Typhoons exert significant but differential impacts on net ecosystem carbon exchange of subtropical mangrove forests in China

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Abstract

Typhoons are very unpredictable natural disturbances to subtropical mangrove forests in Asian countries, but little information is available on how these disturbances affect ecosystem level carbon dioxide (CO_2) exchange of mangrove wetlands. In this study, we examined short-term effect of frequent strong typhoons on defoliation and net ecosystem CO_2 exchange (NEE) of subtropical mangroves, and also synthesized 19 typhoons during a 4-year period between 2009 and 2012 to further investigate the regulation mechanisms of typhoons on ecosystem carbon and water fluxes following typhoon disturbances. Strong wind and intensive rainfall caused defoliation and local cooling effect during typhoon season. Daily total NEE values decreased by 26%-50% following some typhoons (e.g. W28-Nockten, W35-Molave and W35-Lio-Fan), but significantly increased (43-131%) following typhoon W23-Babj and W38-Megi. The magnitudes and trends of daily NEE responses were highly variable following different typhoons, which were determined by the balance between the variances of gross ecosystem production (GEP) and ecosystem respiration (RE). Furthermore, results from our synthesis indicated that the landfall time of typhoon, wind speed and rainfall were the most important factors controlling the CO_2 fluxes following typhoon events. These findings indicate that different types of typhoon disturbances can exert very different effects on CO_2 fluxes of mangrove ecosystem and that typhoon will likely have larger impacts on carbon cycle processes in subtropical mangrove ecosystems as the intensity and frequency of typhoons are predicted to increase under future global climate change scenarios.

1 Introduction

Although mangrove ecosystems only cover a small fraction of world forests, they are highly important component in coastal and global carbon cycle (Bouillon et al., 2008a; Kristensen et al., 2008; Donato et al., 2011). They also provide other numerous ecological services, such as coastal protection, fisheries production, biodiversity maintenance and nutrient cycling (Tomlinson, 1986; Gilbert and Janssen, 1998). However, the global mangrove area has been reduced by 1-2 % per year, and the mangrove areas in China has been greatly lost since the 1980s with only 22 700 ha remaining due to aquaculture, urbanization and other human activities (Alongi, 2002; Duke et al., 2007; Chen et al., 2009).

Changes in tropical cyclone activities are one important component of global climate change, and the characteristics of tropical cyclones are likely to change in a warming climate (Webster et al., 2005; Emanuel, 2007; IPCC, 2013; Knutson et al., 2010). Knutson et al. (2010) predicted that the global mean maximum wind speed of tropical cyclones would increase by 2-11 % in 2100, and the frequency likely to decrease by 6-34 %. Coastal mangrove ecosystems are especially vulnerable to tropical cyclones due to their location along coastlines (Kovacs et al., 2004; Milbrandt et al., 2006; Amiro et al., 2010; Barr et al., 2012). Although mangrove ecosystems exhibit a high degree of ecological stability to these disturbances, the increased intensity and frequency of storms may increase damage to mangroves through defoliation and tree mortality (Alongi, 2008; Gilman et al., 2008). Dietze and Clark (2008) investigated the detailed dynamics of vegetation to hurricane disturbance using designed experimental gaps, and found that sprouts which constitute 26-87 % of early gap regeneration played an important role in the maintenance of diversity. However, little information is available on how these disturbances affect carbon dioxide (CO_2) exchange of mangrove ecosystem, partly due to few direct measurements of canopy level CO_2 fluxes of mangrove ecosystem before and after tropical cyclone disturbances (Amiro et al., 2010; Barr et al., 2010; Barr et al., 2012).

A synthesis of the FLUXNET database underscored the importance of stand-replacing disturbance regulation on carbon budgets of ecosystems (Baldocchi, 2008). Running (2008) also illustrated the less extreme disturbances should be incorporated in future climate change studies. Disturbances such as tropical cyclones (typhoons, hurricanes or cyclones), which have strong impacts on forest structures and functions, are very common but unpredictable to coastal ecosystems (Turner and Dale, 1998; Greening et al., 2006). The most fundamental impact of such disturbances is the redistribution of organic matter from trees to the forest floor, including defoliation and uprooting stems (Kovacs et al., 2004; Milbrandt et al., 2006; Li et al., 2007; Barr et al., 2012). Defoliation could not only greatly reduce LAI (leaf area index) and the daytime carbon uptake, but also increase litter decomposition and result in large ecosystem respiration (RE) following this disturbance (Ostertag et al., 2003; Ito, 2010).

In recent years, several studies examined possible impacts of typhoon or hurricane disturbances on net ecosystem CO_2 exchange (NEE) (Li et al., 2007; Ito, 2010; Barr et al., 2012). After 10 typhoons struck Japan, the canopy carbon gain of forests decreased by 200 g C m^{-2} yr^{-1} (Ito 2010). Li et al. (2007) reported a 22 % decrease of GPP (gross primary production) and a 25 % decrease of RE of a scrub-oak ecosystem after Hurricane France, resulting in no significant change in NEE. Stand-replacing hurricane disturbances generally cause large defoliation and tree mortality, and hence large reduction in CO_2 uptake over a long time period (Amiro et al., 2010; Barr et al., 2012), whereas less extreme disturbances that do not have significant damage to stems have negligible effects on NEE (Li et al., 2007; Powell et al., 2008).

The complex variations of NEE depend on the balance between two interactive processes, GEP (gross ecosystem production) and RE (Valentini et al., 2000; Wen et al., 2010; Zhang et al., 2010). GEP is mainly controlled by PAR (photosynthetically active radiation), high VPD (vapor pressure deficit) and Ta (air temperature) that limit daily photosynthetic rates (Goulden et al., 2004; Powell et al., 2008; Keith et al., 2012). GEP and RE respond independently to microclimate, but RE is regulated by Ts (soil temperature), soil water content and debris on the forest floor (Li et al., 2007; Kwon et al., 2010; Barr et al., 2012). Kwon et al. (2010) observed that NEE depression occurred with different timing, magnitude and mechanism in a deciduous forest and farmland during the Asian monsoon. These results indicate that the relative effects of these microclimatic factors determine the balance between GEP and RE, and hence the different trends and magnitudes in NEE responses following disturbances. However, the relationships among different tropical cyclone disturbances, microclimates and the carbon budgets of ecosystems are not well understood. Moreover, it is essential to investigate the regulations of typhoon characteristics (including wind speed, landfall point, frequency and duration) on CO_2 exchange of mangrove ecosystem.

The main objective of this study was to examine short-term effects of frequent strong typhoons on microclimate, defoliation and net ecosystem CO_2 exchange of two subtropical mangroves in China. We also synthesized 19 typhoons during a four year period between 2009 and 2012 to further investigate possible mechanisms for the regulations of typhoon characteristics on variations of ecosystem carbon dynamics following typhoon disturbances.

2 Materials and Methods

2.1 Site description

The measurements were made in two subtropical mangrove ecosystems located in Gulei Gulf, Fujian Province and Yingluo Bay, Guangdong Province, in southern China. The first site, Yunxiao mangrove study site (thereafter YX), is situated in the Zhangjiangkou National Mangrove Nature Reserve (23°55′14.59″N, 117°25′4.9″E). This nature reserve was established in 1997 as a provincial nature reserve, and was included in the Ramsar List in 2008. This site is dominated by *Kandelia obovata*, *Avicennia marina* and *Aegiceras corniculatum*, with the canopy height of 3-4 m. Based on China Meteorological Administration, the 1981-2011 mean annual temperature and precipitation were 21.1 ℃ and 1285 mm, respectively. For YX, tides are irregular semidiurnal and the high tides can reach up to 1.0 m above the sediment, with tidal water salinity ranging between 1-22 ppt. The second site, Gaoqiao mangrove study site (thereafter GQ), is located in the Zhanjiang National Mangrove Nature Reserve (21°34′3.04″N, 109°45′22.33″E). This nature reserve is the largest mangrove nature reserve in China, and it was included into the Ramsar List in 2002. This site is dominated by *Bruguiera gymnorrhiza*, *A. corniculatum* and *A. marina*, and the canopy height was about 3 m. The 1981-2011 mean annual temperature and precipitation were 22.9 ℃ and 1 770 mm, respectively. The tides of GQ are regular diurnal and the high tides can reach up to 1.8 m above the sediment, with tidal water salinity ranging between 1-30 ppt.

2.2 Eddy covariance and microclimatic measurements

The eddy covariance measurement systems were established in 2008 and 2009 at the YX and GQ sites, respectively. Each system was equipped with a three-dimensional sonic anemometer (CSAT3; Campbell Scientific, Inc., USA) and an open-path infrared gas analyzer (LI-7500; Li-Cor, Inc., USA). The CSAT3 and LI-7500 were mounted at heights of 5.4 m for YX and 8.6 m for GQ. The footprint was in the direction of the local prevailing winds, which is southeast wind for YX and northeast wind for GQ. The eddy flux data were sampled at 10 Hz, and their mean, variance and covariance values were calculated and logged at 30 min intervals using a data logger (CR1000 for YX, CR3000 for GQ; Campbell Scientific, Inc., USA).

Air temperatures and relative humidity were measured with temperature and relative humidity probes (HMP45AC; Vaisala, Inc., Finland) at heights of 3.0 m, 12.6

m for YX and 2.6 m, 7.4 m, 8.6 m, 14.0 m for GQ. Soil temperatures were measured using temperature probes (109; Campbell Scientific, Inc., USA) at three sediment layers (5 cm, 10 cm, 20 cm) for YX and at two sediment layers (10 cm, 20cm) for GQ, and the average soil temperatures were also measured using an averaging soil TC probe (TCAV; Campbell Scientific, Inc., USA) at 10-20 cm sediment layer. Solar radiation, PAR and net radiation were determined with a pyranometer sensor (LI-200SZ; Li-Cor, Inc., USA), a PAR quantum sensor (LI-190SZ; Li-Cor, Inc., USA) and a four-component net-radiation sensor (NR01; Hukseflux Thermal Sensors, Inc., USA), respectively. Soil heat flux was measured with soil heat flux plate (HFP01SC; Hukseflux Thermal Sensors, Inc., USA). Wind speeds (010C; Met One Instruments, Inc., USA) and wind direction (020C; Met One Instruments, Inc., USA) were measured at heights of 3.0 m, 12.6 m for YX and 2.6 m, 7.4 m, 14.0 m for GQ. Precipitation was measured using a tipping bucket rain gauge (TE525MM; Texas Electronics, Inc., USA). The meteorological data were sampled at 1 s intervals and averaged values were recorded at 30-min intervals with a CR1000 data logger (Campbell Scientific, Inc., USA).

2.3 Flux data processing and gap filling

The eddy covariance data were processed with the EC_PROCESSOR software package (http://www4.ncsu.edu/~anoorme/ECP/) (Noormets et al., 2007), using the 2-axis rotation and the Webb-Pearman-Leuning expression (Paw U et al., 2000; Mauder and Foken, 2006). Sonic temperatures were corrected for changes in humidity and pressure (Schotanus et al., 1983). The 30-min fluxes were corrected for the warming of IRGA according to Burba et al. (2006). We also removed anomalous or spurious data were caused by rainfall events, instrument malfunction, power failure or IRGA calibration. These introduced data gaps that were filled following the methods of Falge et al. (2001). The mean diurnal variation method was used to fill short gaps by calculating the mean values of the same half-hour flux data with a 14-day moving window. Larger data gaps were filled using look-up tables. For each site, daytime and nighttime look-up tables were created for each two-month interval, which was sorted by PPFD and Ta. After gap filling, data were extracted and analyzed with the micrometeorological data.

2.4 Typhoon impacts on mangrove ecosystem

In this study, we selected typhoons that were stronger than Category 8 (wind speed > 17.2 m s^{-1}), and landed at a distance less than 300 km from the YX or GQ sites based on data from China Meteorological Agency, which resulted in a total of 19 typhoons passed over the YX and GQ site (Fig. 1) during a 4-year period between 2009 and 2012. The characteristics of each typhoon including typhoon name, DOY_{Land} (the time of year that typhoon made landfall), duration (the length of time when the typhoon occurred at a distance less than 300 km from our study site), category (Beaufort wind force scale), $wind_{Land}$ (the maximum wind speed of typhoon when made landfall), $wind_{min.distance}$ (the maximum wind speed near mangrove ecosystem when the typhoon was the nearest to it), $distance_{min}$ (the minimum distance from mangrove study site during typhoon period) and rainfall are summarized in Supplement Table S1. If the dates of typhoon were very close to each other (less than seven days) or even overlapped, we combined them as a single typhoon. For example, typhoon Lionrock, Namtheum, Meranti and Fanapi formed around late August and middle September, then we combined them as Lio-Fan. To categorize the selected typhoons quantitatively, we used the corresponding maximum wind speed and typhoon name to represent each typhoon. For example, the maximum wind speed of typhoon Lio-Fan was 35 m s^{-1}, and then we used W35-Lio-Fan to represent this typhoon.

For each typhoon, five clear days before and after the typhoon made landfall were selected to calculate the daily mean air and sediment temperature (Ta, Ts), maximum air and sediment temperature (Ta_{max}, Ts_{max}), and photosynthetically active radiation (PAR). The daily gap-filled fluxes (NEE, GEP, RE and ET (evapotranspiration)) were calculated the same way as these microclimatic factors. For NEE values, negative values represent net carbon uptake, and positive values represent net carbon release. The light response was estimated with a form of Michaelis-Menten equation (Barr et al. 2010): $\mathrm{NEE} = -\alpha\mathrm{PAR}/(1-(\mathrm{PAR}/2000)+(\alpha\mathrm{PAR}/\mathrm{GEP}_{2000}))+\mathrm{R_d}$. Where α is the ecosystem quantum yield (μmol CO_2 (μmol PAR^{-1})), GEP_{2000} is the gross ecosystem productivity (μmol CO_2 m^{-2} s^{-1}) when photosynthetically active radiation reach 2000 μmol m^{-2} s^{-1}, and R_d is ecosystem respiration (μmol CO_2 m^{-2} s^{-1}). Delta values (ΔNEE, ΔGEP, ΔRE, ΔET, Δα, ΔGEP_{2000} and ΔR_d) were estimated as their differences between before and after each typhoon made landfall. For delta values, negative values indicate decrease following typhoon, positive values indicate increase after typhoon.

The residuals of NEE ($NEE_{residual}$) from the light response function (Barr et al. 2010) were regressed against VPD and Ta before and after the typhoon to quantify the magnitude they regulate daytime NEE. A more positive $NEE_{residual}$ indicates less photosynthesis or more respiration. To quantify typhoon impacts on daily carbon and water fluxes, we then analyzed the regulatory characteristics of typhoon on them using data from 2009 to 2012 for YX and GQ.

2.5 Litterfall measurements

To quantify litterfall production, we randomly installed 5 litter traps which were baskets constructed by 1.0 mm mesh size nylon mesh under the canopy of each mangrove species around the eddy tower, with litter collected monthly, oven-dried, sorted and weighted as leaf, twig, flower and fruit (including hypocotyle).

2.6 Statistical analysis

The eddy covariance data were processed using software SAS version 9.0 (SAS Institute Inc., USA). All measured parameters before and after typhoon were presented as mean ± standard deviation for five replicates. The differences in microclimatic factors, carbon and water fluxes between before and after typhoon were tested using independent sample *t*-test. The differences in daily carbon and water fluxes among typhoons were analyzed by one-way Analysis of Variance (ANOVA). Then Duncan post hoc tests were applied to examine the differences after ANOVA. The relationships between typhoon characteristics and microclimatic factors, carbon and water fluxes were also analyzed by linear regression. The statistical analyses were conducted with software SPSS version 16.0 (SPSS Inc., USA).

3 Results

3.1 Typhoons and meteorological data

From 1945 to 2012, the annual typhoon initiation frequency was 25.27 ± 6.10, and the frequency of landfalls on China was 9.26 ± 2.65. During 2009 and 2012, the typhoon initiation and landfall frequency was not very high. There were three and one typhoon made landfall particularly near YX and GQ (Fig. 1a, Supplement Table S1). Among them the minimum distance from YX and GQ was 9 km and 29 km, respectively (Supplement Table S1). The duration of the typhoons occurred at a distance less than 300 km from YX or GQ was 28.79 ± 15.44 hour on average, ranging from 9 to 74 hours.

From June to October, typhoon brought strong wind accompanied with torrential rain (Fig. 2, Supplement Table S1). The monthly total rainfall showed significant correlation with monthly maximum wind speed for our study sites (y = 16.29 x - 155.79, R^2 = 0.47, P < 0.001 for YX, and y = 11.05 x – 50.66, R^2 = 0.19, P = 0.004 for GQ). During typhoon period, the strongest wind speed of typhoon reached 40 m s^{-1}, and the strongest observed wind speed near our study site can exceed 35 m s^{-1}. The magnitude of total rainfall during typhoon period ranged from 3 mm to 85.8 mm for YX, and from 0.2 mm to 115.8 mm for GQ during 2009 and 2012. Rainfall showed significant correlation with duration of typhoon for our study sites (y = 2.12 x – 16.40, R^2 = 0.60, P = 0.014 for YX, and y = 1.59 x + 0.19, R^2 = 0.47, P = 0.029 for GQ). Both daily mean and maximum Ta significantly decreased after most of strong typhoon landfalls, while their variations were larger than that before typhoon (Table

1). The cooling effect of typhoon was less apparent in Ts, which led to smaller differences in Ts and Ts_{max} following typhoon. With a few exceptions, significant decreases in daily mean total PAR were observed (Table 1).

3.2 Litterfall production

Mean annual litterfall production was 848.44 g DW m^{-2} yr^{-1} and 728.62 g DW m^{-2} yr^{-1} for YX and GQ from 2009 to 2012. Leaf and twig litter were the largest components of total litterfall, accounting for more than 75% of total litterfall for our mangrove sites. Except leaf litter of *A. corniculatum*, monthly litterfall varied seasonally with two peaks, one in April to May and the other in July to August (Fig. 3). Typhoon with strong wind and heavy rain could cause defoliation. In the typhoon season, the highest monthly litter production accounted for 30% and 13% of annual litterfall for YX and GQ. Moreover, about 5% to 25% green leaves and twigs appeared in litter traps after typhoon made landfall. For *K. obovata* at YX site, monthly twig litter production was significantly correlated with monthly maximum wind speed ($y = 1.63\ x - 12.68$, $R^2 = 0.14$, $P = 0.015$) and monthly total rainfall ($y = 0.06\ x + 6.62$, $R^2 = 0.10$, $P = 0.041$). For *B. gymnorrhiza* at GQ site, monthly leaf litter production was significantly correlated with monthly maximum wind speed ($y = 2.01\ x + 24.29$, $R^2 = 0.22$, $P = 0.004$), and monthly twig litter production also showed significant correlation with monthly maximum wind speed ($y = 0.77\ x - 5.21$, $R^2 = 0.26$, $P = 0.001$) and monthly total rainfall ($y = 0.03\ x + 2.81$, $R^2 = 0.21$, $P = 0.005$). For *A. corniculatum* at GQ site, only monthly twig litter production showed significant correlation with monthly maximum wind speed (y = 0.74 x – 1.34, R^2 = 0.11, P = 0.045).

3.3 Net ecosystem CO_2 exchange

For typhoon effect on carbon and water flux values of mangrove ecosystems, only six strong typhoons that made significant changes on them were taken into account (Fig. 4). Daily total NEE values were reduced following typhoon W28-Nockten (26%), W35-Molave (39%) and W35-Lio-Fan (50%), but significantly increased following typhoon W23-Parma (12%), W23-Babj (43%) and W38-Megi (131%) (Fig. 4a). Daily total GEP values were all reduced significantly following typhoon W28-Nockten (15%) and W35-Molave (8%), but no change in daily total GEP was observed following the typhoon W23-Babj (Fig. 4b). Typhoon W23-Parma and W38-Megi significantly suppressed daily total RE values, but typhoon W23-Babj increased the daily RE (Fig. 4c). Typhoon W23-Parma also reduced daily total ET after typhoon landfalls, but typhoon W23-Parma caused the opposite change in ET (Fig. 4d).

Table 2 summarized light response curve parameters before and after strong typhoons made landfall near our study sites during the four year period between 2009 and 2012. The apparent quantum yields (the α value) slightly decreased following typhoon, but there was no significant difference in α before and after each typhoon. After typhoon W38-Megi made landfall, GEP_{2000} value was smaller than before typhoon values (P < 0.001). RE rate (the R_d value) before typhoon was more than twice the value after typhoon W38-Megi made landfall. However, after typhoon W23-Babj, GEP_{2000} value was greater than before typhoon values (P = 0.035). During the four year period between 2009 and 2012, the annual NEE ranged from -539.98 to -865.80 g C m^{-2} yr^{-1} and -691.86 to -737.74 g C m^{-2} yr^{-1} for YX and GQ, respectively (Table 4). The mean annual GEP was 1871 and 1763 g C m^{-2} yr^{-1}, respectively for YX and GQ during the same period, with corresponding mean annual total RE of 1287 and 1096 g C m^{-2} yr^{-1} and RE/GEP of 0.69 and 0.63, respectively.

PAR was the most important control over daytime NEE, although VPD and Ta also exerted strong controls over daytime NEE (Fig. 5, 6). VPD above 1.5 kPa suppressed daytime NEE (Fig. 5a, e). After typhoon W28-Nockten landed, daytime NEE values were reduced by high VPD, while they were not affected by VPD before the typhoon (Fig. 5e). Although high Ta also reduced daytime NEE values after typhoon W28-Nockten, it had little effect on daytime NEE before this typhoon made landfall (Fig. 5f). After typhoon W38-Megi landed, significant reduction in Ta increased daytime NEE (Fig. 5l).

3.4 Relationships of carbon and water fluxes with typhoon properties

Variations in daily carbon fluxes and the model parameters were explained by variations in typhoon properties (Table 3). ΔGEP values did not show significant relationships with typhoon properties for YX and GQ. However, ΔNEE values were strongly correlated with DOY_{Land} (P=0.025), indicating that typhoon made landfall later in the year could increase daily NEE. $\Delta\alpha$ values were negatively correlated with

DOY_{Land} (P=0.039) and rainfall (P=0.022). ΔRE values were also negatively related to $wind_{min.\ distance}$ (P=0.030), showing that typhoon with strong wind led to lower daily RE.

4 Discussion

4.1 Impact of typhoons on defoliation of mangrove forests

We observed significant increase in litter production in both mangrove forests in China following most typhoon events (Fig. 3), suggesting that great defoliation occurred due to typhoon disturbances. The immediate impacts of typhoon disturbance on canopy included defoliation and twig losses (Xu et al., 2004; Li et al., 2007; Ito, 2010), which led to obvious changes in LAI and albedo values (Barr et al., 2012; O'Halloran et al., 2012). The positive relationship between monthly litter productions and monthly mean wind speed observed here for GQ (Fig. 3) also indicated a strong impact of wind disturbance on defoliation. This is consistent with the results from several previous studies, which demonstrated higher monthly litter production during typhoon season (Tam et al., 1998; Zheng et al., 2000). Milbrandt et al. (2006) observed no significant differences of hurricane impacts on litter production among mangrove species, but they found a negative correlation between canopy loss and the distance to hurricane eyewall. Moreover, typhoon-derived litters could immediately decompose on the forest floor, which increase litter decomposition and nutrient inputs (Ostertag et al., 2003). Thus, significant increases in mangrove litter production following typhoon events are very common, and will increase ecosystem respiration and nutrient supply for mangrove forest recovery. At the same time, Li et al. (2007) reported that lower LAI following wind disturbances could result in lower soil respiration. The intensive and consecutive rainfalls also caused the reduced respiration during the summer monsoon (Kwon et al. 2010). Therefore, the positive correlation between rainfall and maximum wind speed for our study sites indicated strong winds control on RE.

4.2 Impacts of typhoons on mangrove daytime NEE

We found inconsistent changes in daytime NEE following typhoon events, with some typhoons (e.g. W23-Babj, W38-Megi) increasing daytime NEE, some typhoons (W28-Nockten, W35-Molave, W35-Lio-Fan) having the opposite effect and one typhoon (W23-Parma) having no effect (Fig. 4). Ito (2010) observed that defoliation caused by typhoon greatly reduced CO_2 uptake of a deciduous broad-leaf forest. Li et al. (2007) also reported a decrease in GPP because of the reduction in LAI after hurricane disturbance. In our study, after typhoon W28-Nockten, W35-Molave and W35-Lio-Fan made landfall, the decrease in GEP was larger than that of RE, which resulted in significant decrease in NEE. Although typhoon W38-Megi caused a reduction in GEP, the large reduction of RE resulted in increased NEE. Kwon et al. (2010) also reported that intensive rainfalls could reduce respiration during the Asian monsoon. GEP and RE also controlled the NEE values after typhoon W23-Parma and W23-Babj (Fig. 4). However, Barr et al. (2012) demonstrated that local heating effect following stand-replacing hurricane disturbances caused high respiration. Therefore, possible effects of typhoons on daytime NEE depend on forest types, forest locations and various changes in micrometeorological conditions due to typhoon events.

For our subtropical mangrove forest sites, the mean annual NEE values were smaller than that reported for tropical mangrove ecosystems (Barr et al. 2010). But the annual NEE values for our study site were substantially greater than that observed in other temperate forest ecosystems in China (eg., Wen et al. 2010, Zhang et al. 2010). Lower RE in mangrove ecosystems was largely responsible for relatively high NEE values, which also has been reported by Barr et al. (2010, 2012). At the same time, tidal events generally result in substantial lateral fluxes of particulate organic carbon, dissolved organic carbon and dissolved inorganic carbon, which might overestimate the NEE values observed by eddy covariance measurement (Bouillon et al. 2008a, Barr et al. 2010).

VPD and Ta were important secondary factors controlling daytime NEE values, especially after typhoon made landfall (Fig. 5). The less negative GEP_{2000} values following typhoon were likely due to carbon assimilation suppressed by high VPD and Ta. Our results for VPD also have been reported in previous studies (Goulden et al., 2004; Powell et al., 2008; Keith et al., 2012). Daytime photosynthetic rates of leaves could be limited by lower stomatal conductance as a result of high VPD (Sano et al., 2010). Additionally, the daytime NEE was much more sensitive to VPD following typhoon W28-Nockten. Although Ta values were reduced following typhoon, high Ta also could cause depression in daytime NEE. This regulation can be explained by temperature controls on both photosynthesis and respiration (Powell et al., 2008). Goulden et al. (2004) also demonstrated positive correlation between $NEE_{residual}$ and Ta in the afternoon, which was likely caused by high Ta, high VPD, or a circadian rhythm.

Large amount water from the rains induced by the typhoons could significantly reduce the salinity in the tidal water surrounding the mangrove forest within the footprint of the eddy flux tower, which could exert significant effect on daytime CO_2 flux by increasing light use efficiency as shown in Table 3. The negative effects of salinity on light use efficiency of mangrove forests also have been reported by Barr et al. (2010), who observed small but significant linear decreases in light use efficiency with increasing salinity during either wet or dry season. Thus, although rainfall from the typhoons plays a minor role in controlling CO_2 flux in term of water availability, the reduction in tidal water salinity because of such rainfall could influence the daytime CO_2 flux of mangrove ecosystems during the typhoon season.

4.3 Regulation mechanisms of typhoons on ecosystem carbon and water fluxes in mangrove forests

Although many studies have examined the impacts of typhoon or hurricane disturbances on CO_2 fluxes in various ecosystems, few have explored the regulation mechanisms of typhoon characteristics on mangrove carbon fluxes (Li et al., 2007; Ito, 2010; Sano et al., 2010; Barr et al., 2012; Vargas, 2012). Results from our synthesis indicated that variations of carbon fluxes following typhoon were strongly controlled by DOY_{Land}, $wind_{min.\ distance}$ and rainfall (Table 3). Rainfall controls on RE was consistent with the finding of Kwon et al. (2010) that intensive and consecutive rainfall reduced respiration during summer monsoon. $Wind_{min.\ distance}$ regulations on RE could be explained by wind damage on canopy loss immediately after typhoon (Ito, 2010). Although we did not measure the changes in leaf area following typhoon, the large litter production and their correlations with wind speed and rainfall during typhoon season demonstrated the damage of typhoon on mangrove forest. These differ from the findings of extreme disturbance, which stand-replacing damages cause significant large RE in a long term (Amiro et al., 2010; Barr et al., 2012). However, no difference in RE after typhoon W28-Nockten, W28-Molave and W35-Lio-Fan observed in this study was consistent with the findings of Li et al. (2007) who found that less extreme disturbance did not increase respiration of forest ecosystem.

The dynamics of daily NEE before and after typhoon were complex because NEE depends on both photosynthesis and respiration processes. They interact with each other, and are controlled by relative independently environmental factors (Li et al., 2007; Wen et al., 2010). Extreme hurricane disturbances generally caused significant defoliation and plant uprooting, and then resulted in significant reduction in GEP and increase in RE of mangrove ecosystems (Barr et al., 2012). Reduced NEE values also have been reported by Lindroth et al. (2008), who observed the reduction of NEE were caused by increased RE. However, less extreme disturbances have negligible effects on NEE (Li et al., 2007). Hurricane disturbance has no significant effects on NEE due to the compensatory reduction in GEP and RE (Li et al., 2007). Actually, there is great agreement between our results and those from previous studies, which indicate climatic drivers on the balance between carbon and uptake (Powell et al., 2008; Wen et al., 2010; Zhang et al., 2010). These indicated typhoon disturbances reduced NEE or did not have significant impact on our mangrove study sites. However, a significant increase in NEE was observed at our study site after typhoon W38-Megi made landfall in early autumn, which was due to the decrease in Ta and RE. In this case, the strong correlation between ΔNEE values and DOY_{Land} conformed that the timing that typhoon made landfall also had important control on carbon exchange of mangrove ecosystems. Although only six typhoons caused significant changes in carbon flux of mangrove ecosystem, these results indicated that carbon flux dynamics were highly variable following typhoons.

5 Conclusions

Typhoon disturbances frequently influence the subtropical mangrove ecosystems in China. Strong wind and intensive rainfall caused defoliation and local cooling effect during typhoon periods. The magnitudes and trends of daily NEE responses were highly variable following different typhoons, which were dependent on the balance between the changes of GEP and RE. Furthermore, the results from our synthesis of 19 typhoons demonstrated that DOY_{Land}, $wind_{min.\ distance}$ and rainfall were the most important factors controlling the carbon fluxes following typhoon. These findings indicated that the CO_2 exchange of mangrove ecosystems responds differently to various types of typhoon disturbances, and future typhoon with increasing frequency and intensity will likely have large influence on carbon cycle processes of subtropical mangrove ecosystems.

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Table 1. Daily average microclimatic factors before and after typhoon made landfall for Yunxiao (YX) and Gaoqiao (GQ) in 2010, including daily means of air temperature (Ta), maximum air temperature (Ta_{max}), soil temperature (Ts), maximum soil temperature (Ts_{max}) and total photosynthetically active radiation (PAR).

Typhoon		Ta (℃)	Ta_{max} (℃)	Ts (℃)	Ts_{max} (℃)	PAR (mol m^{-2} d^{-1})
W23-Parma	Before	28.29±0.65	32.05±1.37	27.68±0.28	27.90±0.14	28.81±8.35
	After	27.57±0.80	32.11±2.21	26.41±0.51	26.86±0.53	29.65±6.68
W23-Babj	Before	29.28±0.30	33.76±0.90	27.65±0.13	27.81±0.12	38.65±1.94
	After	27.55±0.29	31.10±0.67	26.54±0.13	26.68±0.12	28.67±4.13
W28-Nockten	Before	29.45±0.29	33.34±0.95	28.15±0.28	28.41±0.34	37.08±3.37
	After	28.49±0.86	32.37±1.31	28.47±0.32	28.73±0.29	29.28±7.21
W35-Molave	Before	29.38±0.73	33.43±1.34	27.71±0.56	28.64±0.51	47.40±5.12
	After	29.12±0.14	32.96±1.18	27.99±0.25	28.86±0.28	40.72±8.11
W35-Lio-Fan	Before	29.10±0.49	33.99±0.84	27.91±0.28	29.41±0.32	34.12±6.49
	After	26.52±0.51	32.95±0.92	26.26±0.18	27.91±0.38	28.31±7.36
W38-Megi	Before	24.98±0.56	28.51±0.88	24.65±0.15	24.86±0.24	20.78±6.16
	After	19.08±1.38	22.94±0.80	22.05±0.90	22.42±0.89	28.81±5.35

Table 2. Model parameters of light response curves before and after each typhoon landfall during 2009 and 2012. α is the ecosystem quantum yield, GEP_{2000} indicates the gross ecosystem productivity when photosynthetically active radiation reach 2000 μmol m^{-2} s^{-1}, R_d represents ecosystem respiration, *P* represents significant difference in model parameters comparing before and after typhoon.

Typhoon		α (μmol CO_2 (μmol PAR^{-1}))	*P*	GEP_{2000} (μmol CO_2 m^{-2} s^{-1})	*P*	R_d (μmol CO_2 m^{-2} s^{-1})	*P*
W23-Parma	Before	0.03±0.01	0.538	21.46±3.15	0.085	2.53±1.06	0.462
	After	0.02±0.01		17.86±2.61		1.92±1.42	
W23-Babj	Before	0.03±0.03	0.988	22.57±4.16	0.035	3.43±1.92	0.775
	After	0.03±0.01		30.74±5.92		3.80±1.96	
W28-Nockten	Before	0.03±0.01	0.884	17.65±2.09	0.654	4.50±1.42	0.218
	After	0.03±0.02		17.08±1.76		2.70±2.65	
W35-Molave	Before	0.04±0.02	0.182	15.42±1.08	0.651	4.91±2.02	0.363
	After	0.02±0.01		16.07±2.90		3.97±0.85	
W35-Lio-Fan	Before	0.03±0.02	0.613	25.38±2.09	0.434	5.64±3.11	0.294
	After	0.03±0.02		24.34±1.93		3.58±2.68	
W38-Megi	Before	0.03±0.01	0.079	28.18±1.42	< 0.001	3.43±1.19	0.009
	After	0.02±0.01		20.85±1.43		1.46±0.47	

Table 3. Linear regression coefficient (Coef.) and significance probability (*P*) between daily ecosystem carbon fluxes change (ΔNEE, ΔGEP and ΔRE), model parameters change of light response curves ($\Delta\alpha$, ΔGEP_{2000} and ΔR_d) before and after typhoon made landfall and typhoon characteristics (DOY_{Land}, duration, category, $wind_{Land}$, $wind_{min.\ distance}$, $distance_{min}$, rainfall). The daily data from 2009 to 2012 for Yunxiao (YX) and Gaoqiao (GQ) were used. The *p* value less than 0.05 was marked as bold number.

Factor	ΔNEE		ΔGEP		ΔRE		$\Delta\alpha$		ΔGEP_{2000}		ΔR_d	
	Coef.	*P*	Coef.	*P*	Coef.	*P*	Coef.	*P*	Coef.	*P*	Coef.	*P*
DOY_{Land}	0.816	**0.025**	0.547	0.204	-0.621	0.137	-0.779	**0.039**	-0.600	0.154	-0.684	0.090
Duration	-0.196	0.674	0.041	0.931	0.147	0.752	-0.481	0.275	-0.099	0.832	-0.303	0.509
Category	0.160	0.732	-0.165	0.724	-0.536	0.214	-0.287	0.533	-0.516	0.235	-0.307	0.503
$Wind_{Land}$	0.100	0.831	-0.226	0.626	-0.506	0.246	-0.238	0.608	-0.501	0.252	-0.289	0.530
$Wind_{min.\ distance}$	0.314	0.493	-0.281	0.541	-0.802	**0.030**	-0.043	0.927	-0.514	0.238	-0.320	0.485
$Distance_{min}$	-0.371	0.412	-0.301	0.511	0.381	0.399	0.518	0.233	0.274	0.552	0.507	0.245
Rainfall	0.006	0.989	0.111	0.813	-0.061	0.897	-0.826	**0.022**	-0.473	0.284	-0.627	0.132

Table 4. Mean annual net ecosystem CO_2 exchange (NEE), gross ecosystem production (GEP), ecosystem respiration (RE) for Yunxiao (YX) and Gaoqiao (GQ) during 2009 and 2012.

Year	NEE ($g\ C\ m^{-2}\ yr^{-1}$)	GEP ($g\ C\ m^{-2}\ yr^{-1}$)	RE ($g\ C\ m^{-2}\ yr^{-1}$)
YX site			
2009	-539.98	1762.55	1238.46
2010	-588.051	1875.07	1336.70
2011	-751.10	1928.32	1296.84
2012	-856.80	1919.33	1275.91
GQ site			
2009	N. A.	N. A.	N. A.
2010	-737.74	1889.72	1214.82
2011	-691.86	1698.19	1026.89
2012	-735.34	1703.14	1045.25

Figure captions

Fig. 1. **(a)** Paths of the 19 typhoons that passed over Yunxiao (YX) and Gaoqiao (GQ) mangrove sites during a four year period between 2009 and 2012, and **(b)** category of each typhoon and its $distance_{min}$ (the minimum distance from mangrove sites) during 2009 and 2012.

Fig. 2. **(a, c)** Maximum wind speed, **(b, d)** total weekly rainfall for Yunxiao (YX) and Gaoqiao (GQ) during a four year period between 2009 and 2012. The name and occurrence date of each typhoon are also shown.

Fig. 3. Monthly **(a, c, e, g)** leaf litter and twig litter **(b, d, f, h)** production for Yunxiao (YX) and Gaoqiao (GQ) in 2010. YX-Am: *Avicennia marina* at YX, YX-Ko: *Kandelia obovata* at YX, GQ-Bg: *Bruguiera gymnorrhiza* at GQ, GQ-Ac: *Aegiceras corniculatum* at GQ. The name and occurrence date of each typhoon are also shown.

Fig. 4. Average daily **(a)** net ecosystem CO_2 exchange (NEE), **(b)** gross ecosystem production (GEP), **(c)** ecosystem respiration (RE), and **(d)** evapotranspiration (ET) before and after six typhoons made landfall. Dark grey bars represent the values during the typhoons occurred at Yunxiao, and light grey bars are for those during the typhoons occurred at Gaoqiao. One asterisk (*) represents significant at $P < 0.05$, two asterisks (**) represent highly significant at $P < 0.01$, and three asterisks (***)

represent extremely significant at $P < 0.001$.

Fig. 5. Residuals of daytime net ecosystem CO_2 exchange (NEE) at photosynthetically active radiation (PAR) as a function of vapor pressure deficit (VPD) and air temperature (Ta) before and after a typhoon made landfall. Residual NEE was calculated by subtracting the NEE expected based on light response function using observations (PAR > 500) from the observed NEE.

Fig. 6. Light response curves before (grey circles) and after (dark circles) 6 typhoons made landfall.

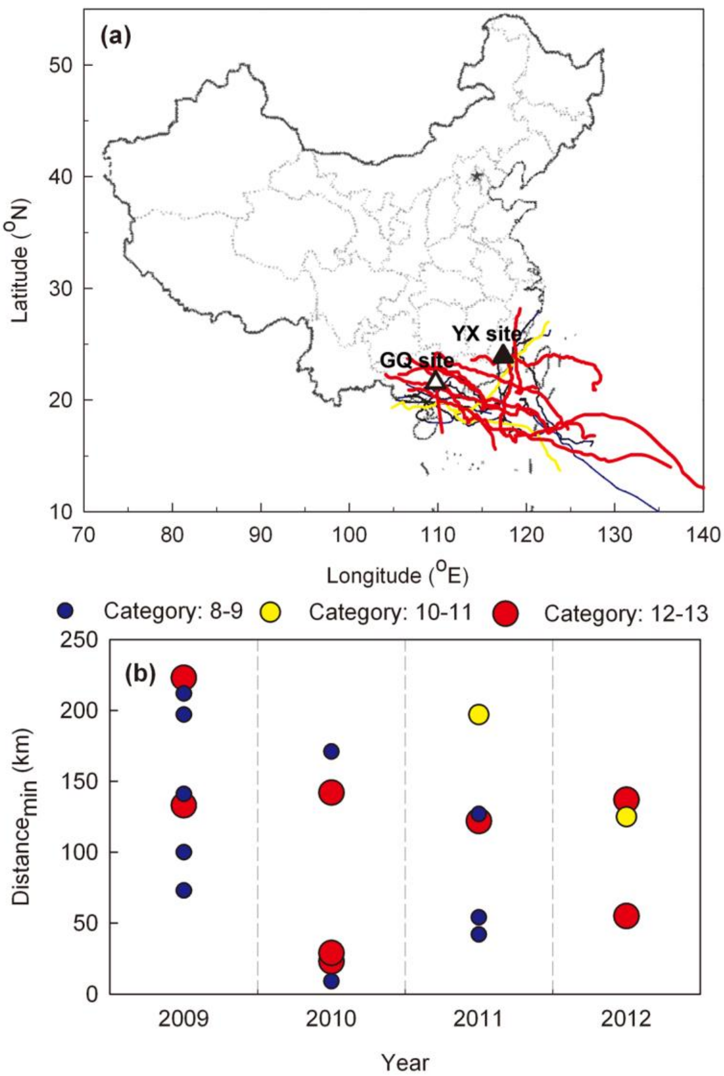

Fig. 1

Fig. 1. **(a)** Paths of the 19 typhoons that passed over Yunxiao (YX) and Gaoqiao (GQ) mangrove sites during a four year period between 2009 and 2012, and **(b)** category of each typhoon and its distance$_{min}$ (the minimum distance from mangrove sites) during 2009 and 2012.

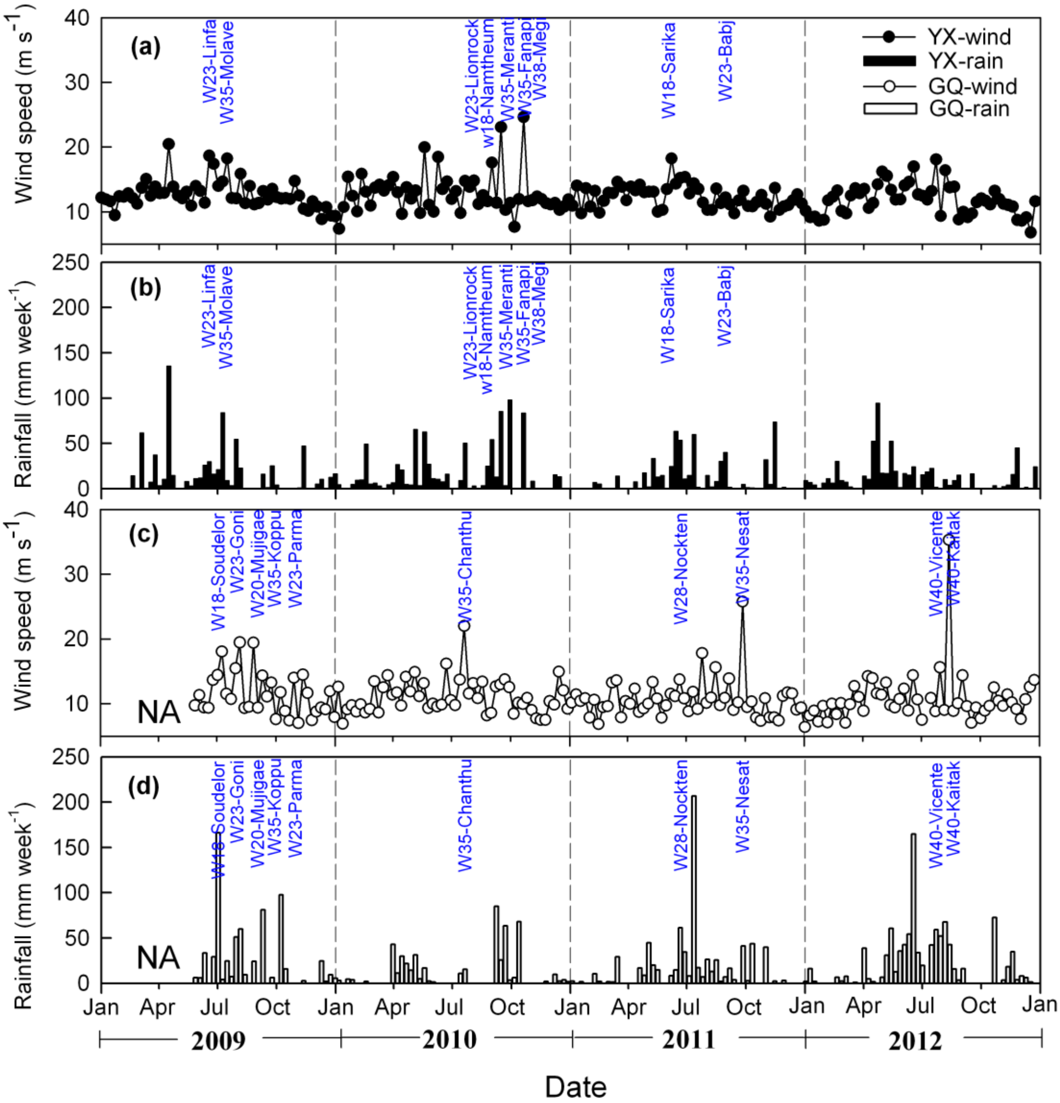

Fig. 2

Fig. 2. **(a, c)** Maximum wind speed, **(b, d)** total weekly rainfall for Yunxiao (YX) and Gaoqiao (GQ) during a four year period between 2009 and 2012. The name and occurrence date of each typhoon are also shown.

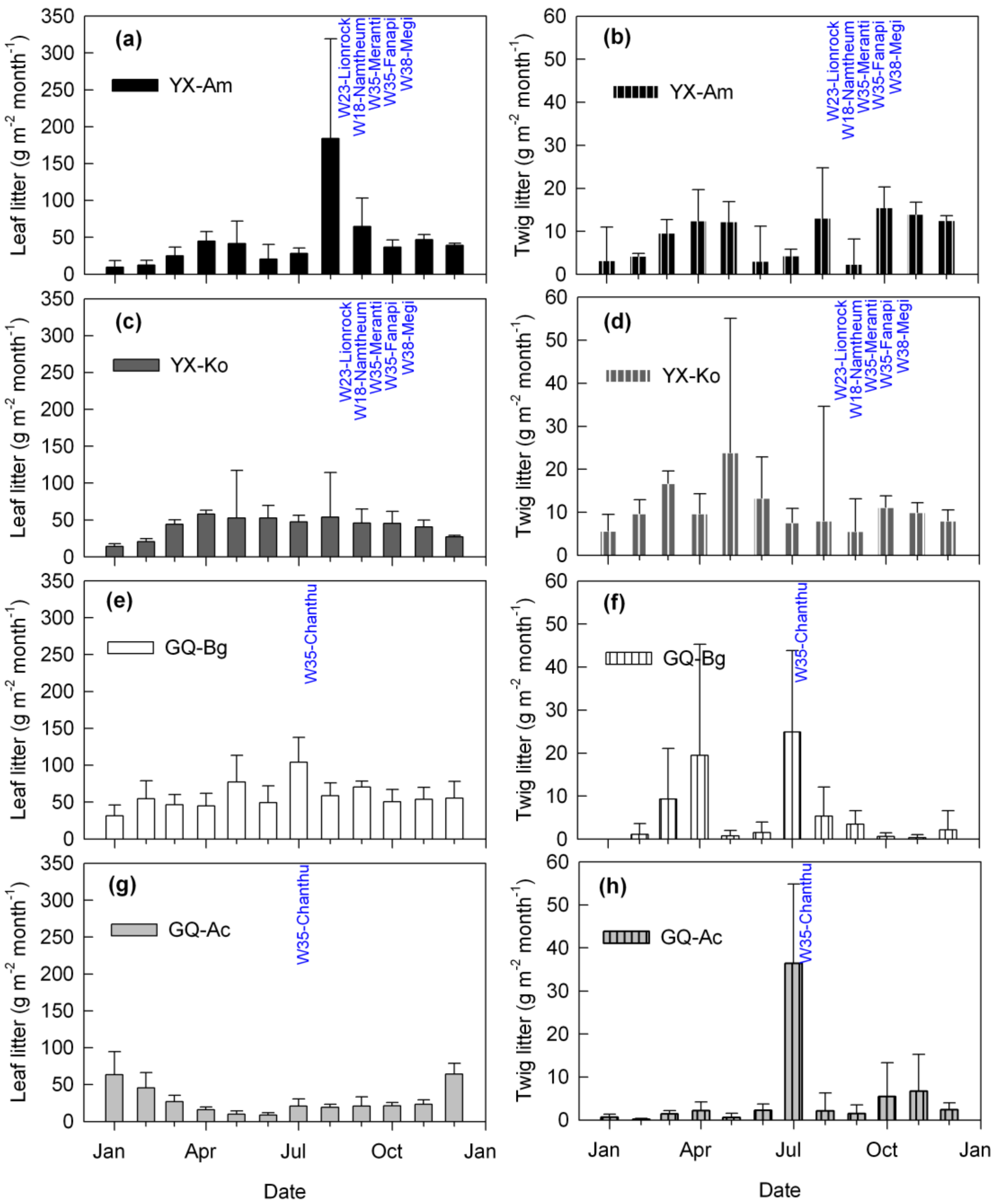

Fig. 3

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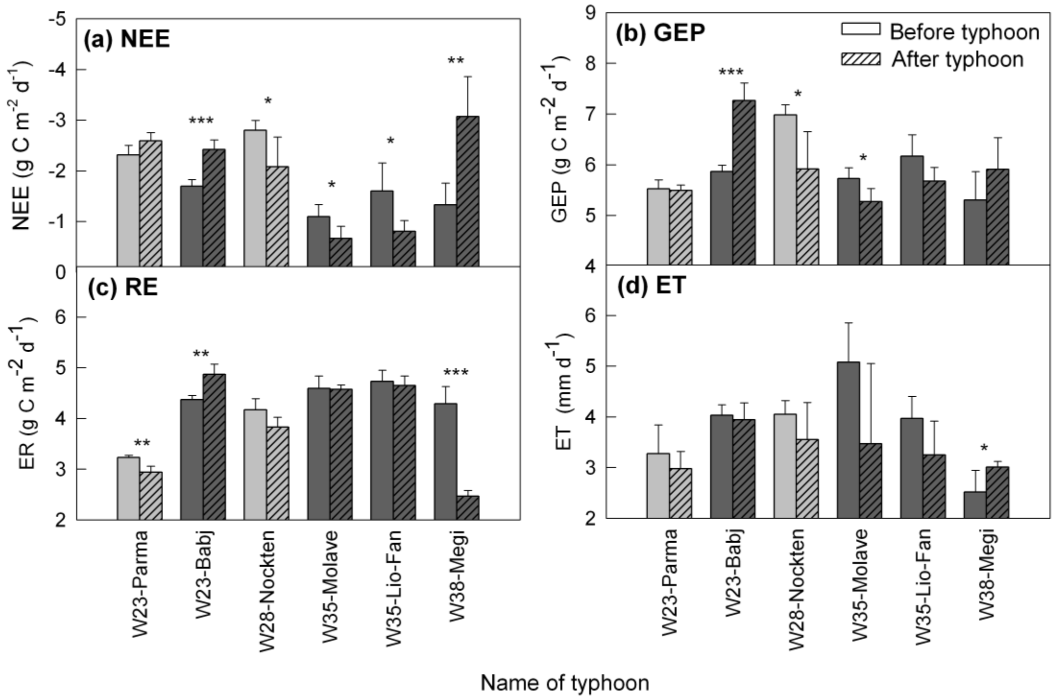

Fig. 4

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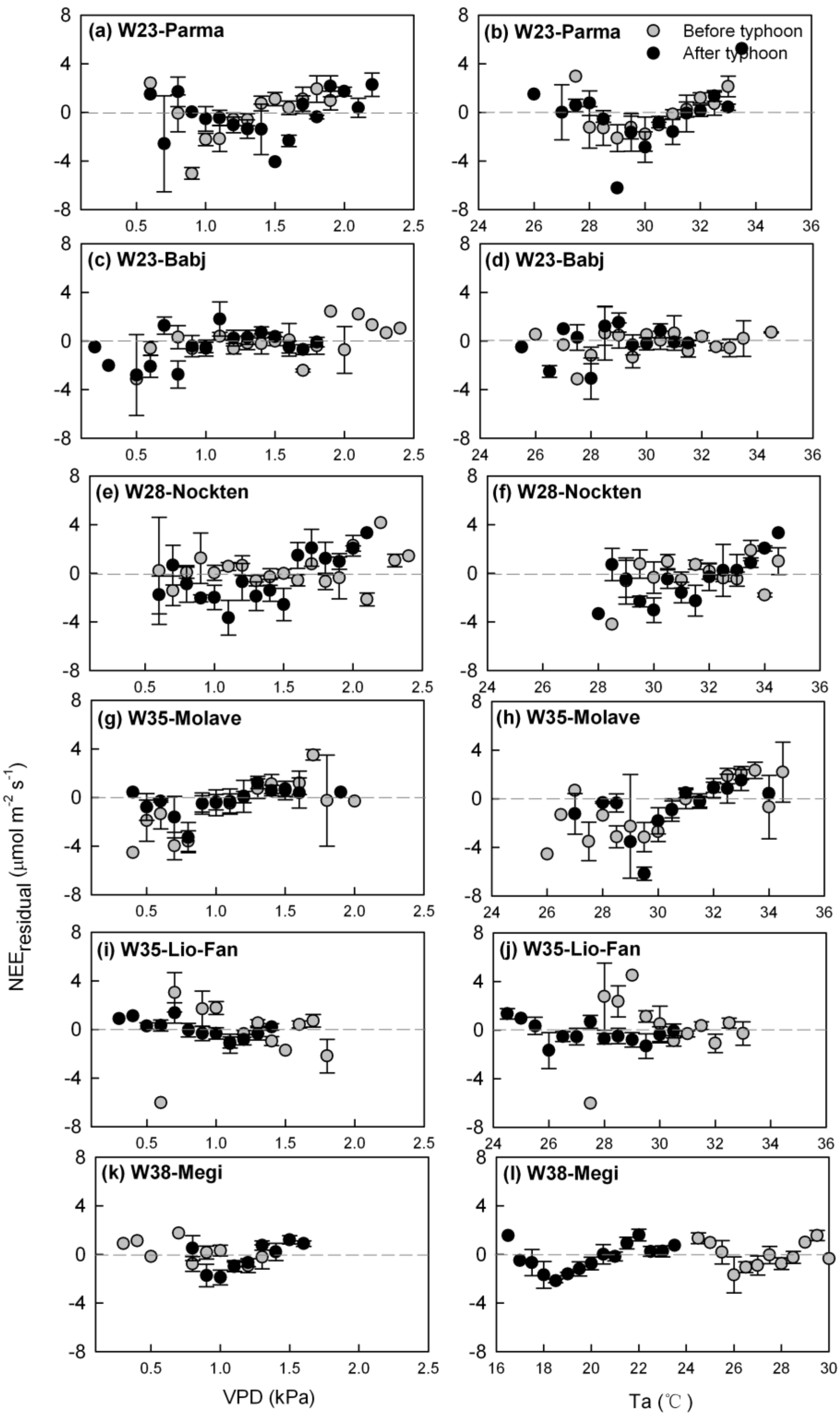

Fig. 5

Fig. 5. Residuals of daytime net ecosystem CO_2 exchange (NEE) at photosynthetically active radiation (PAR) as a function of vapor pressure deficit (VPD) and air temperature (Ta) before and after a typhoon made landfall. Residual NEE was

calculated by subtracting the NEE expected based on light response function using observations (PAR $>$ 500) from the observed NEE.

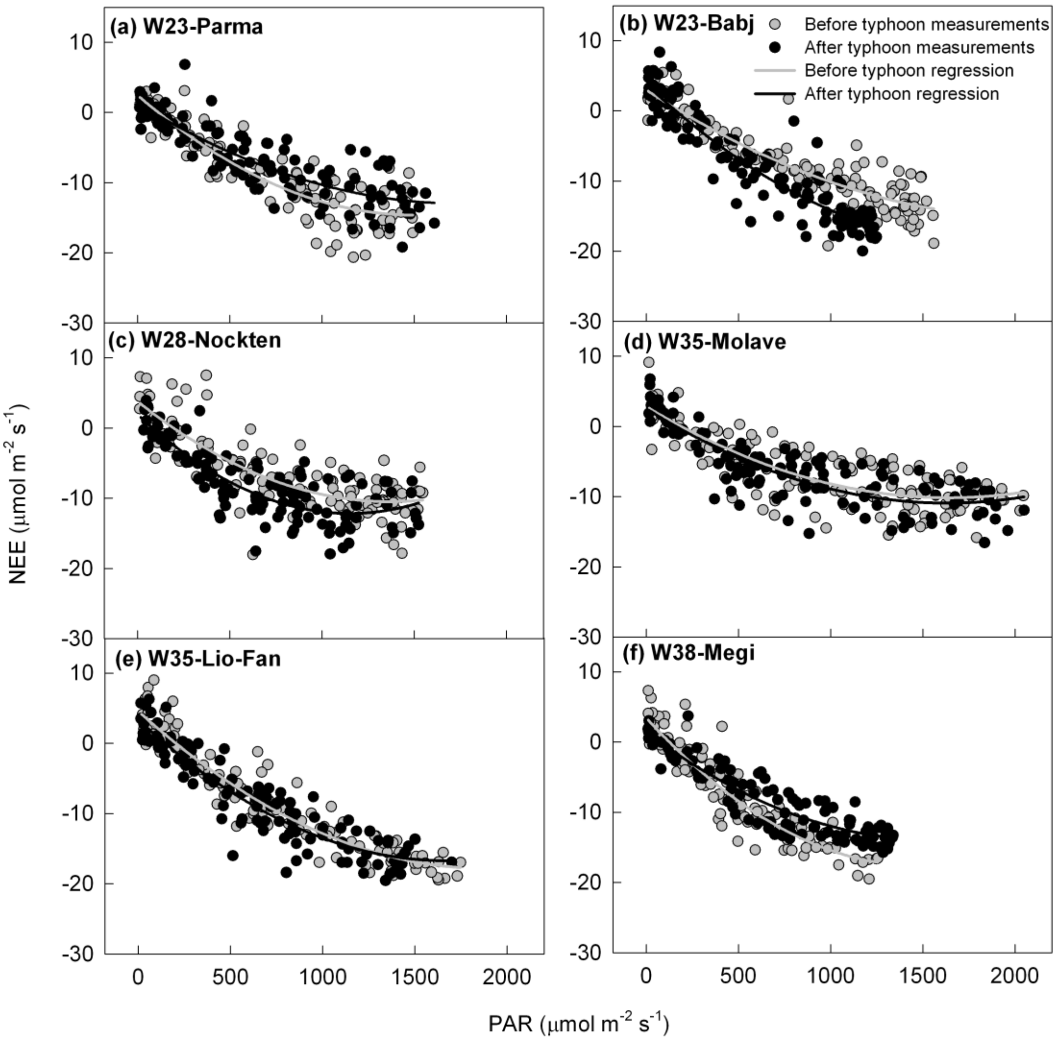

Fig. 6

Fig. 6. Light response curves before (grey circles) and after (dark circles) 6 typhoons made landfall.