Investigating effect of environmental controls on dynamics of CO$_2$ budget in a subtropical estuarial marsh wetland ecosystem

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Investigating effect of environmental controls on dynamics of CO_2 budget in a subtropical estuarial marsh wetland ecosystem

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Abstract

In this study, we quantified the ecosystem-scale CO_2 exchange of two different but typical low-latitude vegetation types, para grass and reed, in a subtropical wetland ecosystem by integrating flux observation with the parameterization of environmental variables. In addition, we explored how seasonal dynamics of environmental factors affected variations in CO_2 budget. The results suggest that gross primary production (GPP, in the order of 1700 gC m^{-2} yr^{-1}) of CO_2 was higher in this site than in previous studies of northern peatlands and estuarial wetlands because of the direct effect of environmental factors. Temperature and radiation had a larger effect than water status (soil moisture content and vapor pressure deficit) on GPP for the two low-latitude ecosystems, which differ from the results for high-latitude regions. Environmental variables had a strong but different impact on the CO_2 budget for para grass and reed areas. This diversity led to different potential shifts and trends of biomass accumulation and distribution of these two typical low-latitude vegetation types under different scenarios of environmental change. The findings from this study can sufficiently provide quantitative understanding of CO_2 budgets in low-latitude wetlands.

1. Introduction

Concerns related to regional and global environmental change have stimulated much interest in investigating the control mechanisms on potential shifts of carbon (C) exchange over different ecosystems. Wetlands cover only 6%–7% of the Earth's surface (Lehner and Döll 2004), but the C storage is estimated to be up to 450 Gt C or approximately 20% of the total C storage in the terrestrial biosphere (Gorham 1991, Maltby and Immirzi 1993). A recent report by Intergovernmental Panel on Climate Change stated that coastal wetlands are highly sensitive to climate change, and one of the greatest challenges in understanding the functioning of estuarine ecosystems is to accurately estimate their C storage and budget (Nicholls *et al* 2007).

On the global scale, wetlands are found over different latitudes under varying climate conditions and have a unique role in regulating global biogeochemical cycles (Reddy and DeLaune 2008). The characteristics of worldwide wetland ecosystems vary widely because of differences in environmental factors and human disturbance. In recent years, despite

some studies on C storage and budget in wetland ecosystems, most were of northern peatlands (Leverenz 1987, Battin *et al* 2009). Northern peatlands mainly function as long-term sinks for atmospheric carbon dioxide (CO_2) and sources of atmospheric methane (CH_4), and their net primary productivity is mainly controlled by the environmental factors and the availability of nutrients (Alm *et al* 1997, Friborg *et al* 2003, Sottocornola and Kiely 2005, Dunn *et al* 2007).

In contrast, estuarine wetland ecosystems are important for C storage for terrestrial ecosystems and are very productive because of the regular input of nutrients (Sverdrup *et al* 2002, Thornton and McManus 1994). Several recent studies concluded that although the global estuarine area is relatively small, its CO_2 degassing flux is as large as the CO_2 uptake by the continental shelf, ranging from 0.4 to 0.6 PgC yr^{-1} and that both flux terms are substantial in terms of global CO_2 flux (Borges 2005, Borges *et al* 2005, Cai *et al* 2006, Chen and Borges 2009). The range of CO_2 flux reflects the heterogeneity and complexity of these highly active biogeochemical environments at the

interface between land and ocean. To date, regions of estuarine CO_2 flux studies are mostly in Europe and eastern North America (Laruelle *et al* 2010); little attention has been paid to estimating CO_2 flux over low-latitude tropical and subtropical estuarine wetland ecosystems.

In addition to determining C budget, quantifying the ecosystem response to seasonal variations of environmental factors is an important issue. Several studies have addressed how the C cycle in peatlands react to seasonality in middle to high-latitude ecosystems (Howes *et al* 1985, Roulet *et al* 1992, Moore *et al* 1998, Waddington *et al* 1998, Ågren *et al* 2007). A recent study of an estuarial reed ecosystem in northern China found strong seasonal variation in the diurnal course of net ecosystem exchange (NEE) (Zhou *et al* 2009). A substantial proportion of this variation could be explained by environmental variables; indeed, soil water content (SWC) and temperature had greater effect on gross primary production (GPP) than photosynthetically active radiation (PAR) and vapor pressure deficit (VPD) in this study site (Zhou *et al* 2009). However, most studies related to environmental controls were conducted in high-latitude ecosystems, and few have investigated estuarial wetlands in tropical or subtropical areas.

Low-latitude wetlands have a broad array of ecosystem services. The ecosystems often show high productivity and feature a unique assembly of aquatic and terrestrial biodiversity. Because of the great influence of tropical and subtropical wetlands on global C cycling, considerable scientific efforts have been invested in quantifying wetland C storage, turnover, hydrologic exports and C interchange between wetland soils and the atmosphere (Mitsch *et al* 1988, Zhuang *et al* 2004, Cui *et al* 2005).

In this study, to quantify the CO_2 exchange and characterize how environmental factors affect the seasonal dynamics of this exchange in low-latitude estuarial wetland ecosystems, we used continuous eddy-covariance (EC) measurement to conduct an investigation in a subtropical estuarine wetland ecosystem in northern Taiwan. In this site, two flux towers were built over two different but representative tropical-to-subtropical ecosystems, para grass and reed. We used EC techniques to analyze temporal variation in CO_2 exchange and determined the effect of environmental factors on the dynamics of CO_2 budget in these two different ecosystems. We aimed to (1) quantify the CO_2 budget, including GPP, ecosystem respiration (R_{eco}), and NEE by examining EC data in terms of environmental variables; (2) analyze the effect of environmental factors on the CO_2 budget; and (3) interpret possible shifts and trends in CO_2 dynamics in this representative subtropical estuarine wetland ecosystem under environmental change.
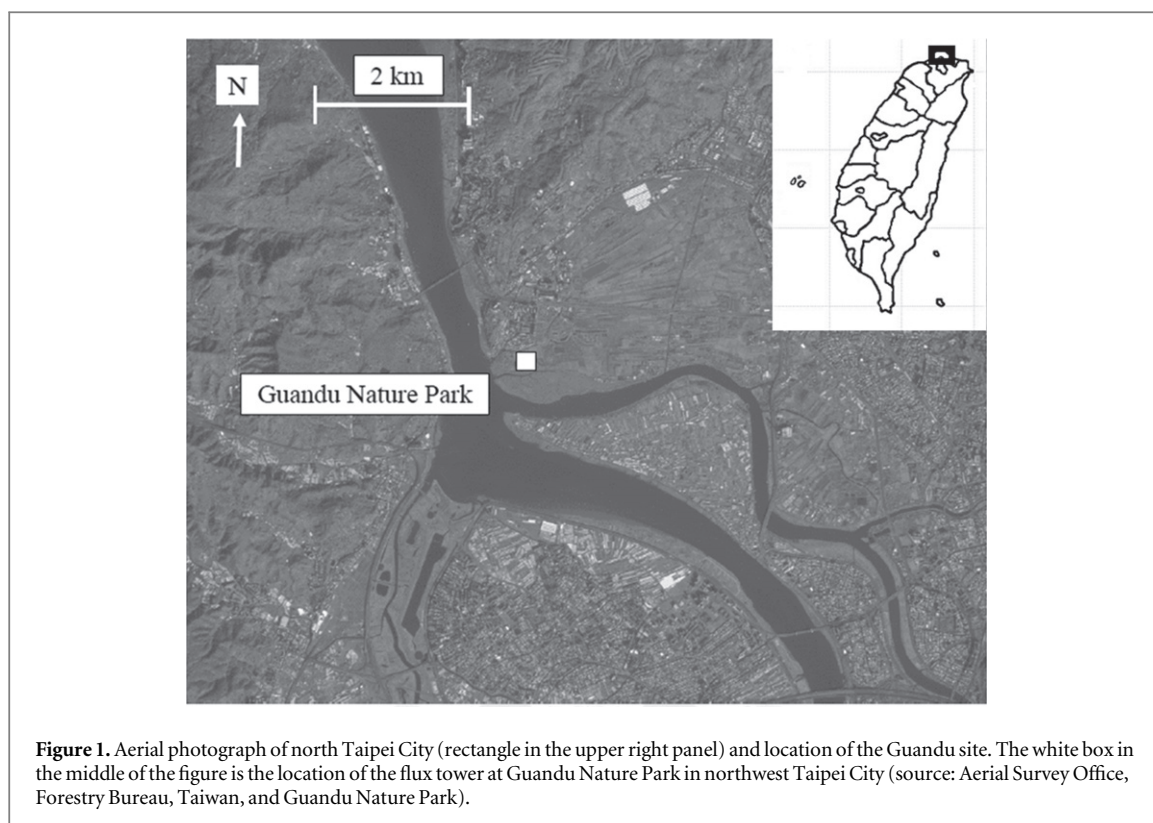
2. Methods

2.1. Study site

Data was collected from an EC flux site (25°7'N, 121°28'E, and 4 m a.s.l.) in the western part of Guandu Nature Park in northwest Taipei City (figure 1). This site is a grass Marsh ecosystem along the riverbank of the Tamsui River, the major river system of the Taipei Basin and is a natural succession-processing area without direct artificial management on the landscape and ecosystem within the study area. The predominant species are para grass (*Brachiaria mutica*) and reed (*Phragmites australis*) (Chang 2011), with mean canopy heights of about 1.2 and 3.0 m, respectively. The major soil type is alluvium clay and is uniformly distributed through the entire rooting zone. The climate is humid subtropical and is strongly influenced by typhoons during the summer and the East Asian monsoon over different seasons. The annual mean temperature is 23.0 °C, and the annual precipitation is 2405.1 mm, with a very mild dry–wet seasonal variation. As for the surface water status, the soil moisture content in reed is mostly close to saturation (from 41.0% to 45.5%) while the variation of soil moisture content for para grass is relatively greater (from 24.5% to 45.5%). Because the precipitation in this study site is more abundant during the summertime, the SWC is high during the wet season and the reed area occasionally experiences surface inundation up to 10 cm in depth for couple hours.

Because the location of the site is only 10 km away from the estuary of Tamsui River, the impact caused by interactions of the estuarial tides and stream flow should play important roles in the hydrological properties, energy budget, and biogeochemical cycles in the area. Several studies provided sufficient information and data on the patterns of nutrients and soil characteristics (Lee 2011) and basic dataset for the local vegetation distributions (Shao 1999) in this subtropical wetland ecosystem.

2.2. Instruments

The EC flux and micrometeorological data were collected from two observation towers in the center of the site. The first tower (hereafter $T1$) is a 3.5 m high walk-up tower located in the center of the site and covered by para grass. Data have been collected at $T1$ since November 2010. The sensors for EC flux were mounted at 3 m and included an open-path infrared gas analyzer (Li-7500, LI-COR, Lincoln, NE, USA) for measuring molar densities of CO_2 and water vapor (H_2O), and a 3D ultrasonic anemometer (Young-81000, R M Yang Corp., Traverse City, MI, USA) for simultaneously measuring wind speed components, wind direction, and virtual temperature.

The second tower (hereafter $T2$) is a 5 m high walk-up tower located 125 m to the east of $T1$ and covered by reeds. Data collection at $T2$ began in January

Figure 1. Aerial photograph of north Taipei City (rectangle in the upper right panel) and location of the Guandu site. The white box in the middle of the figure is the location of the flux tower at Guandu Nature Park in northwest Taipei City (source: Aerial Survey Office, Forestry Bureau, Taiwan, and Guandu Nature Park).

2013. The EC-system sensors were mounted at 5.0 m and include a Li7500 gas analyzer and a 3D ultrasonic anemometer (CSAT-3, Campbell Scientific, Logan, UT, USA). All scalars and fluxes on both towers were sampled at 10 Hz and averaged every 30 min. Data from these two towers were collected by use of a data logger (CR3000, Campbell Scientific, Logan, UT, USA) mounted on $T1$. To estimate the source area of the flux measurement of these two towers, the footprint model developed by Kormann and Meixner (2001) was applied, and the results show that 90% of the footprint is 56 m for $T1$ and 82 m for $T2$. According to the results, the footprint extents for both ecosystem areas are spatially homogeneous and are representative of both towers.

In addition to the EC data, meteorological variables were collected at both sites. Data for PAR (collected by LI-190 quantum sensor, LI-COR, Lincoln, NE, USA) and radiation components (CNR1 four-component net radiometer, Kipp and Zonen, Delft, The Netherlands) were collected at the top of $T1$ and $T2$. Meanwhile, PAR (BF5 sunshine sensor, Delta-T Devices, Cambridge, UK) and radiation components were sampled at the top of $T2$. Air temperature (T_a) and relative humidity were measured by use of HMP45C probes (Campbell Scientific) at both towers. SWC was measured at 0.02 and 0.20 m by using time-domain reflectometry probes (CS616, Campbell Scientific). Precipitation were measured with use of a tipping-bucket rain gauge (RS-102-D, Ogasawara Keiki, Japan) mounted on $T1$. All meteorological data were

recorded by use of the CR3000 data logger on $T1$ and averaged every 30 min.

In this study, the data from January 2011 to May 2014 for para grass and from January 2013 to May 2014 for reed was used for analysis and comparison. Energy, momentum, and scalar fluxes were calculated for each 30 min period. Data quality control in this study applied the following standard procedure widely used in FluxNet, AsiaFlux, and CarboEurope (Webb *et al* 1980, Foken and Wichura 1996, Vickers and Mahrt 1997, Wilczak *et al* 2001, Foken *et al* 2004). The high-frequency raw data quality check, spike detection, and data quality classification (Foken *et al* 2004) were performed by using the EdiRe software developed by University of Edinburg (Clement 2004). Afterwards, the half-hourly flux data was calculated by applying planner-fit correction (Wilczak *et al* 2001), stationarity test (Vickers and Mahrt 1997, Foken *et al* 2004), and Webb–Pearman–Leuning correction (Webb *et al* 1980).

According to the statistics of the measurement data, the gaps (missing data) of the entire study period were 17.8% for para grass and 21.1% for reed, and the gaps are mainly due to the interference caused by precipitation on the LI-7500 open-path gas analyzer, as well as the thermal stratification during the nighttime. To fill the gap, the gap less than 3 h were recovered by using a simple interpolation and the gaps of several hours were filled by applying the mean diurnal variation method (Falge *et al* 2001).

2.3. Quantifying CO_2 budget

On the ecosystem scale, the NEE of CO_2 could be partitioned into two components, GPP and R_{eco}, by the following equation:

$$NEE = GPP + R_{eco}, \qquad (1)$$

where the sign of NEE (CO_2 flux) indicates the uptake (negative) or release (positive) of CO_2. Usually, R_{eco} could be obtained from the relationship between nocturnal NEE and T_a, in terms of data measured directly by the EC tower during nighttime under strong turbulence conditions (friction velocity, U_{star}, > 0.15 m s^{-1}). The relationship between R_{eco} and T_a was estimated by the Van't Hoff equation (Waddington and Roulet 2000):

$$R_{eco} = R_{T_{ref}} e^{B(T_a - T_{ref})}, \qquad (2)$$

where $R_{T_{ref}} = 10\,°C$ is the R_{eco} at reference temperature and B is a site-specific fitted parameter ($B = \frac{\ln Q_{10}}{10}$, where Q_{10} is the temperature coefficient), an indicator of sensitivity to temperature, and defined as the change rate of R_{eco} on increasing the temperature by 10 °C (Xu and Qi 2001).

In addition to R_{eco}, NEE could be parameterized by appropriate environmental factors. During the daytime, maximum ecosystem photosynthesis rate A_{max} (mg CO_2 m^{-2} s^{-1}) and apparent quantum yield α (μmol CO_2 μmol^{-1} photon) were used to indicate plant photosynthetic capacity and characterize the response pattern to radiation (Ruimy *et al* 1995, Frolking *et al* 1998, Zhang *et al* 2006). These two parameters were derived from the relationship between daytime NEE (mg CO_2 m^{-2} s^{-1}) and PPFD (μmol photon). For this purpose, mean daytime values (binned-averages by time of day) for NEE and PPFD were calculated for parameterization. From the daytime 30 min averaged data, the values for A_{max} and α on the ecosystem scale were estimated by the Michaelis–Menten model (Ruimy *et al* 1995):

$$NEE = R_{eco} - \frac{\alpha PPFD \cdot A_{max}}{\alpha PPFD + A_{max}}. \qquad (3)$$

From the measured NEE, the GPP was calculated by equation (1). Daily and monthly values for GPP and R_{eco} were summed from the 30 min data.

2.4. Path analysis

To evaluate how environmental variables affect GPP of CO_2, we performed path analysis (Li 1981, Liu *et al* 2011) with flux data for both ecosystem areas at Guandu to characterize the detailed relationship between environmental factors and components of CO_2 budgets for the two ecosystem areas at seasonal to annual temporal scales. Path analysis, an extension of multivariable regression analysis, provides estimates of the magnitude and significance of hypothesized causal connections of different environmental variables. The method has been widely used in many

ecological studies (Mitsch *et al* 1988, Xu and Qi 2001, Zhuang *et al* 2004, Whittaker *et al* 2009, Mitsch *et al* 2010).

In this study, we assumed that T_a, PAR, SWC and VPD were the primary factors in driving or constricting photosynthetic CO_2 fixation, and their interrelated paths provide the means to evaluate direct and indirect responses (primarily of PPFD). To quantify the path coefficient for each component, we conducted four multiple linear regressions on data collected during the entire study period that did not violate conditions of statistical stationarity in the measured turbulent fluxes. We used standardized partial-regression coefficients to describe the path strengths generated from the following analyses: (1) GPP regressed on T_a, PAR, SWC and VPD; (2) environmental factors regressed on each other. In addition, the test of statistical significance was performed for each regression to characterize how significant the effect was based on a given significance level (0.05).

In order to process the regression analysis, an appropriate time step was determined first to maintain the statistical stationarity (Liu *et al* 2011). Because flux components of grass ecosystems could be affected by short-term weather events (typhoons, fronts, etc) for the time scale of a couple of days (typically three to five days in subtropical East Asia) (Chen and Chen 2003), we used the time step of four days as an average duration to smoothen the effects of meteorological fluctuations.

3. Results

3.1. Comparison of temporal variations of NEE

Climate data suggests there is no onset or end of the growing season in terms of temperature and water status at this site, and the seasonality was relatively mild compared to other wetlands at higher latitudes. To characterize the difference in seasonal variations, we simply divided the data into two groups: the 'fast growing season' for the summer months from May to September, with monthly mean temperature $\geqslant 27\,°C$, and the 'slow growing season', from October to April. Here the terms 'fast' and 'slow' are just for naming of groups.

At $T1$, the hourly dynamics of NEE during fast and slow growing seasons showed similar trends but different magnitudes (figure 2). Mean NEE was −8.0 and −0.4 μmol m^{-2} s^{-1} during the fast and slow growing seasons, respectively, and annual mean NEE was about −5.6 μmol m^{-2} s^{-1}. At $T2$, the difference between the fast and slow growing seasons was smaller than that at $T1$. The mean NEE was −10.8 and −8.7 μmol m^{-2} s^{-1} during the fast and slow growing seasons, respectively, and the annual mean NEE was −9.6 μmol m^{-2} s^{-1}. As for the components of CO_2 budget in the annual scale, from the EC data and the corresponding environmental factors, NEE, R_{eco} and GPP were estimated to
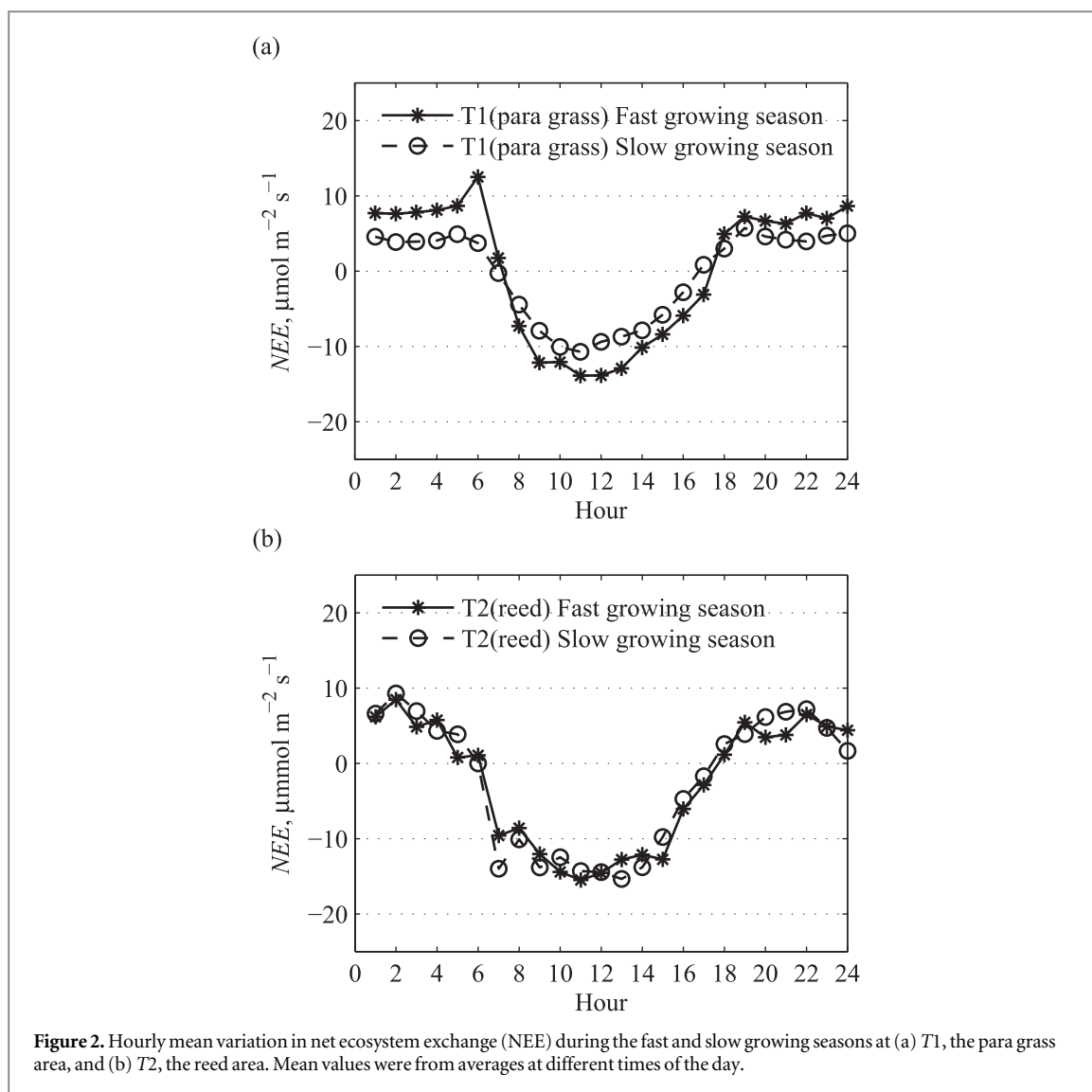
Figure 2. Hourly mean variation in net ecosystem exchange (NEE) during the fast and slow growing seasons at (a) *T*1, the para grass area, and (b) *T*2, the reed area. Mean values were from averages at different times of the day.

be -53.48, 1732.13 and -1785.64 gC m^{-2} yr^{-1}, respectively, for the para grass area and -376.12, 1351.44 and -1727.62 gC m^{-2} yr^{-1}, respectively, for the reed area (table 1).

The comparison of NEE dynamics for these two ecosystems showed that seasonal variation in CO_2 flux between the fast and slow growing seasons for the para grass was relatively larger than reed. The results imply that variations in environmental factors over different seasons were more important for CO_2 uptake in para grass than in reed in this area.

3.2. Responses of NEE to environmental factors

To parameterize R_{eco}, we analyzed the relationship between nocturnal NEE and T_a by equation (2) for both areas (figure 3(a)). At an annual time scale, the temperature dependence of R_{eco} was lower for reeds (*T*2) than para grass (*T*1). The temperature coefficient Q_{10} was estimated at 1.97 for *T*1 and 1.49 for *T*2. Therefore, the results suggest that reeds had higher adaptive resilience to fluctuation in environmental temperature than did para grass in this study site. In

addition, the difference in surface water status (the flooding is more frequent in *T*2 than in *T*1) is expected to be another cause to suppress CO_2 release of reed.

To parameterize NEE in terms of radiation, we used the Michaelis–Menten curve (equation (3)) to fit the whole observed NEE data at both towers. However, the regression curve underestimated NEE at low radiation and could not properly capture the patterns throughout the entire PPFD range. Previous studies suggested that the light response curve may have distinct patterns under different radiation conditions (Leverenz 1987, Kull and Kruijt 1998). Therefore, we divided the data into two groups with different radiation regimes: the data with PPFD < 600 μmol m^{-2} s^{-1} was calculated by linear regression (Kull and Kruijt 1998, Leverenz 1987, Lewis *et al* 2000), and the other group with PPFD $\geqslant 600$ μmol m^{-2} s^{-1} was estimated with the Michaelis–Menten model. The fitted curves suggest that the magnitude of daytime NEE at both towers could be appropriately parameterized by the Michaelis–Menten model ($R^2 = 0.695$ for *T*1 and $R^2 = 0.680$ for *T*2) (figure 3(b)). The difference in NEE patterns in the comparison implies that the two

Table 1. Comparison of annual CO_2 budgets, including net ecosystem exchange (NEE), ecosystem respiration (R_{eco}), and gross primary production (GPP) with previous studies (gC m^{-2} yr^{-1}).

No. site (location)	Vegetation type	NEE	R_{eco}	GPP	Reference
1. Guandu $T1$		−53.48	1732.13	−1785.64	This study
2. Guandu $T2$		−376.12	1351.44	−1727.62	This study
3. Panjin Wetland Ecosystem Research Station (41°08' N, 121°54'E)	Freshwater tidal wetland	−65			Zhou et al (2009)
4. Florida Coastal Everglades Long Term Ecological Research (25°26'N, 80°36'W)	Short-hydroperiod Marsh	−50	446.1	−496	Schedlbauer et al (2012)
5. Western peatland flux station of the Fluxnet-Canada Research Network (FCRN) (54°57'N, 112°50'W)	Moderately rich fen	−144	569	−713	Syed et al (2006)
6. San Joaquin Freshwater Marsh (33°39'N, 117°50'W)	Typha wetland	−867	561	−1428	Rocha and Goulden (2009)
7. Yellow River Delta Ecological Research Station (37°46'N, 118°59'E)	Warm-temperate coastal wetland	−237.4[a]	348.3[a]	−585.7[a]	Han et al (2013)
8. Shidler Tallgrass Prairie (36°55'N, 96°40 W)	Tallgrass prairie	−362	1353	−1715	Falge et al (2002)
9. Little Washita Watershed (34°58'N, W97°59'W)	Temperate grassland	212	754	−542	Falge et al (2002)
10. Mer Bleue peatland (45°25'N, 75°40'W)	Ombrotrophic bog	−15.8	415.78	−431.52	St-Hilaire et al (2010)
11. Mirabel peatland (47°42'N, 73°55'W)	Ombrotrophic bog	−75.9	178.1	−254	Roehm and Roulet (2003)

[a] During the growing season from May to October.
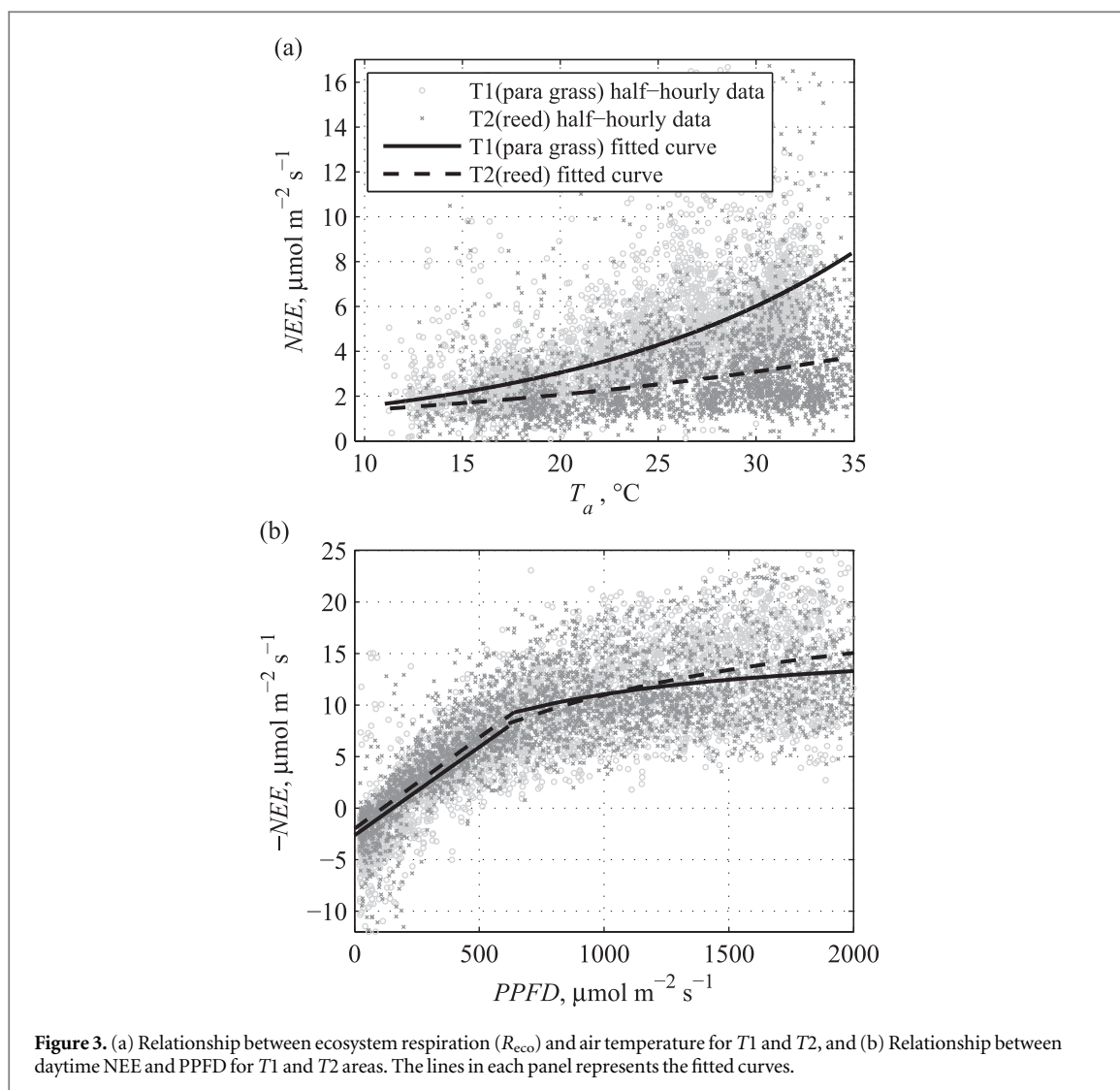
Figure 3. (a) Relationship between ecosystem respiration (R_{eco}) and air temperature for *T*1 and *T*2, and (b) Relationship between daytime NEE and PPFD for *T*1 and *T*2 areas. The lines in each panel represents the fitted curves.

ecosystems react differently over different range of PAR. The result in figure 3(b) shows that CO_2 assimilation was 20% higher for reeds at lower radiation condition, but para grass was more capable of assimilate CO_2 at higher radiation condition of PPFD $\geqslant$ 1200 μmol m^{-2} s^{-1}.
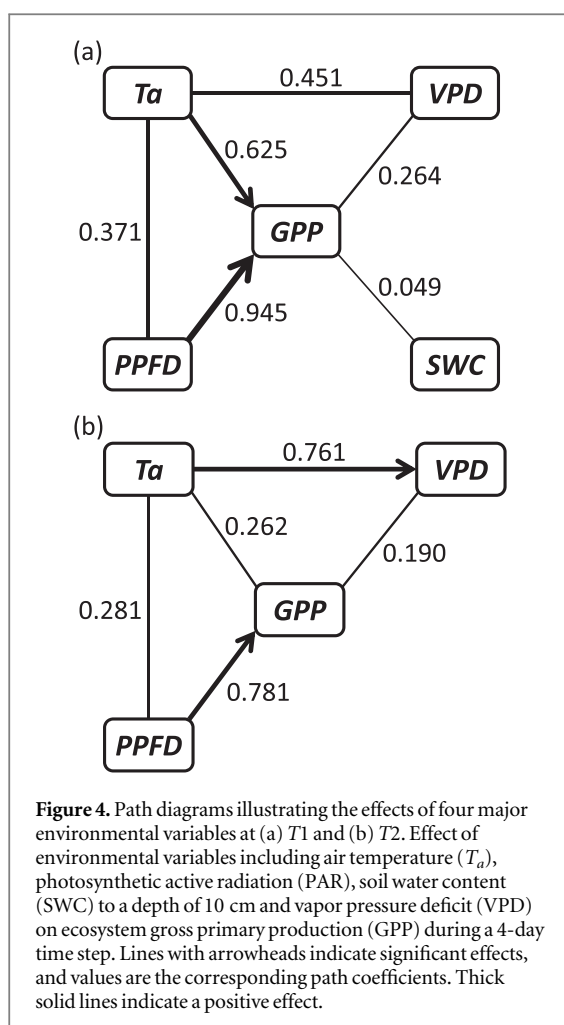
3.3. Path analysis

We used path analysis to examine the effects of major environmental variables on controlling GPP at 4-day time step as mentioned earlier in the method section for both para grass and reed areas. The environmental variables included T_a, PAR, and VPD for both ecosystems. In addition, we considered SWC for *T*1 only because the swamp-covered land surface around *T*2 caused saturated condition all the time.

At *T*1 (figure 4(a)), all four environmental variables had significant and positive effects on the magnitude of GPP. However, T_a and PAR had greater path coefficients than did VPD and SWC (figure 4(a)), for stronger control on GPP. At *T*2 (figure 4(b)), path analysis revealed a similar pattern, with both T_a and PAR playing more

important roles than VPD on GPP. However, the path coefficients for the environmental variables were smaller than at *T*1. The ecosystem response in terms of GPP was relatively less sensitive to fluctuations of environmental factors for reeds than para grass at this study site.

To further investigate how the environmental factors affect the dynamics of GPP throughout the entire 'fast growing season', we quantified the relationship between environmental factors and EC-based GPP during the 4-day time step over three different periods of the summer season (May–September, the 'fast growing season' in this study) as well as the transition periods just before (April) and after (October) (Liu *et al* 2011). These three periods include the early stage (from April to May), the middle stage (from June to August), and the late stage (from September to October), and the relationship was regressed by using scatter plots (figure 5). At *T*1 (figure 5(a)), at all three stages of the growing season, PAR and T_a had the greatest effect on GPP. However, at *T*2 (figure 5(b)), these effects were relatively mild. The result was consistent with the path analysis findings.
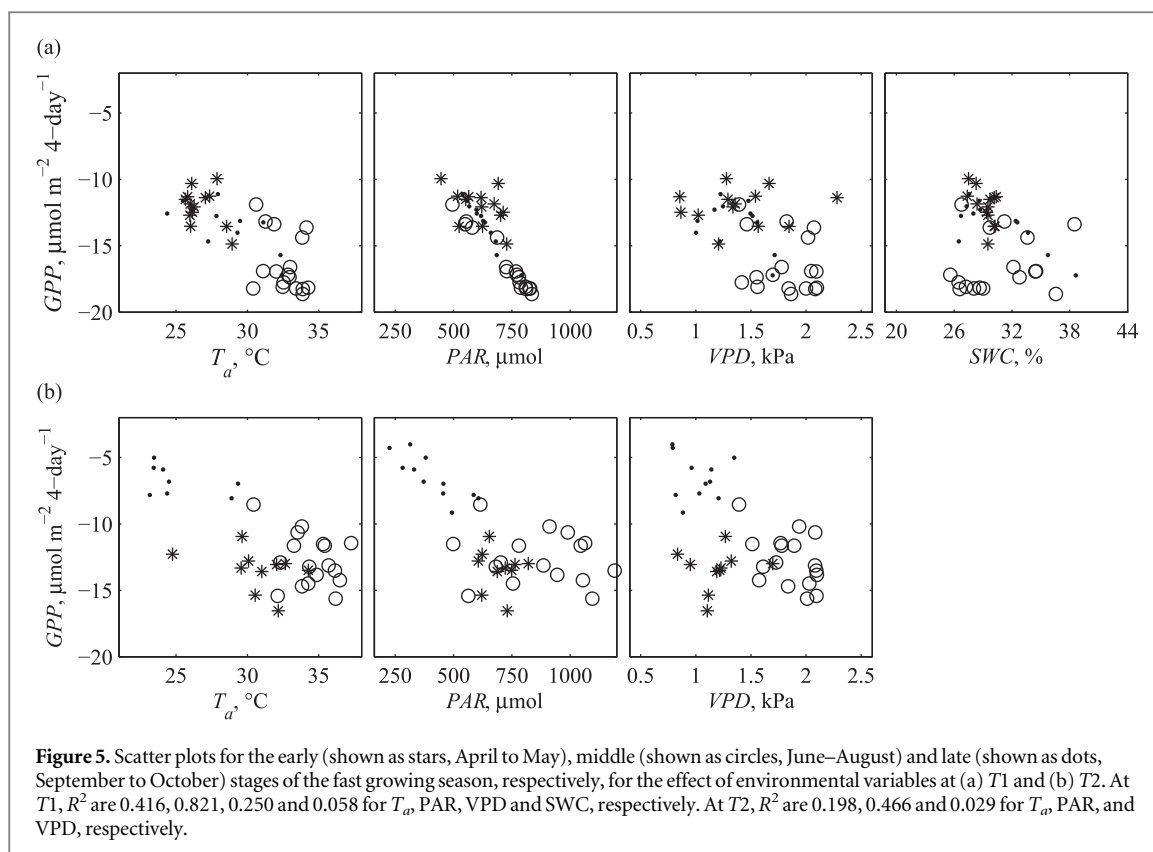
Figure 4. Path diagrams illustrating the effects of four major environmental variables at (a) T1 and (b) T2. Effect of environmental variables including air temperature (T_a), photosynthetic active radiation (PAR), soil water content (SWC) to a depth of 10 cm and vapor pressure deficit (VPD) on ecosystem gross primary production (GPP) during a 4-day time step. Lines with arrowheads indicate significant effects, and values are the corresponding path coefficients. Thick solid lines indicate a positive effect.

4. Discussion

4.1. Comparison of CO_2 budget for para grass and reed

The two ecosystems in this study are adjacent to each other and experience almost identical environmental conditions. It makes these two ecosystems good examples to characterize their sensitivity to environmental changes. The results of CO_2 flux show stronger seasonality for para grass than reeds (figure 2). Thus, according to results shown in table 1, the quantities of GPP for these two areas are almost identical, but NEE and R_{eco} are showing different magnitudes in annual scale. The annual ecosystem respiration was 28% higher at $T1$ than at $T2$. One of the reasons is probably because of relatively more plant debris in para grass area, which provided more sources for CO_2 release. Another reason to cause such difference is mainly attributed to the difference in surface water status between this two sites. As stated earlier, soil moisture content in $T2$ is close to saturation, which could significantly suppress the release of CO_2 around $T2$ (Pezeshki 2001).

The analysis revealed that CO_2 assimilation was 20% higher for reeds than para grass at PPFD $\leqslant 800 \, \mu$mol m^{-2} s^{-1}, but para grass was more capable of uptaking CO_2 than reeds at higher radiation condition of PPFD $\geqslant 200 \, \mu$mol m^{-2} s^{-1} (figure 3(b)). Thus, para grass was more sensitive to the light environment than reeds and less productive at lower radiation. According the observation data, about 63.6% of the PAR records were $\leqslant 800 \, \mu$mol m^{-2} s^{-1}, and only 20.3% were $\geqslant 1200 \, \mu$mol m^{-2} s^{-1}. Therefore, daytime NEE was relatively greater for reeds than para grass in this area. This finding agreed with path analysis results, which suggests that PAR had a greater effect on para grass than reeds. The results of path analysis and scatter plots also indicate that the variations in both T_a and atmospheric water status (in terms of VPD) had stronger effects on para grass than reeds.

Para grass is native to tropical areas of western and northern Africa (Thornton and McManus 1994, Chanson *et al* 2004) and spread to Southeast Asia, Australia and Latin America. In contrast, reeds are found on every continent over different latitudes, except Antarctica (Marks *et al* 1994, Chambers *et al* 1999). Over the last 150 years, the distribution of reeds has greatly increased and the species are now considered aggressive invaders in many regions (Chambers *et al* 1999, Rice *et al* 2000). A previous study found that when the invasion of reeds progresses from pre-invasion conditions to 90% cover, C sequestration in wetlands significantly increases (Battin *et al* 2009). Similar conditions were also found in Guandu site. According to the long-term field observation conducted by Guandu Nature Park (Shao 1999, Lee 2011), these two species are native in the area. However, in the early 1990s, the area was dominated by para grass and the coverage of reeds was small, yet over time, reed dominated ecosystem expanded into areas previously dominated by para grass. Because the two ecosystems in this study showed different sensitivity to environmental factors and both are widely distributed in tropical and subtropical regions, variations in environmental factors under global or regional environmental changes may lead to changes in C budgets in low-latitude wetland ecosystems. Our results suggest that the para grass is relatively more sensitive than reed to the influences of environmental factors. Therefore, under the variations in environmental controls, the change rate of CO_2 exchange will be greater for para grass than other species such as reed. The highly sensitive para grass has less resilience than other species, which may lead to the less-sensitive species such as reeds becoming more abundant in low-latitude areas. Such changes in coverage can alter ecosystem processes and change biogeochemical cycling (Roehm and Roulet 2003) via an aggressive growth strategy over different temporal scales.

Figure 5. Scatter plots for the early (shown as stars, April to May), middle (shown as circles, June–August) and late (shown as dots, September to October) stages of the fast growing season, respectively, for the effect of environmental variables at (a) $T1$ and (b) $T2$. At $T1$, R^2 are 0.416, 0.821, 0.250 and 0.058 for T_a, PAR, VPD and SWC, respectively. At $T2$, R^2 are 0.198, 0.466 and 0.029 for T_a, PAR, and VPD, respectively.

4.2. CO_2 flux compared with other wetland ecosystems

We used EC measurement with environmental factors to estimate the CO_2 budget for two ecosystem areas in the subtropical wetland site and compared our data with those from other studies with different methods conducted in other wetland ecosystems (table 1). We found the C sequestration at Guandu is greater than most studies.

The diversity of C budgets among these study sites is due first to differences in biomass among the study sites (the leaf area index LAI is 1.7 for the bog in The Netherlands, 1.5 for the peatlands in Canada, 4.0 for reed wetland in Panjin and 8.0 for para grass in this study). Ecosystems with lager biomass have more capacity for C fixation, which is consistent with other studies (Frolking *et al* 1998, Moreno-Sotomayor *et al* 2002). Furthermore, environmental factors play key roles in influencing C exchange over different sites. Our study site had no dry season, which is a typical climatic condition in tropical to subtropical regions in East Asia and Southeast Asia. However, in other studies, the monthly precipitation at higher latitudes showed large seasonal variation, so the dry condition in these sites may suppress the photosynthetic capacity. As well, low temperature restricts ecosystem photosynthesis (Lafleur *et al* 2001, Zhang 2006). Therefore, low temperatures at high-latitude sites results in short growing seasons, low photosynthetic capacity, and lower annual GPP.

4.3. Factors affecting ecosystem CO_2 exchange

Several previous studies tried to characterize how environmental controls alter C exchange in grassland ecosystems. However, most of these studies focused on patterns in northern ecosystem. An analysis of a high-latitude northern European peatlands area showed that PAR was the dominant factor controlling gross and net uptake of CO_2 (Lindroth *et al* 2007). In addition, soil water status played an important role as well (Forrest and Smith 1975, Moore 1989). Other studies of high-latitude peatlands ecosystems found that the fixation and transformation of N could alter dynamics of C cycling by a complicated mechanism (Hemond 1983, Urban and Eisenreich 1988, Rochefort *et al* 1990, Li and Vitt 1997, Williams and Silcock 1997, Williams *et al* 1999).

Therefore, understanding the key ecological properties such as CO_2 dynamics and the influences of environmental fluctuations on estimating CO_2 storage is important for characterizing low-latitude wetlands. In this study, we provide solid quantitative evidence to conclude that the seasonal dynamics of CO_2 exchange in a typical tropical-to-subtropical wetland ecosystem is strongly associated with the seasonality of several environmental factors. CO_2 storage and flux of different dominant species in low-latitude Marsh wetlands have different sensitivities to seasonal variations in meteorological conditions. For low-latitude Marsh wetland ecosystems such as at Guandu and all other ecosystems in East to Southeast Asia, temperature and PAR have stronger effects than do soil water status and

VPD on CO_2 exchange. These findings differ from those for high-latitude estuarial wetland ecosystems in Northeast China (Zhou *et al* 2009), which found that SWC and temperature had greater effect on GPP than PAR and VPD for high-latitude wetlands.

5. Conclusions

In this study, we used EC measurement to quantify the ecosystem-scale budget of CO_2 exchange at two different but representative wetland ecosystem in northern Taiwan. These two vegetation types showed different NEE response during different seasons. Temperature and radiation (PAR) had a greater effect than water status (SWC and VPD) on GPP for these two low-latitude ecosystems, which differs from findings for high-latitude regions. The results from path analysis and regression revealed that environmental variables have strong but different impacts on CO_2 budget for para grass and reed in this area. It implies that in this low-latitude wetlands area, the sensitivities of these species to the variations in environmental controls are statistically different, and these two ecosystem types would possibly respond at different magnitudes under different environmental conditions. Furthermore, such discrepancy indicates different capabilities of CO_2 exchange, so this diversity leads to different potential shifts and trends of biomass accumulation and distribution of these two typical low-latitude vegetation types under environmental changes. The finding from this study can sufficiently provide quantitative understanding on managing wetland ecosystem at different temporal and spatial scales.

    Understanding the dynamics of C stocks, release and sequestration in subtropical wetlands would improve current understanding of C cycling at regional and global scales. Adequate approaches to quantifying these fluxes and stocks remain challenging. Standardized methods of monitoring, reporting and verification need to be developed. Finally, CO_2 temporal variability ranges from daily to interannual. C-rich tropical and subtropical wetland ecosystems should be considered high priorities in climate-change adaptation and mitigation strategies throughout the world. For a more robust evaluation of C flux in these areas, an intensive, integrated, international and interdisciplinary program of observational efforts is required.

Acknowledgments

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