.

Recently, several studies have been made of the inter-comparison of CO<sub>2</sub> fluxes on regional and global scales as continuous data for CO<sub>2</sub> fluxes from the eddy covariance technique have been accumulated. Valentini et al. (2000) showed the relationship between carbon accumulation and geography in Europe. Law et al. (2002) investigated the response of vegetation to environmental variables using the North American and European flux data collected by FLUX-NET. Falge et al. (2002) compared seasonal variations in net ecosystem exchange (NEE) for various vegetations. Amiro et al.

(2006) studied the affect of disturbance on carbon balance in boreal forests by the comparing flux data for several sites in Canada. However, systematic inter-comparative studies of CO<sub>2</sub> fluxes in Asia have been limited.

In East Asia, which is the East Eurasian continent in the Northern Hemisphere, a humid region spreads continuously from the arctic to the tropics because of the East Asian monsoon and rain front (Kohyama, 2006). Seasonal variation in temperature is clear in the subarctic and temperate zones while it is small in the tropical zone. Snow covers the land for 1–7 months in the subarctic and cool-temperate zones. There is also a permafrost period in the subarctic and cool-temperate zones. The temperate zone has four seasons and a rainy period for about 1 month before the summer dry season. Typhoons hit marine countries at mid-latitude. In the tropical zone; the year is divided into rainy and dry seasons. Drought occurs every few years in an El Niño event in the tropical zone (Hirano et al., 2007).

In East Asia, forest ecosystems, which adjust for humid regions, are continuously distributed from subarctic, through temperate, to tropical climate zones from north to south (Ohta et al., 1993; Kohyama, 2006). In the present study, sites are distributed widely from the subarctic to tropical zones in East

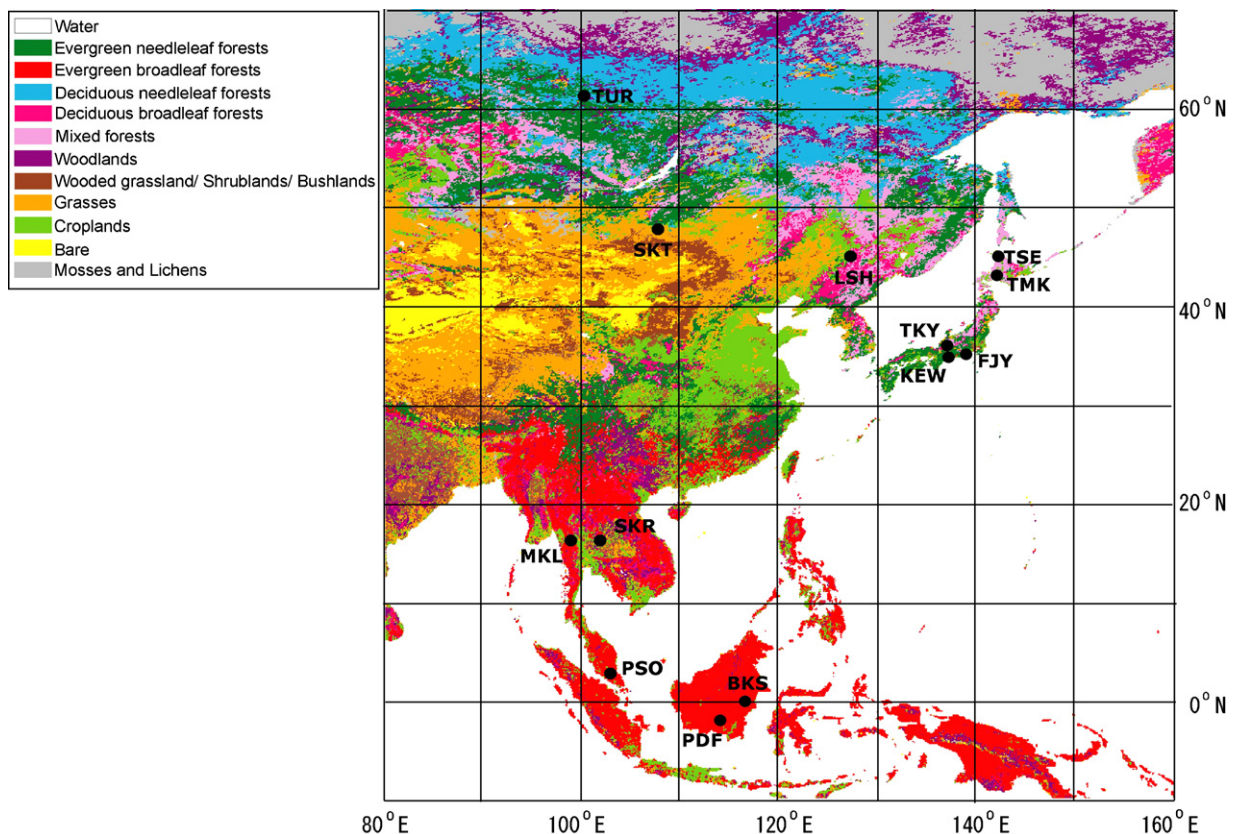


Fig. 1 – Location of study sites in East Asia in a land classification map (De Fries et al., 1998).

Asia, and cover typical vegetation types found in East Asia. Boreal forests are considered to play an important role in global climate and the global scale carbon cycle, as they are large carbon stocks (e.g. Bonan et al., 1992; Otto-Bliesner and Upchurch, 1997). The eastern Siberian boreal forest is dominated by deciduous conifer forest (larch: *Larix*) over permafrost (Gower and Richards, 1990; Matsuura et al., 2005). However, there are few studies for CO<sub>2</sub> exchange between forest ecosystems and the atmosphere over larch forest (Hollinger et al., 1998). Therefore, we have collected data at four larch forest sites. There are many forest types in the temperate zone. Deciduous broadleaf, larch, mixed, and evergreen forest were examined in this report. The tropical zone is mainly dominated by evergreen broadleaf forest. However, reports on NEE are still limited from Asian tropical ecosystems (Yasuda et al., 2003; Saitoh et al., 2005). Therefore, we collected data for five different types of tropical forest.

The objectives of this paper are to clarify environmental control factors that regulate NEP, gross primary production (GPP), and ecosystem respiration (RE) in various forest ecosystems across East Asia and to compare these with those in the North America and Europe.

## 2. Materials and methods

### 2.1. Sites description

We analyzed CO<sub>2</sub> flux data from 13 flux tower sites, which are distributed geographically from 2°S to 64°N in latitude and from 98°E to 141°E in longitude. Fig. 1 shows the site location, and Table 1 shows the details of the site characteristics. The climatic zones include subarctic (2 sites), temperate (6 sites) and tropical (5 sites) zones. The forest biomes are constituted of deciduous coniferous (4 sites), deciduous broadleaf (1 site), mixed evergreen and deciduous (1 site), evergreen coniferous (2 sites), and tropical forests (5 sites). Eleven sites in the present study are relatively close to the ocean, and two sites are located deeper within the continent.

Most sites are natural forests, secondary forests, or planted forests with a tree age more than approximately 45 years. This study also includes two naturally or artificially disturbed sites in the tropics; one is a young forest regenerating after a severe wild fire (BKS), and the other is a peat swamp forest where the ground water level is artificially controlled (PDF). At the BKS site, forest burned severely in 1998 and most of the trees were killed. During our study period, a shrub species *Macaranga gigantea* was re-growing with a tree age of 4 years or less. At the PDF site, a drainage canal was built near the study site in the late 1990s. The ground water level slowly reduced and the soil surface layer became dry (Hirano et al., 2007).

### 2.2. Measurements

Net ecosystem CO<sub>2</sub> exchange (NEE = -NEP) was calculated as the sum of the eddy CO<sub>2</sub> flux ( $F_c$ ) and the rate of change in CO<sub>2</sub> storage below the flux measurement height ( $F_s$ ).  $F_c$  was measured using the eddy covariance technique with three-dimensional sonic anemometer-thermometers and open- or closed-path CO<sub>2</sub>/H<sub>2</sub>O analyzers. Measurement systems and

calculation protocols were mostly based on EUROFLUX methodology (Aubinet et al., 2000). The CO<sub>2</sub> storage change was calculated by the vertical profile of the atmospheric CO<sub>2</sub> concentration or a single height measurement of CO<sub>2</sub> concentration at the flux measurement height. At KEW and PSO sites,  $F_s$  was neglected since the measurement of CO<sub>2</sub> concentration was not conducted at the site. The measurement instruments used at each site are shown in Table 2.

### 2.3. Estimation of GPP and RE, gap filling, and data procedure

At each site, principal investigators performed quality control for high frequency data (4–10 Hz) including the removal of spikes, raw data tests (Vickers and Mahrt, 1997), a non-stationary test and an integral turbulence test (Foken and Wichura, 1996) and calculated 30-min or 60-min fluxes. The detailed protocols used at each site are described in the references listed in Table 1. This study collected 30-min- or 60-min-average meteorological observations and CO<sub>2</sub> fluxes with data gaps, and applies nighttime correction and gap-filling. Positive or negative NEP represents the forest ecosystem absorbing or releasing CO<sub>2</sub>, respectively. NEP data with low turbulence were excluded using the threshold of friction velocity ( $u_*$ ) (Massman and Lee, 2002). We examined whether temperature-normalized nighttime NEE responds to turbulent intensity from all nighttime data categorized into  $u_*$  classes of 0.1 m s<sup>-1</sup>. We statistically distinguish the  $u_*$  classes for dropping RE from each other (Tukey's HSD,  $p < 0.05$ ) (Hirata et al., 2007), and obtained the threshold of  $u_*$ , which varied among the sites (Table 2).

At the TUR site (a larch forest in central Siberia), measurement periods were limited to the growing season. Therefore, we used long-term (1968–1992) meteorological data from a meteorological station near the site for annual mean air temperature and annual precipitation data. An eddy covariance measurement was performed from June to the first half of September 2005 (Nakai et al., in press). NEP estimated by the eddy covariance technique at TUR is not based on year-round data but on the measurement in the growing season from June to early September. At the site, GPP during the dormant season can be ignored because the larch trees were leafless, and winter CO<sub>2</sub> efflux from the snow surface estimated by chamber measurement was negligibly small for a whole-year estimation (Matsuura et al., 2007). Therefore, we considered the NEP and RE in the growing season at TUR to be almost equivalent to the annual NEP and RE, however, the annual values might have some overestimation (NEP) and underestimation (RE) due to disregarding RE in the dormant season.

We used the following equation of Lloyd and Taylor (1994) to fill gaps in nighttime NEE ( $F_{NEE, \text{night}}$ ):

$$F_{NEE, \text{night}} = F_{RE, T_{ref}} \exp \left\{ \frac{E_0}{R} \left( \frac{1}{T_K + T_{ref} - T_0} - \frac{1}{T_K + T_a - T_0} \right) \right\} \quad (1)$$

Here  $T_a$  is the air temperature (°C),  $E_0$  is activation energy (J mol<sup>-1</sup>),  $R$  is ideal gas constant (J mol<sup>-1</sup> K<sup>-1</sup>).  $F_{RE, T_{ref}}$  is  $F_{NEE, \text{night}}$  at the reference temperature ( $T_{ref}$ ), which was 10 °C.  $T_K$  and  $T_0$  are 273.15 and 227.13 K, respectively.  $F_{RE}$ ;  $T_{ref}$  and  $E_0$

Table 1 – Site characteristics

Site name (Site code), Country	Location	Elevation (m)	Forest type	Soil type	Maximum LAI (m <sup>2</sup> m <sup>-2</sup> )	Tree height (m)	Tree age (years)	Dominant species	Reference
Tura (TUR), Russia	64°12'N, 100° 27'E	250	Subarctic larch forest (DC)	Gelisol	<0.3	3	105	Gmelin larch ( <i>Larix gmelinii</i> ), lichen and moss ( <i>Cladina stellaris</i> , <i>Pleurozi schreberi</i> )	Kajimoto et al. (2006) Nakai et al. (in press)
Southern Khentei Taiga (SKT), Mongolia	48°21'N, 105°39'E	1630	Subarctic larch forest (DC)	Alfisol (Soil Survey Staff (1999))	2.7	20	70–300	Siberian larch ( <i>Larix sibirica</i> ), White birch ( <i>Betula platyphylla</i> )	Li et al. (2005)
Laoshan (LSH), China	45°20'N, 127°34'E	370	Temperate planted larch forest (DC)	Alfisol	2.5	IS	35	Gmelin larch ( <i>Larix gmelinii</i> )	Wang et al. (2005)
CC-LaG experiment site (TSE), Teshio, Japan	45°03'N, 142°06'E	70	Conifer-Hardwood mixed forest (MX)	Inceptisol	7.5 (PAI) (Canopy3, Forest floor 4.5)	25	–	Oak ( <i>Quercus crispula</i> ), Birch ( <i>Betula ermanii</i> ), Sakhalin fir ( <i>Abies sachalinensis</i> ), Bamboo grass ( <i>Sasa senanensis</i> )	Koike et al. (2001) Takagi et al. (2005)
Tomakomai Flux Research Site (TMK), Japan	42°44'N, 141°31'E	140	Temperate planted larch forest (DC)	Entisol	9.2 (Canopy 5.6, Forest floor 3.6)	16	45	Japanese larch ( <i>Larix Kaempferi</i> ), Birch ( <i>Betula ermanii</i> , <i>Betula platyphylla</i> ), fern ( <i>Dryopteris crassirhizoma</i> )	Hirano et al. (2003) Wang et al. (2004) Hirata et al. (2007)
Takayama (TKY), Japan	36°05'N, 137°25'E	1420	Temperate deciduous forest (DB)	Inceptisol	3.5 (PAI)	15–20	50	Deciduous oak ( <i>Quercus crispula</i> ), Bamboo grass ( <i>Sasa veitchii</i> )	Saigusa et al. (2002) Saigusa et al. (2005)
Fujiyoshida forest meteorology research site (FJY), Japan	35°27'N, 138°46'E	1030	Naturally regenerated red pine forest (EC)	Entisol	5.5	20	90	Japanese redpine ( <i>Pinus densiflora</i> ), Japanese holly ( <i>Ilex pedunculosa</i> )	Ohtani et al. (2005)
Kiryu Experiment Watershed (KEW), Japan	34°58'N 135°59'E	250	Temperate planted Japanese cypress forest (EC)	Entisol	5.5 (PAI)	IS	45	Japanese cypress ( <i>Chamaecyparis obtusa</i> )	Takanashi et al. (2005a) Ohkubo et al. (2007)
Mae Klong (MKL), Thailand	14°35'N, 98°51'E	160	Tropical seasonal deciduous forest (TR)	Ultisol	4.0 (PAI)	30	–	Dipterocarp ( <i>Shorea siamensis</i> , <i>Vitex peduncularis</i> , <i>Xylia xylocarpa</i> )	Kondo et al. (submitted for publication)
Sakaerat (SKR), Thailand	14°29'N, 101°55'E	535	Tropical dry evergreen forest (TR)	Ultisol	4.0 (PAI)	35	–	Dipterocarp ( <i>Hopea ferrea</i> )	Gamo et al. (2005)
Pasoh Forest Reserve (PSO), Malaysia	2°58'N, 102°18'E	75–150	Tropical rain forest (TR)	Ultisol	6.5 (PAI)	35–45	–	Dipterocarp ( <i>Hopea ferrea</i> )	Takanashi et al. (2005b) Kosugi et al. (2008)
Bukit Soeharto (BKS), Indonesia	0°52'S, 117°03'E	20	Tropical secondary forest (TRF)	Ultisol	3.0 (PAI)	11	4	Dipterocarp ( <i>Macaranga gigantea</i> )	Gamo et al. (2005)
Palangkaraya drained forest (PDF), Indonesia	2°21'S, 114°02'E	30	Tropical peat swamp forest (TRD)	Histosol	5.6 (PAI)	26	–	Tumih ( <i>Combretocarpus rotundatus</i> ), Clusiaceae ( <i>Cratoxylum arborescens</i> ), <i>Buchanania</i> ( <i>Buchanania sessifolia</i> ) <i>Entuyut</i> ( <i>Tetramerista glabra</i> )	Hirano et al. (2007)

Description of ecosystem type—DC: deciduous coniferous forest; MX: mixed forest; DB: deciduous broadleaf forest; EC: evergreen coniferous forest; TR: tropical forest; TRF: tropical forest disturbed by forest fire; TRD: tropical forest influenced by drainage changes from a constructed canal. Soils were classified into soil orders of the USDA Taxonomy (Soil Survey Staff, 1999). For soils that lacked information in the articles, we determined soil orders by soil map.



**Table 2 – Measurement systems**

Site code	Sonic anemometer model	IRGA model	Flux measurement height (m)	Sampling frequency (Hz)	Average period for flux calculation (min)	$u_*$ threshold ( $m s^{-1}$ )
TUR	R-3, Gill <sup>a</sup>	LI-7500, Licor <sup>d</sup>	20	10	30	0.1
SKT	SAT-550, Kaijo <sup>b</sup>	LI-7500, Licor <sup>d</sup>	30	10	30	0.3
LSH	SAT-550, Kaijo <sup>b</sup>	LI-7000, Licor <sup>d</sup>	29	10	30	0.2
TSE	DA600-3TV, Kaijo <sup>b</sup>	LI-7000, Licor <sup>d</sup>	32	10	30	0.0
TMK	DA600-3TV, Kaijo <sup>b</sup>	LI-6262, Licor <sup>d</sup>	27	10	30	0.3
TKY	DA600-3TV, Kaijo <sup>b</sup>	LI-6262, Licor <sup>d</sup>	25	5	30	0.5
FJY	DA600-3TV, Kaijo <sup>b</sup>	LI-6262, Licor <sup>d</sup>	26	5	30	0.2
KEW	DA-600T, Kaijo <sup>b</sup>	LI-7500, Licor <sup>d</sup>	29	10	30	0.4
MKL	SAT540, Kaijo <sup>b</sup>	LI-6262, Licor <sup>d</sup>	42	4	30	0.2
SKR	Wind Master, Gill <sup>a</sup>	LI-6262, Licor <sup>d</sup>	45	4	30	–
PSO	SAT-550, Kaijo <sup>b</sup>	LI-7500, Licor <sup>d</sup>	54	10	30	–
BKS	Wind Master, Gill <sup>a</sup>	LI-6262, Licor <sup>d</sup>	14	10	30	0.2
PDF	CSAT3, Campbell <sup>c</sup>	LI-7500, Licor <sup>d</sup>	41	10	60	0.1

<sup>a</sup> Gill Instruments Ltd., Lymington, UK.

<sup>b</sup> KAIJOSONIC Corporation, Tokyo, Japan.

<sup>c</sup> Campbell Scientific, Inc., Logan, USA.

<sup>d</sup> LI-COR Inc., Lincoln, USA.

were determined each day for a 29-day moving window by the least-squares method.

Data gaps in daytime NEE ( $F_{NEE, day}$ ) were filled by the following non-rectangular hyperbola equation as a function of photosynthetic photon flux density (PPFD;  $Q$ ) (Prioul and Chartier, 1977).

$$F_{NEE, day} = \frac{-\phi Q - P_{max} + \sqrt{(\phi Q + P_{max})^2 - 4\phi Q \theta P_{max}}}{2\theta} + R_d \quad (2)$$

In the equation,  $P_{max}$ ,  $\phi$ ,  $\theta(=0.9)$  and  $R_d$  are the maximum GPP at light saturation ( $\mu mol m^{-2} s^{-1}$ ), the initial slope ( $mol mol^{-1}$ ), the convexity of the light-response curve and daytime respiration ( $\mu mol m^{-2} s^{-1}$ ), respectively. The parameters for Eq. (2) were determined each day for a 15-day moving window by the least-squares method. Gaps of observed NEP were filled by estimated NEP using non-linear empirical models (Eqs. (1) and (2)).

The relationship between the net ecosystem exchange, NEE ( $F_{NEE}$ ), the net ecosystem production, NEP ( $F_{NEP}$ ), the gross primary production, GPP ( $F_{GPP}$ ), and the total ecosystem respiration, RE ( $F_{RE}$ ), is expressed:

$$F_{NEP} = -F_{NEE} = F_{GPP} - F_{RE} \quad (3)$$

In this equation, where GPP represents CO<sub>2</sub> assimilation by photosynthesis in vegetation. RE represents CO<sub>2</sub> release by soil, stem, branch, and foliage respiration. The values of NEE in nighttime and winter season are identical to RE because GPP equals zero. Daytime RE was estimated by extrapolation using Eq. (1). GPP was calculated by the subtraction of daytime NEE from daytime RE.

Here we explain some site specific procedures for flux calculation (Saigusa et al., 2008). Flux measurement involves particular problems caused by advection and low turbulence at night (Massman and Lee, 2002). The effects of these factors are different at each site, because they relate to site specific

conditions such as complex topography, canopy structure and frequency of calm nights. We applied  $u_*$  correction to nighttime NEE for most sites. However, at two tropical forest sites (SKR and PSO), there was a significant underestimation of nighttime NEE even if  $u_*$  filtering was applied. At both sites, the annual NEP was estimated by biometric methods, and the underestimation in the total ecosystem respiration estimated by the eddy covariance method was obvious from the comparison with these other methods (Saigusa et al., 2008). At the PSO site, we replaced all the nighttime NEE values by values of ecosystem respiration that was calculated by an empirical equation based on the chamber method (Kosugi et al., 2008). van Gorsel et al. (2007) proposed a method for correction of nighttime NEE, which uses the maximum value of nighttime NEE of each night to construct a temperature response function (such as Eq. (1)). At the SKR site, in addition of this method, we used nighttime data only during turbulent night (high  $u_*$ ) in order to exclude low turbulent data continuing whole night (Saigusa et al., 2008).

### 3. Results

#### 3.1. Annual values of GPP, RE and NEP

Annual values of carbon budget components and meteorological variables are listed in Table 3 for each site and year. GPP ranged from 40 to 2 tC ha<sup>-1</sup> year<sup>-1</sup> and RE from 40 to 1 tC ha<sup>-1</sup> year<sup>-1</sup>. In the tropical forest (< 20°N), values of GPP reached 33.3 ± 3.3 tC ha<sup>-1</sup> year<sup>-1</sup>, while RE varied from 23 tC ha<sup>-1</sup> year<sup>-1</sup> at BKS (TRF; 1°S) to 40 tC ha<sup>-1</sup> year<sup>-1</sup> at PDF (TRD; 2°S) (Table 3).

The annual values of NEP ranged widely from -7 to 5 tC ha<sup>-1</sup> year<sup>-1</sup> from 2°S to 64°N in latitude. NEP was small at high latitude, relatively large at mid-latitude, and there was large scattering at low latitude. Above 40°N, CO<sub>2</sub> exchange was almost balanced or absorbed slightly with small scatter. The NEP of evergreen forests (FJY, KEW) was larger than that of

**Table 3 – Climatic conditions of the study sites including annual sum of NEP, GPP, RE, photosynthetic photon flux density (PPFD) and precipitation (P), annual mean air temperature, soil water content (SWC), daytime vapor pressure deficit (VPD),  $P_{\max}$ , and maximum  $P_{\max}$ , and growing season length for NEP and GPP**

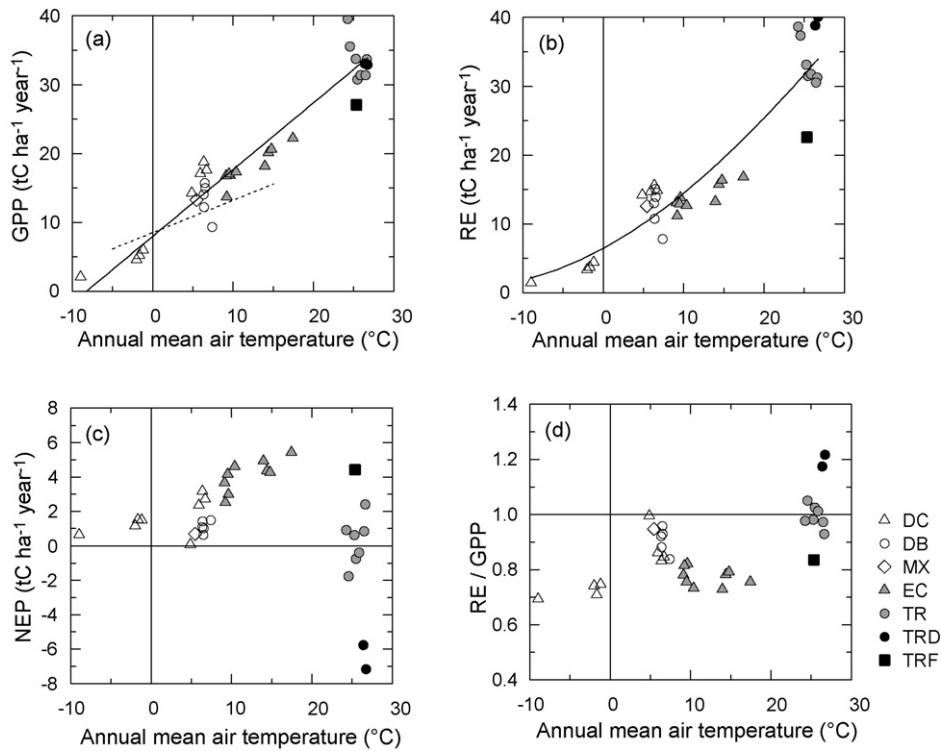
Site	Year	NEP (tC ha <sup>-1</sup> )	GPP (tC ha <sup>-1</sup> )	RE (tC ha <sup>-1</sup> )	PPFD (mol m <sup>-2</sup> )	P (mm)	T <sub>a</sub> (°C)	SWC (m <sup>3</sup> m <sup>-3</sup> )	Daytime VPD (kPa)	Annual mean $P_{\max}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	Maximum $P_{\max}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	Growing season length (days)
TUR	2004	0.7 <sup>a</sup>	2.1 <sup>a</sup>	1.5 <sup>a</sup>	1918 <sup>b</sup>	360 <sup>b</sup>	-9.0 <sup>b</sup>	0.48 <sup>b</sup>	1.6 <sup>b</sup>	4.0 <sup>a</sup>	5.8	102 <sup>b</sup>
SKT	2003 <sup>c</sup>	1.2	4.5	3.4	11582	276	-2.0	0.07	0.5	2.8	12.0	115
	2004	1.5	6.0	4.5	11582	267	-1.2	0.07	0.7	4.0	14.1	187
	2005	1.5	5.2	3.7	11929	230	-1.7	0.05	0.6	3.9	13.2	168
LSH	2004	0.1	14.3	14.2	9295	639	4.8	0.28	1.1	9.2	27.0	198
TSE	2002	0.7	13.3	12.6	7546	973	5.4	0.39	0.7	9.9	25.4	223
TMK	2001	2.4	17.1	14.7	8125	1208	5.9	0.33	0.6	14.0	42.6	202
	2002	2.7	17.6	14.9	8433	885	6.7	0.35	0.6	13.5	41.8	224
	2003	3.2	18.8	15.6	9028	1034	6.4	0.29	0.6	14.8	47.6	199
TKY	2000	0.6	15.8	15.1	10012	1912	6.4	0.39	0.5	9.0	28.1	227
	2001	1.1	14.1	13.0	10003	1655	6.3	0.39	0.5	8.4	25.7	202
	2002	1.0	15.0	14.0	9840	1912	6.5	0.40	0.5	9.5	35.9	195
	2003	1.4	12.2	10.8	9307	2294	6.3	0.40	0.4	8.3	31.9	215
	2004	1.5	9.3	7.8	10337	2392	7.3	0.39	0.5	5.9	20.5	238
FJY	2000	3.0	16.8	13.8	10464	1599	9.6	-	0.8	14.8	28.2	365
	2001	3.7	16.8	13.1	10344	2414	9.1	-	0.7	14.0	29.3	361
	2002	4.2	17.1	12.9	10576	1858	9.5	-	0.8	14.4	28.5	364
	2003	2.5	13.7	11.2	9777	2201	9.2	-	0.6	14.2	26.8	363
	2004	4.6	17.3	12.7	10883	2201	10.4	-	0.8	15.6	30.3	366
KEW	2001	4.9	18.2	13.2	9493	1437	14.0	-	1.2	13.9	22.9	365
	2002	4.4	20.1	15.8	9424	1179	14.4	-	1.2	14.4	21.5	364
	2003	4.3	20.7	16.4	8430	1971	14.8	-	1.1	15.0	26.3	362
	2004	5.4	22.3	16.8	9239	1797	17.4	-	1.5	15.4	23.5	365
MKL	2003	0.6	33.8	33.1	11941	1708	25.3	0.32	1.8	33.3	55.4	365
	2004	-0.8	30.7	31.5	11449	-	25.5	0.26	2.0	30.9	49.1	365
SKR	2002	-1.8	35.6	37.4	13660	1813	24.5	1.42	1.4	22.0	32.8	365
	2003	0.9	39.6	38.7	14570	1152	24.3	0.12	1.4	25.0	39.2	365
PSO	2003	-0.4	31.4	31.8	12603	1896	25.9	0.25	1.3	21.6	25.9	365
	2004	2.4	33.7	31.3	12335	1655	26.6	0.26	1.3	24.4	29.2	366
	2005	0.8	31.4	30.5	13100	1649	26.5	0.25	1.4	23.1	27.4	365
BKS	2002	4.4	27.1	22.7	11853	2015	25.3	0.27	1.3	22.4	37.0	365
PDF	2002	-7.2	32.9	40.1	6425	1853	26.7	0.30	1.5	23.7	31.8	365
	2003	-5.8	33.1	38.8	7197	2291	26.4	0.28	1.5	25.5	34.1	365

Daytime VPD is the annual mean VPD for PPFD above 1000  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . Growing season length is the number of days of positive GPP.

<sup>a</sup> Data are from June to early September 2005.

<sup>b</sup> Data are from long-term (1968–1992) meteorological data at a meteorological station near the site.

<sup>c</sup> Data are from April 2003 to March 2004.



**Fig. 2 – Relationships between annual mean air temperature ( $T_a$ ) and (a) GPP, (b) RE, (c) NEP and (d) ratio of RE to GPP (RE/GPP). Data is categorized by forest type (Table 2) using symbols. A solid line in (a) is the regression line, which is calculated from non-disturbed forests (that is, except for disturbed sites (TRF, TRD));  $GPP = 0.97T_a + 7.99$ ,  $r^2 = 0.92$ ,  $RMS = 2.84 \text{ tC ha}^{-1} \text{ year}^{-1}$ . The dashed line in (a) is the regression between annual GPP and annual mean air temperature in North America and Europe (Law et al., 2002);  $GPP = 0.42T_a + 8.53$ ,  $r^2 = 0.50$ . The solid line in (b) is the regression curve, which is calculated from non-disturbed forests excluding disturbed sites (TRF, TRD);  $F_{\text{night, Tref}} = F_{\text{RE, Tref}} e^{E_0/R[(1/(T_K+T_{\text{ref}}-T_0)) - (1/(T_K+T_0-T_a))]}$ ,  $F_{\text{RE, Tref}} = 14.47 \text{ tC ha}^{-1} \text{ year}^{-1}$ ,  $E_0 = 24.99 \text{ J mol}^{-1} \text{ K}^{-1}$ ,  $r^2 = 0.89$ ,  $RMS = 3.45 \text{ tC ha}^{-1} \text{ year}^{-1}$ .**

deciduous forests (LSH, TMK, TKY) at mid-latitude. At low latitude, NEP varied from being a large  $\text{CO}_2$  sink in tropical secondary forest BKS (TRF; 1°S), almost at equilibrium in tropical rain forest PSO (TR; 3°N) and a large  $\text{CO}_2$  source ( $-5.8$ – $-7.2 \text{ tC ha}^{-1} \text{ year}^{-1}$ ) in tropical peat swamp forest PDF (TRD; 2°S). This large negative NEP was mainly caused by enhanced ecosystem respiration due to the affect of the artificial disturbance, in which the ground water level decreased due to excavated drains, and the decomposition of soil organic matter significantly accelerated as the surface soil dried (Hirano et al., 2007). This resulted in the highest RE/GPP value of 1.2 of all sites. The values of RE/GPP ranged from 0.8 to 1.0 in other tropical forests ( $<20^\circ\text{N}$ ), from 0.7 to 1.0 in temperate forests ( $30$ – $45^\circ\text{N}$ ), and were about 0.7 for subarctic forests ( $>48^\circ\text{N}$ ). In the young tropical secondary forest BKS (TRF; 1°S), RE/GPP was about 0.8, which was smaller than other tropical forests due to low RE.

### 3.2. Relationships between air temperature and GPP, RE and NEP

The responses of annual values of NEP, GPP, RE, and RE/GPP to environmental factors are examined in the following sections. Fig. 2 shows the relationships between annual carbon fluxes and annual mean air temperature. Data was categorized by

forest types, which were deciduous coniferous (DC; TUR, SKT, LSH, TMK), deciduous broadleaf (DB; TKY), mixed (MX; TSE), evergreen coniferous (EC; FJY, KEW), tropical (TR; MKL, SKR, PSO), tropical swamp (TRD; PDF), and tropical secondary (TRF; BKS) (Table 2). As is clearly shown in Fig. 2(a), the annual values of GPP linearly increased with the air temperature, which varied between  $-10$  and  $27^\circ\text{C}$  from the subarctic zone to the tropical zone. The solid line in Fig. 2(a) shows the result of linear regression between GPP and the annual temperature obtained in the present study ( $GPP = 0.97 \times T_a + 8.4$ ,  $r^2 = 0.92$ ,  $RMS = 2.84 \text{ tC ha}^{-1} \text{ year}^{-1}$ ), except for the two disturbed sites: BKS (TRF) and PDF (TRD) (Table 4). The dashed line shows the result based on forests in North America and Europe from Law et al. (2002) ( $GPP = 0.47 \times T_a + 8.52$ ,  $r^2 = 0.50$ ).

The annual values of RE also had a significant positive correlation with the annual air temperature (Fig. 2(b)), however, the relation was rather more exponential than linear. The solid curve in Fig. 2(b) was the result of regression with the Lloyd and Taylor equation. The determination coefficient of the regression curve was 0.89 and RMS was  $3.45 \text{ tC ha}^{-1} \text{ year}^{-1}$ , which indicates the RE–temperature relationship was relatively more scattered than the GPP–temperature relationship.

It should be noted that the regression lines shown in Fig. 2(a) and (b) were calculated only from the data of mature forests, not using data from the two disturbed forests; BKS (TRD) and PDF

**Table 4 – Regression results where the equation is  $y = aX + b$** 

Y variable	X variable	Slope, $a$	Intercept, $b$	$r^2$	RMS
Annual GPP (tC ha year <sup>-1</sup> )	Annual mean air temperature (°C)	0.97	7.99	0.92	2.84
Annual GPP (tC ha year <sup>-1</sup> )	Annual cumulative PPFD (mol m <sup>-2</sup> year <sup>-1</sup> )	0.00	-7.64	0.37	7.83
Annual GPP (tC ha year <sup>-1</sup> )	Annual mean $P_{\max}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	1.17	2.09	0.87	3.63
Annual GPP (tC ha year <sup>-1</sup> )	Maximum $P_{\max}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	0.54	3.07	0.38	7.78
Annual GPP (tC ha year <sup>-1</sup> )	Maximum LAI (PAI) (m <sup>2</sup> m <sup>-2</sup> )	3.09	7.42	0.23	10.23
Annual GPP (tC ha year <sup>-1</sup> )	Annual mean SWC (m <sup>3</sup> m <sup>-3</sup> )	-16.15	23.61	0.03	11.68
Annual RE (tC ha year <sup>-1</sup> )	Annual mean SWC (m <sup>3</sup> m <sup>-3</sup> )	-17.40	22.94	0.03	12.11

The data includes non-disturbed sites (DC, DB, MX, EC and TR) and excludes disturbed sites (TRF and TRD).

(TRF). The data from the disturbed sites was also plotted in Fig. 2(a) and (b), and the relations between GPP and the annual temperature at the disturbed forests were quite similar to those for the mature forests (Fig. 2(a)), however, the relations between RE and the annual temperature at the disturbed forests were much more scattered (Fig. 2(b)).

Fig. 2(c) shows the relationship between annual NEP and annual mean air temperature. Observed annual NEP rapidly increased with air temperature, when the temperature was lower than about 10 °C, from 1 to 5 tC ha<sup>-1</sup> year<sup>-1</sup>, and stayed at 4–5 tC ha<sup>-1</sup> year<sup>-1</sup> in the temperature range between 10 and 20 °C. In the tropical zone with a temperature from 24 to 27 °C, the annual NEP showed a large scatter from -7 to 4 tC ha<sup>-1</sup> year<sup>-1</sup>.

The ratio of RE to GPP increased with temperature (Fig. 2(d)). RE/GPP was almost 0.7 when the annual mean temperature was below 0 °C. In the temperate zone with a temperature range between 5 and 20 °C, values of RE/GPP ranged from 0.7 to 1.0, where the values of RE/GPP for temperate deciduous coniferous (temperate larch) (DC) and temperate mixed (MX) forests (~1.0) were higher than that for temperate deciduous (DB) and temperate evergreen coniferous (EC) forests (0.7–0.8). In the tropical zone, the RE/GPP of mature forests ranged between 0.8 and 1.0; 0.8 for young secondary forest (TRF, BKS sites), was the smallest and 1.2 for drainage forest (TRD, PDF sites) was the largest.

### 3.3. Maximum GPP at light saturation ( $P_{\max}$ )

The forest sites included in the present study have different dominant species, different light-photosynthesis responses for individual leaves, and different growing periods. In order to make clear the controlling factors for the annual GPP, we examined the significance of the parameters for the maximum and the mean levels of photosynthetic ability. Table 4 shows the regression results for the relationship between the annual GPP and the maximum  $P_{\max}$  and the annual mean  $P_{\max}$ , respectively. Annual mean  $P_{\max}$  clearly increased with annual GPP (Fig. 3, Table 4), although maximum  $P_{\max}$  had a poor relationship with annual GPP (Table 4). In Section 4.1, we discuss the reason that the annual mean  $P_{\max}$  correlates strongly with annual GPP.

### 3.4. Other climatic factors

Table 4 shows linear regression results for the annual values of several variables with GPP and RE. Annual PPFD did not influence annual GPP, although PPFD influenced seasonal or interannual variations of GPP at a specific site (e.g. Li et al.,

2005; Hirano et al., 2007; Hirata et al., 2007). These results were because GPP saturated at high PPFD and PPFD had no affect during the defoliated season.

The annual GPP had a positive correlation with the maximum leaf area index (LAI), although the correlation coefficient was poor ( $r^2 = 0.23$ ). A caution should be given that the LAI data at several sites included not only leaf area but also plant area such as stems and branches. Moreover, the evaluation method for LAI was different among the sites.

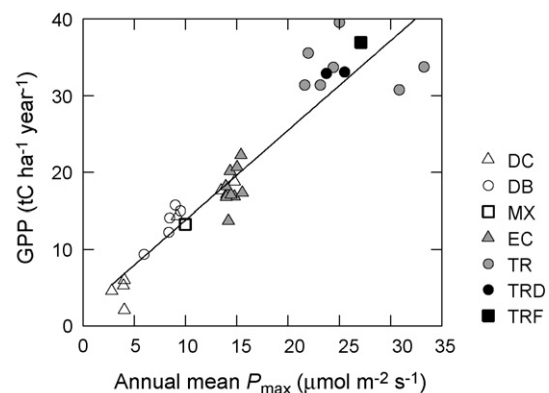
The correlation was also relatively low between the annual values of soil water content (SWC) and both GPP and RE across East Asia, although SWC influenced the RE of tropical forests at a site scale (Gamo et al., 2005; Hirano et al., 2007; Kosugi et al., 2008). In contrast, it did not influence the RE of a subarctic forest (SKT) (Li et al., 2005) or a temperate larch forest (TMK) (Liang et al., 2004) at a site scale.

Both GPP and RE decreased with annual precipitation when precipitation was below 1000 mm year<sup>-1</sup>. However, there was no significant relationship between NEP and precipitation (Table 3).

## 4. Discussion

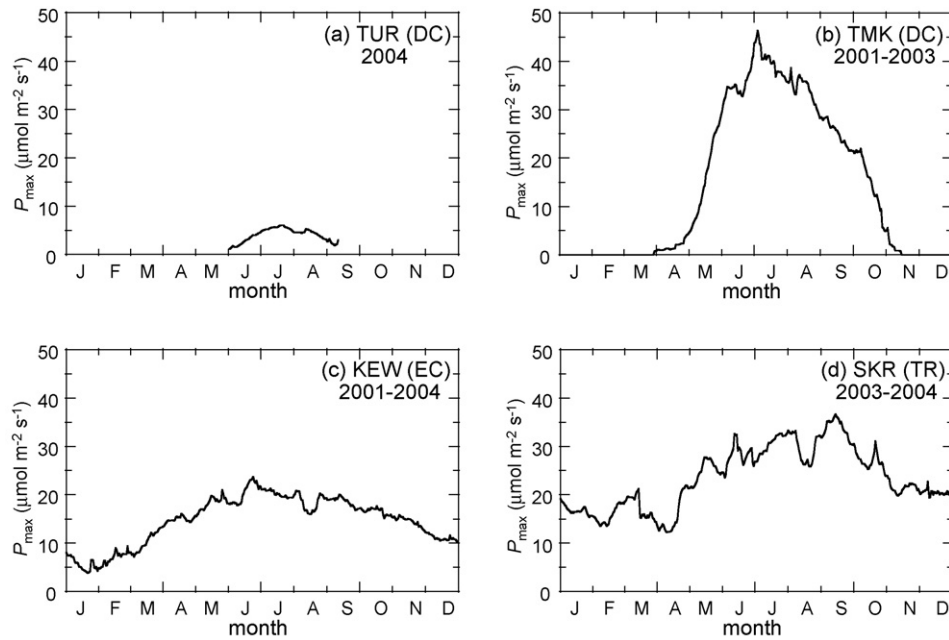
### 4.1. GPP

This study clearly shows that annual GPP has a significant positive correlation with the annual air temperature across East Asia, and the relationship is quite linear even though the study sites covered diverse forest ecosystems with a wide climatic range from subarctic to tropical zones and different



**Fig. 3 – Relationship between annual GPP and annual mean  $P_{\max}$ ;  $Y = 1.17X + 2.09$ ,  $r^2 = 0.87$ ,  $RMS = 3.63$  tC ha<sup>-1</sup> year<sup>-1</sup>.**





**Fig. 4** – Seasonal variation in  $P_{\max}$  at the (a) TUR, (b) TMK, (c) KEW and (d) SKR sites.

ecosystem types such as deciduous, evergreen, broadleaved, and coniferous (Fig. 2(a)). At the same time, the annual GPP shows a strong linear relationship with the annual mean  $P_{\max}$  (Fig. 3). We are, therefore, able to hypothesize that there is a significant interdependence among the annual air temperature, the annual mean  $P_{\max}$ , and the annual GPP in the forest ecosystems across East Asia. In the following sections, we discuss how meteorological elements and biological characteristics regulate annual GPP.

It is generally said that GPP is determined by growing season length, photosynthetic capacity, and LAI (Chapin et al., 2002). The annual air temperature can influence all three of the above conditions, and in particular, the temperature is the most important factor in regulating the growth period length (Saigusa et al., 2008). As listed in Table 3, the growing season length for GPP, which means the number of days when GPP was positive, could be longer than 360 days when the annual air temperature was above 9 °C for evergreen forests in temperate and tropical zones, and decreased to only about 100 days with the decrease in annual temperature in temperate and subarctic zones.

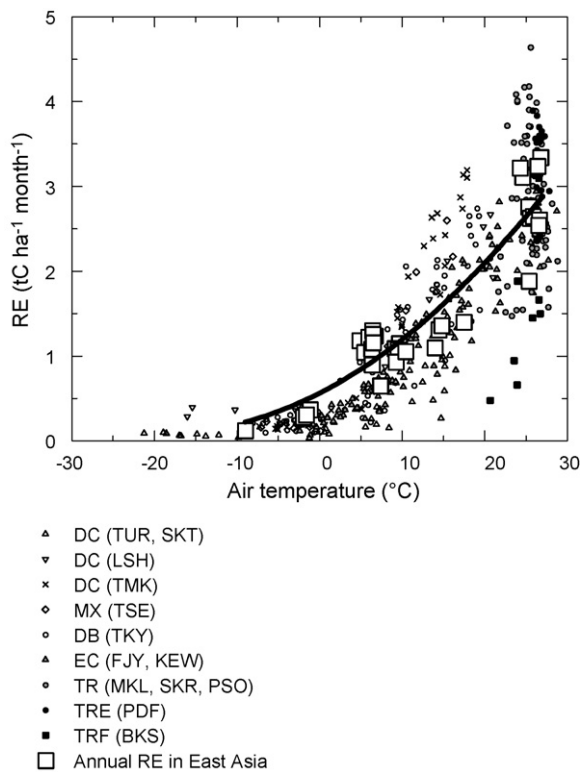
The seasonal change of the photosynthetic capacity was an important factor in regulating the annual GPP. Seasonal changes in  $P_{\max}$ , which represents the highest level of photosynthetic capacity, are plotted in Fig. 4 for a subarctic larch forest in central Siberia (TUR), a temperate larch forest in northern Japan (TMK), a temperate evergreen coniferous forest in central Japan (KEW), and a tropical evergreen forest in Thailand (SKR). In the larch forest in central Siberia (TUR), the growing season was quite short (from June to August), and the maximum value of  $P_{\max}$ , which appeared in the early stage of the growing period (July), was the lowest of all sites. At the temperate larch forest (TMK), the growing season was longer than TUR (from May to October), with the highest  $P_{\max}$  observed in June. At the evergreen site (KEW), the growing

season was the longest (the whole year), however, the maximum value of  $P_{\max}$  was less than the temperate deciduous forest.  $P_{\max}$  of the tropical dry evergreen forest (SKR) peaked at the end of the rainy season or the beginning of the dry season (September to October), but kept relatively high throughout the year.

According to Table 3,  $P_{\max}$  values observed in the temperate larch forest ( $44.0 \mu\text{mol m}^{-2} \text{s}^{-1}$  at TMK) was higher than those in the two tropical forests (SKR, PSO) where the annual values of GPP were extreme ( $>30 \text{ tC ha}^{-1} \text{ year}^{-1}$ ). This result was interpreted to mean that higher annual GPP in the tropical forests was mainly attributable to relatively high  $P_{\max}$  maintained throughout the year. The strong positive correlation between the annual mean  $P_{\max}$  and the annual GPP supports this. The reason the annual mean  $P_{\max}$  showed higher correlation with the annual GPP compared to the maximum  $P_{\max}$  was that the annual mean  $P_{\max}$  takes into account the affect of growing period length.

In previous studies, Law et al. (2002) found that there is a significant positive correlation between the annual air temperature and the annual GPP estimated at various flux sites in North America and Europe. The regression lines of both studies are plotted in Fig. 2(a), with a dashed line for Law's result and a solid line for the present study. The present study covers a wide temperature range from  $-9$  to  $27$  °C, and the determination coefficient of the regression line was much higher (0.92) than that in Law's study (0.57). This result suggests that the annual GPP in East Asian forests is primarily related to annual temperature.

One of the reasons the annual GPP so strongly correlates with temperature was possibly that forests in East Asia are not exposed to severe stresses other than temperature. For example, photosynthetic capacity of forests in North America and Europe is influenced by the limitation of soil water content and high vapor pressure deficit (VPD) caused by summer



**Fig. 5 – Relationship between monthly RE and air temperature. Relationship between annual RE and annual mean air temperature represented by white square symbols, and its regression curve**  
 $(F_{\text{night, Tref}} = F_{\text{RE, Tref}} e^{E_0/R((1/(T_K+T_{\text{ref}}-T_0))-(1/(T_K+T_0-T_a)))}$ ,  
 $F_{\text{RE, Tref}} = 1.20 \text{ tC ha}^{-1} \text{ month}^{-1}$ ,  $E_0 = 25.73 \text{ J mol}^{-1} \text{ K}^{-1}$ ),  
 represented by a solid line, are the same as those in Fig. 2(b) except that the annual RE has been converted from annual to monthly.

drought (e.g., Anthoni et al., 1999; Scott et al., 2004). In comparison, the annual precipitation at the present study sites in East Asia was mostly higher than 600 mm, up to 2400 mm, except for the two subarctic sites (230–270 mm at SKT; 360 mm at TUR). This is fairly high compared to North America and Europe (198–1700 mm). Furthermore, there is a rainy season at mid-latitudes in East Asia in the early stage of the growing season typically from June to July, which provides sufficient water to ecosystems every year. As a result, less summer drought stress is a strong candidate for the main cause of the simple relationship between the annual GPP and the annual air temperature in East Asia. On a site scale, the diurnal, seasonal or interannual variation of GPP is affected by VPD conditions (Gamo et al., 2005; Li et al., 2005; Wang et al., 2004; Hirano et al., 2007).

#### 4.2. RE

A strong exponential relationship between the annual RE and the annual mean air temperature was observed throughout East Asia (Fig. 2(b)). Similar results were observed at a site scale. In Fig. 5, we superimpose the monthly RE–air tempera-

ture relationship on the annual relationship (Fig. 2(b)) (the unit of RE has been converted from annual to monthly) in order to compare the dependency of RE on air temperature between an East Asia scale and an individual site scale. The white squares and solid curve represent the relationship between annual RE and air temperature. Most monthly RE–air temperature relationships almost overlap annual RE–air temperature relationships, except for temperate larch and mixed forests in northern Japan (TMK; DC, TSE; MX), which have ratios of GPP to air temperature that increase at a quicker rate than those of other forests. At TMK site, RE values should be enhanced by the high photosynthetic activity of larch forest during the growing season (Hirata et al., 2007).

In contrast, previous studies such as Law et al. (2002) reported a less clear relationship between annual RE and annual mean temperature in North America and Europe. One of the advantages of this study was that the sites were distributed over a wide latitude range from 2°S to 64°N with an annual temperature from –9 to 27 °C, while the previous study sites in North America and Europe typically covered from 30 to 70°N. The wide latitude range of the present study enabled us to detect a clear temperature dependence of the annual RE in East Asia in a wide temperature band.

The annual RE is regulated by numerous components, such as respiration in the stem (Liang et al., 2005; Miyama et al., 2006), branch (Miyama et al., 2003), root (Lee et al., 2003; Dannoura et al., 2006), foliage (Miyama et al., 2003), microorganisms (Uchida et al., 2005), and decomposition of litter (Kim et al., 2005a, Kim et al., 2005b), soil organic carbon (Lee et al., 2003; Dannoura et al., 2006) and coarse wood debris (Jomura et al., 2007). The total annual ecosystem respiration is affected by various processes, not only by meteorological factors such as temperature and soil water content, but also by biological and biochemical factors such as plant biomass, soil organic matter content, nutrient resources, chemical substances and physical characteristics of the soil, type of disturbance, tree age, seasonal changes in photosynthesis, leaf area, and other phenological events. Responses of the ecosystem respiration to the environment are different depending on the ecosystem (Bond-Lamberty et al., 2004; Subke et al., 2006; Trumbore, 2006). Thus, the respiratory processes could be far more influenced by any number of factors other than the photosynthetic processes. This interpretation is supported by the fact that the RE–temperature relationship was more scattered than the GPP–temperature relationship.

Although the respiration processes includes complicated mechanisms, the annual total ecosystem respiration from diverse ecosystems across East Asia was expressed by one simple curve as a function of the annual mean air temperature. On the other hand, the seasonal or interannual variation of RE was affected by seasonal changes in water resources in some tropical forests such as MKL, SKR (Gamo et al., 2005), PSO (Kosugi et al., 2008) and PDF (Hirano et al., 2007).

#### 4.3. NEP

In the present study, the NEP–temperature relationship in Fig. 2(c) shows that NEP is close to zero in subarctic larch forests (DC) with low annual temperatures (<0 °C). In the mid-

temperature zone (5–20 °C), the annual NEP tends to increase with temperature, and the CO<sub>2</sub> uptake rate is highest in the temperature range around 10–20 °C. For high temperatures (>20 °C) the values of annual NEP show a significant scatter from a large CO<sub>2</sub> source (–8 tC ha<sup>–1</sup> year<sup>–1</sup> at TRD) to a large sink (4 tC ha<sup>–1</sup> year<sup>–1</sup> at TRF). The large scatter in the annual NEP in the high temperature zone was due to the large scatter in the annual RE, not in GPP.

The influence of disturbance was more significant on RE than on GPP. A large CO<sub>2</sub> release was observed at the PDF site (TRD) affected by the artificial drainage and acceleration of peat decomposition by drying soil, although the annual GPP of the PDF site was relatively close to those of non-disturbed natural forests (TR). The annual GPP of BKS (TRF) is also close to that of other natural tropical forests; however, the annual RE of the BKS site was smaller than that of non-disturbed natural tropical forest, probably because the trees were quite young (<4 years old) and the above-ground and below-ground plant biomass was less than those at the mature forests. Except for the two disturbed sites, the annual NEP in tropical mature sites was mostly less than that in the mid-temperature zone, due to the increased rate of annual RE with temperature being much higher than that of GPP in higher temperature conditions. In the Amazon region, Saleska et al. (2003) also reported that recent disturbance influences RE rather than GPP; old-growth forests lost CO<sub>2</sub>, which was mainly released from large coarse wood debris (CWD) pools despite high growth rates (Rice et al., 2004) because of the recent disturbance such as drought associated with a strong El Niño event.

While annual GPP is simply regulated by annual mean air temperature (Section 4.1), annual RE is much more sensitive to factors other than air temperature when compared to GPP (Section 4.2). The annual NEP was not simply determined by annual mean air temperature only. Caution should be exercised as NEP is small in comparison to large gross fluxes such as GPP and RE. Therefore, factors other than annual mean air temperature (e.g. site history, disturbance, and soil characteristic) are responsible for the scatter in the RE–temperature relationship (Figs. 2(b) and 5), and that they have a great impact on the resultant NEP. Consequently, annual NEP should be understood in terms of a wide variety factors via RE. In temperate and boreal European forests, which are N-limited, Magnani et al. (2007) reported that NEP was strongly driven by nitrogen deposition resulting from anthropogenic activities while GPP and RE were regulated by air temperature.

#### 4.4. Validity of NEP

It is important to evaluate the uncertainty of the annual NEP by crosschecking with different methods. In this section, we compare the annual NEP estimated by the eddy covariance technique with that obtained by the biometric and chamber methods in order to evaluate the uncertainty.

There are many sources of uncertainty in the eddy covariance technique: horizontal advection and nighttime data correction, topography, surface roughness, and nighttime atmospheric stability (e.g. Massman and Lee, 2002). Moreover, the different instrumentation and installation of the measurement system among sites may cause systematic

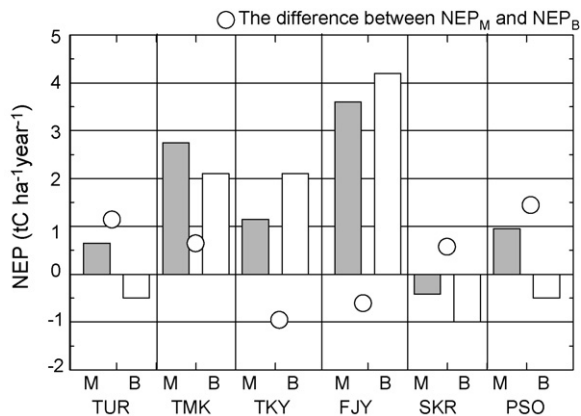
errors when we use the data for the purpose of inter-site comparisons (Loescher et al., 2005). In addition, even though the flux measurement was ideally conducted on flat and horizontal-homogeneous surfaces, the temporal average of fluxes observed at a single point may have an inherent distortion compared with the spatial average (Kanda et al., 2004).

Here we use data from the biometric and chamber methods to evaluate uncertainty in the annual NEP, since both methods have advantages and disadvantages. The advantage of the biometric method for NEP evaluation is that long-term changes in plant biomass and carbon stock in the soil are detectable and is, hence, suitable for verification of long-term integration of NEP (Jia and Akiyama, 2005; Ohtsuka et al., 2005). The disadvantage is that the method still has a large uncertainty in estimating carbon stock in the soil, such as soil organic matter and fine root production (Satomura et al., 2006; Fukuzawa et al., 2007). The advantage of the chamber method is that we can use the data for validation of specific processes on a short time scale such as nighttime ecosystem respiration and daytime canopy photosynthesis, while the disadvantage is that it requires an enormous number of measurements to establish spatial heterogeneity and there are large uncertainties in the process of scaling up space and time because many assumptions need to be made (Malhi et al., 1999).

Other sources of uncertainty may be in the carbon loss from the foliage as volatile organic compounds (Tani et al., 2002; Ieda et al., 2006), and from the soil through leaching by herbivores (Chapin et al., 2002). We neglected these affects in the present study.

It is important to point out that the spatial and temporal results of ground research such as micrometeorological, biometric, and chamber method base analysis are limited. For instance, our eddy flux data was obtained within about 1 km. Therefore, our observation data cannot completely cover the long-term and wide areas including whole forests, tree age, and disturbance in East Asia. Our results are, however, informative and useful to validate terrestrial ecosystem models to investigate the response of forest to climate and disturbance (Sasai et al., 2005; Friend et al., 2007; Ito et al., 2007).

Since the early 2000s, many studies have been conducted in various terrestrial ecosystems in Asia to estimate the annual values of carbon budget components using biometric measurements and the chamber method. The annual NEP had been estimated by the biometric method at the TUR (Matsuura et al., 2007), TMK (Yone et al., 2005; Yone et al., 2006; Hirata et al., 2007), TKY (Ohtsuka et al., 2007), FJY (Sugita, 2005), SKR (Yamamoto et al., 2005), and PSO sites (Yamamoto et al., 2005). Fig. 6 shows the annual NEP from micrometeorological and biometric methods and the difference between the two. Both methods resulted in similar variation of NEP between sites. The differences of NEP between the two methods were  $0.4 \pm 1.0$  tC ha<sup>–1</sup> year<sup>–1</sup>. Attention should be paid to uncertainty arising from the difference of measuring period for the eddy covariance technique and the biometric method at each site. If we simply scaled the difference ( $0.4 \pm 1.0$  tC ha<sup>–1</sup> year<sup>–1</sup>) over the present study area (2.1 Gha; East and Southeast Asia and Russia (FAO, 2006)), the uncertainty in the different methods



**Fig. 6 – Comparison of NEP between the meteorological (M) and the biometric method (B). Circles show the subtraction of NEP obtained by the biometric method from that calculated by the meteorological method.**

reached  $0.86 \pm 2.05 \text{ PgC year}^{-1}$ . Ground measurement of NEP still contains uncertainties in the present study; these should be minimized by improving long-term measurements for both methods in future study.

The chamber method for soil, trunk and foliar respiration was applied to the KEW and TMK sites. Ohkubo et al. (2007) validated that nighttime NEP of the KEW site by chamber method with identical results to that by eddy covariance technique with a  $u$ -threshold. At the TMK site, Liang et al. (2006) also verified that total NEP of the eddy covariance technique was close to that of the chamber method (Hirata et al., 2007).

In the temperate zone, some sites, such as TKY and KEW, were located in mountainous regions and the topography around the tower was quite complex. The uncertainty caused by the horizontal advection and nighttime data correction is large, however, the annual NEP estimated by the two methods were relatively close at both sites (Ohtsuka et al., 2007; Ohkubo et al., 2007). This result suggests that the eddy covariance data can be used for estimating ecosystem carbon cycle components even in complex topography if the data is well validated by other methods (Hammerle et al., 2006).

Kosugi et al. (2008) reported that many calm nights caused continuous underestimation of nighttime NEP by the eddy covariance technique at the PSO site. In contrast, at the PDF site, Hirano et al. (2007) observed large nighttime NEE by eddy covariance technique with small  $u$ -similar to that at the PSO site. Nighttime NEE estimation remained difficult and the uncertainty was significantly higher in tropical forests for reasons such as a large amount of respiration under high temperature conditions throughout the year, many calm nights (Kosugi et al., 2008), and tall canopy with a wide variety of tree height (Finnigan, 2004).

## 5. Conclusions

This paper compares annual values of NEP, GPP, and RE among 11 mature forests and 2 disturbed forests across East Asia

including different ecosystem types such as evergreen and deciduous, coniferous and broadleaf, planted and natural forests, with a wide climatic range from subarctic, through temperate, to tropical zones.

In East Asia, where sufficient precipitation is supplied to most ecosystems in every growing season, summer drought stress is less severe than in North America and Europe. Thus the environmental influence on forest NEP, GPP, and RE differs in several aspects between these areas.

The findings we obtained from the present inter-site comparison are summarized as follows:

- (1) The annual GPP and RE are simply regulated by annual mean air temperature across East Asia. The annual GPP has a very strong linear relationship with the annual air temperature, and the annual RE also has a clear exponential relationship with temperature.
- (2) There is a clear inter-dependency among the annual GPP, annual mean  $P_{\text{max}}$ , and the annual temperature; which means that the annual GPP is regulated by both growing period length and the seasonal variation in maximum photosynthetic ability. Air temperature is the most important influence on these values.
- (3) The RE–temperature relationship is more complicated than the GPP–temperature relationship. This is because annual RE is much more sensitive to factors other than the annual temperature compared to GPP. Some factors other than annual mean air temperature (e.g. site history, disturbance, and soil characteristic) are responsible for the scatter in the RE–temperature relationship (Figs. 2(b) and 5), and that they have a great impact on the resultant NEP. This indicates that annual NEP should be understood in terms of a wide variety factors via RE.
- (4) Annual NEP is small at high latitude, relatively large at mid-latitude, and is widely scattered at low latitude. The site-specific characteristics of NEE are influenced more by RE than GPP.
- (5) Compared with North America and Europe, the regression coefficients of the GPP–temperature and RE–temperature relationships are high. Moreover, the slope of the GPP–temperature relationship in East Asia is greater than that of North America and Europe. One of the reasons for this relates to less restriction of GPP and RE by severe environmental stresses such as summer drought. As a result, the temperature dependence of the annual values of GPP and RE can be expressed in a relatively simple form in East Asia.

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