Metabolic changes and the resistance and resilience of a subtropical heterotrophic lake to typhoon disturbance

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Abstract: We studied how typhoon strength affects the daily dynamics of ecosystem metabolism of a subtropical alpine lake in Taiwan. We identified proximal agents of typhoon disturbance and assessed the resistance (the extent of change induced by a disturbance) and resilience (the rate of recovery after a disturbance) of lake metabolism to them. Gross primary production (GPP), ecosystem respiration (ER), and net ecosystem production were estimated from high-frequency dissolved oxygen and water temperature data provided by an instrumented buoy. There were 15 typhoons of various magnitude (accumulated precipitation [AP] ranged from 51.5 to 816.5 mm) recorded during this study. Typhoons resulted in significantly lower GPP (3%–81% decrease), and higher ER (7%–828% increase) compared to immediately before the events, and thus the lake became more heterotrophic (28%–852% increase in heterotrophy). The resistance and resilience of lake metabolism depended on the intensity of the typhoon. Smaller typhoons (with average daily AP (ADAP) < 200 mm•d^{-1}) had greater effects on lake metabolism than medium (ADAP 200–350 mm•d^{-1}) and large (ADAP >350 mm•d^{-1}) typhoons. However, metabolism also recovered more quickly after smaller typhoons than after medium or larger typhoons. Typhoon effects on ecosystem metabolism is likely mediated by the magnitude and duration of typhoon-induced changes in lake mixing, the quantity and quality of dissolved organic carbon, and the biomass of primary producers.

Keywords: lake metabolism, typhoon, resistance, resistance, high-frequency measurements

Introduction

Factors influencing lake metabolism (defined here as those processes determining gross primary production (GPP), ecosystem respiration (ER) and net ecosystem production (NEP)) are topical because lake metabolism is an indicator of trophic status. In addition, lake metabolism is a factor determining the extent to which lakes are net sources or sinks of atmospheric carbon (Hanson et al. 2003; Kortelainen et al. 2006). Globally, lakes and reservoirs may be a net carbon source to the atmosphere as well as sequestering an amount of carbon in their sediments similar to that reaching the world's oceans from streams and rivers (Dean 1999).

Global warming is expected to alter the spatial and temporal distribution of precipitation, potentially causing large functional changes in ecosystems (Kerr 2007; Zhang et al. 2007). Although debates still exist, the number and frequency of intense tropical storm and typhoon events is predicted to increase in subtropical areas (Hoyos et al. 2006; Vecchi et al. 2008). More precipitation and greater frequency may increase surface runoff from watersheds to recipient aquatic ecosystems, thus changing their biogeochemical cycling, food web structures and ecosystem metabolism.

Subtropical alpine lakes are usually characterized by highly variable environmental perturbations including typhoon-induced rapid flushing, high diel variation in irradiation, and temperature fluctuations (ranging from 14 ^{o}C to 25 ^{o}C in summer), all of which might be expected to affect physical and biogeochemical processes and, thus, lake metabolism (Frenette et al. 1996; Dodds 2002). Because most lake metabolism studies are from temperate dimictic lakes, metabolism of tropical and subtropical polymictic lakes, especially those subject to severe, episodic events such as typhoons, is poorly understood. Several studies have focused on the effect of typhoon disturbances on hydrodynamics, nutrient cycling, phytoplankton structures and CO_2 flux in Lake Biwa, Japan, and Yuan Yang Lake (YYL), Taiwan (Frenette et al. 1996; Robarts et al. 1998; Jones et al. 2009). Previous studies revealed that ecosystem metabolism in YYL has seasonal patterns similar to those of temperate lakes; however, monthly averages of GPP and ER are decreased by 50% and 25%, respectively, during the typhoon season (July to October) from their peaks in mid-May (Tsai et al. 2008). Nevertheless, the response to and recovery of lake metabolism from typhoon disturbances and proximal drivers of change are still not understood at the time scales that are relevant to the lake's dynamics. Because typhoons bring strong winds and large amounts of precipitation, they likely cause vertical mixing of the water column as well as nutrient and dissolved organic carbon (DOC) loading (Gaiser et al. 2009). The effects on lake metabolism are difficult to predict *a priori* because nutrient loading would tend to push the lake toward autotrophy while DOC loading would push the lake toward heterotrophy (Hanson et al. 2004).

Limited information about the impact of typhoons on lake metabolism results from difficulties accessing study sites and research facilities, especially during or immediately after the storm events. The advent of wireless sensor networks providing high-frequency data immediately before, during and after these storm events has allowed researchers to fill in these data gaps (Porter et al. 2005, 2009). The GPP and ER of freshwater ecosystems provide a fundamental indication of cross-ecosystem connectivity responding to natural and human disturbances. They are useful parameters for evaluating aquatic ecosystems’ response to disturbances because both processes integrate energy and material flows through the ecosystem (Uehlinger 2000; Williamson et al. 2008). The resistance (the amount of change caused by a disturbance) and resilience (the speed of recovery following a disturbance) of an ecosystem are key factors determine its ability to continue functioning under changing conditions (Orwin and Wardle 2004). Understanding an ecosystem’s resistance and resilience to natural or anthropological disturbances can help predict response to anticipated changes in the future.

Yuan Yang Lake (YYL) is a small, shallow, subtropical alpine lake located in northern

Taiwan. The lake experiences multiple typhoon events each year. A single typhoon can deliver more than a meter of precipitation on the 4.5-m-deep lake, which results in rapid flushing (Tsai et al. 2008). Here we present the results of 18 months of study of the metabolism of YYL by *in situ* high-frequency diel dissolved oxygen (DO) measurements. Fifteen typhoon events were recorded during this study. We aimed to assess how physical, chemical and biological changes due to typhoons altered daily lake metabolic dynamics.

In a smaller lake ecosystem, we hypothesized that lake metabolism recovers more quickly from small- and medium-sized typhoons (the size of typhoon was classified by their average daily precipitation, for details please see Table 1) than from large typhoons. Small to moderate precipitation events may tend to flush terrestrial nutrients or chemicals from the watershed and lead to obvious changes in the lake's metabolism. In contrast, large typhoons might bring more materials into the lake, however, extra precipitation associated with large typhoons may act to dilute inputs to the lake. After large typhoons, lakes may be slower to recover than after small to moderate events because primary producers and heterotrophs would be flushed out of the system with the massive precipitation. To test this hypothesis and better understand the mechanism of the impact of a typhoon on lake metabolism, we aimed to (1) assess how typhoon strength affects lake metabolism and potential metabolic drivers, (2) clarify the potential mechanisms causing these effects, and (3) assess the resistance and resistance of lake metabolism to typhoon disturbances.

Materials and methods

Study site

Yuan Yang Lake (YYL) is in the north-central region of Taiwan (24°35'N, 15 121°24'E) and is a small (3.6×10^4 m^2), shallow (4.5 m maximum depth) lake in a mountainous catchment 1730 m above sea level (Fig. 1). The lake has no defined inlet and one outlet. The lake and watershed (3.7×10^6 m^2) was selected for long-term ecological study by the Taiwan

National Science Council in 2004 and joined the Global Lake Ecological Observatory Network (GLEON) in 2004. The steep catchment is dominated by pristine Taiwan false cypress forest. The lake is slightly colored, with an average DOC concentration of 6.1 mg•L^{-1} and mean pH of 5.9. The mean annual temperature is approximately 13 ^{o}C (monthly average ranges from -5 to 15 ^{o}C), and annual precipitation can exceed 4 m. The water column is stratified from early spring to late autumn and is usually completely mixed in winter. Anoxia is commonly observed in the hypolimnion during summer and autumn. The lake experiences three to seven typhoons (in summer and autumn) each year, during which more than 40% of the annual precipitation may fall.

High-frequency data collection

An instrumented buoy was deployed in April 2004 above the deepest location in YYL to record surface DO concentration, water temperature and wind speed every 10 min (Fig. 1). Surface DO concentrations were measured at 0.25 m depth by a Sonde (600-XLM, YSI, Inc. Yellow Springs, OH, USA) fitted with a rapid-pulse oxygen-temperature electrode (YSI, model 6562). The DO Sonde was calibrated in air, with a correction for barometric pressure before deployment. This air calibration was checked during weekly calibration/maintenance visits by placing the Sonde in water-saturated air for 60 min. Additional calibrations were performed by measuring the DO concentration at 0, 0.25, 0.5, 1, 2, 3.5 m with a portable water-quality multiprobe (Hydrolab minisonde 4a, Hach Environmental, Loveland, CO, USA) to eliminate the potential bias induced by drift of *in situ* Sonde while being deployed. Water temperature was measured through the water column at 0.5-m increments by use of a thermistor chain (Templine, Apprise Technologies, Inc. Duluth, MN, USA). Wind speed was measured 2 m above the lake by use of an anemometer (model 03001, R.M. Young, Traverse, MI, USA). Precipitation, air temperature and downward photosynthetically active radiation (PAR) were measured at a land-based weather station approximately 1 km from the lake using a tipping bucket rain gauge, temperature probe (41382VC; R.M. Young) and a PAR sensor (LI-190; Li-cor, Lincoln, NE, U.S.A.), respectively. Over the entire period of observation (May 2004 to October 2005), data were successfully recorded on 446 days.

Limnological sample

Associated lake surface water samples were collected manually at weekly intervals during the typhoon season (June or July to October). Additional sampling was conducted before the onset of typhoons and immediately after typhoons when access permitted. Samples for DOC (45 mL), Chl *a* (200 mL) and water color (18 mL) analyses were collected using a portable hand pump with inline filters (Whatman, 47 mm GF/F, the nominal pore size is 0.7 μm, Maidstone, Kent, UK). DOC samples were stored on ice no longer than two days after collection until analysis with an O.I. TOC analyzer (Model 1010, O.I. Analytical, College Station, TX, USA) with persulfate digestion. Filters of Chl *a* sample were stored in the dark at 4^{o}C until Chl *a* was extracted with methanol and then was measured by a Portable Fluorometer (10-AU-005-CE; Turner Designs, Sunnyvale, CA, U.S.A.) (Hanson et al. 2003). Total phosphorus (TP) and total nitrogen (TN) were measured from unfiltered surface water samples. TP samples (50 mL) were digested with concentrated sulphuric acid and later analysed by the molybdenum blue method. TN samples of 6 mL were combined with potassium peroxydisulphate and then digested in an autoclave. Nitrite content was determined by using a Shishin flow injection analyser (FIA, ZC4000; Taipei, Taiwan). Water color samples were kept on ice and brought back to the laboratory. Absorbance was measured by spectrophotometry (Spectroquant, VEGA 400, Serial No: 00060093, Merck, Whitehouse Station, NJ, USA) in a 10-cm cuvette. Water color was expressed as wavelength-specific (440 nm) absorbance coefficient: (a_{440}, m^{-1}): $a_{440} = 2.303 \times$ (absorbance at 440 nm/0.1 m) (Houser 2006).

Estimation of lake metabolism

Daily GPP and ER were estimated from high-frequency measurements (every 10 min) of

DO concentration at 0.25 m depth. The metabolism model described by Cole et al. (2000) and Hanson et al. (2003) was adopted for estimating GPP, ER and NEP from diel DO data. We assumed that the additional loading of DO induced by external loadings of surface inflow, and groundwater were negligible in the lake. In brief, ER was calculated as the atmospheric diffusion-corrected changes in DO during nighttime. In keeping with previous work (Cole et al. 2000; Hanson et al. 2003; Tsai et al. 2008), we calculated GPP by assuming that ER during the day and night was equal. NEP (=GPP-ER) was calculated as the diffusion-corrected increase in surface-layer DO during daytime. Metabolic parameters were calculated for each day except for the days of typhoons, because entraining of anoxic bottom waters (Tsai et al. 2008) and potential DO loading from incoming waters may render the model invalid during (but not immediately before or after) typhoon events.

Because of the effect of alpine topography and foggy weather on the availability of PAR to primary producers, light intensity data from the meteorological station were examined at an hourly time step to estimate the actual timing of photosynthesis. We considered “daytime” to be the period when the measured light intensity was >10 μmole photons $m^{-2}\bullet s^{-1}$ (Lauster et al. 2006). Exchange of oxygen between water column and atmosphere (F_{atm}) was estimated as $F_{atm}= k(O_{2sat}–O_2)/Z$ ($\mu mol\bullet m^{-3}\bullet h^{-1}$) (Cole et al. 2000, 2002), where Z is the depth of mixing layer (m) and k is the transfer coefficient ($m\bullet h^{-1}$) for oxygen. k is expressed as (Wanninkholf, 1992)

$$k = k_{600} \times \left(\frac{SC_{oxy}}{600}\right)^{-0.67}, \qquad (1)$$

where k_{600} (k for a Schmidt number of 600) was estimated as a function of wind speed at 10 m (U_{10}, $m\bullet s^{-1}$) above the lake by the equation of $k_{600} = 2.07 + 0.21 \times U_{10}{}^{1.7}$ (Cole et al. 1994), and

SC_{oxy} is the Schmidt number for oxygen and is calculated as follows (Wanninkholf, 1992):

$$SC_{oxy}=1800.6-120.1\times t+3.78\times t^2-0.05\times t^3, \tag{2}$$

where t is the water temperature (°C).

$O_2(t)$ and $O_{2sat}(t)$ are the measured DO concentration and saturation concentration of oxygen (mg•L^{-1}) at t °C, respectively. O_{2sat} is a function of water temperature and altitude and was estimated by the empirical equation given in Dodds (2002).

Data analysis

We used the difference between 3-day means of GPP, ER, and NEP immediately before and after a typhoon event to quantify typhoon-induced metabolic change. The duration of typhoon event itself was determined by the in-situ measured timing of typhoon-induced precipitation in YYL. The index for resistance (*RS*) was calculated as follows (Orwin and Wardle 2004):

$$RS(t_0)=1-\frac{2|D_0|}{(C_0+|D_0|)}\ , \tag{3}$$

where D_0 is the difference between the last measurement of metabolic parameters before typhoon events (C_0) and the maximal disturbed metabolic parameter occurring at time t_0 after the end of the typhoon. The index for resilience (*RL*) at time t_x was calculated as follows:

$$RL(t_x)=\frac{2|D_0|}{(|D_0|+|D_x|)}-1, \tag{4}$$

where t_x is 3 days after the occurrence of the maximum disturbed parameter and D_x is the difference between the C_0 and the disturbed metabolic parameters at time t_x. *RS* and *RL* both range between -1 and 1. A value of 1 indicating that the disturbance has no effect in the metabolic parameters (maximal resistance) and full recovery (maximal resilience) of response variables to the level before the disturbance. An *RS* value of 0 indicates a 100% reduction or enhancement and an *RL* value of 0 represents no recovery (i.e., $D_0 = D_X$) in the metabolic parameters after the end of the disturbance, respectively. Negative values of *RS* indicate more than 100% change (i.e., where $|D_0| > C_0$) and negative values for *RL* indicate negative recovery (i.e., the system continued to move away from its pre-typhoon state even after the typhoon had ended).

We used one-way ANOVA with Tukey's post-hoc test to evaluate the impact of typhoon on lake metabolism by comparing 3-day averages of GPP, ER, and NEP values before a typhoon with corresponding parameters measured in the subsequent post-typhoon periods. A paired *t*-test was used to compare the *RS* and *RL* of GPP, ER, and NEP. Pearson correlation was used to determine the quantitative relation between change in environmental and limnological variables and the three ecosystem metabolic parameters (i.e., GPP, ER, and NEP). Stepwise multiple linear regression analysis was performed to identify the factors that simultaneously account for the *RS* and *RL* of lake metabolism. We used Statistica® software (StatSoft, Tulsa, OK, USA) to calculate the coefficient of determination (R^2). A $p < 0.05$ was considered statistically significant.

Results

Typhoon disturbance regimes

Typhoon and storm disturbances were prevalent in YYL (Table 1), with seven typhoon events in 2004 and eight events in 2005. The accumulated precipitation (AP) of a single typhoon ranged from 51.5 to 816.5 mm, and the 10-min average wind speed ranged from 0.72

to 3.45 m•s^{-1}. The AP was positively correlated with the corresponding wind speed (r=0.88, p<0.05, n=15, Table 2 and Fig. 2d). Total precipitation in typhoon seasons accounted for 69.6% and 67.8% of the annual total precipitation in 2004 and 2005, respectively. Typhoon disturbances changed a number of measured limnological variables. Although water color and DOC concentrations increased quickly after the typhoons, the opposite was noted for Chl *a* and TP. (Fig. 3). The change in limnological variables (%) was negatively correlated with the AP of typhoons except for TP. Decreases in water color, DOC and TN were observed after large typhoon (e.g., L1) (Fig. 3).

Response of lake metabolism to typhoons

Results of one-way ANOVA indicated that most of the typhoon events resulted in lowered GPP (3.3%–81.0% decrease) and increase ER (7.1%–827.7% increase). The lake, therefore, became more heterotrophic after typhoon events (27.6%–852.4% increase in heterotrophy) (p<0.05, Figs. 2a-c). Daily changes in NEP were mainly controlled by ER dynamics. The daily changes in NEP were mainly controlled by the dynamics of ER, because ER was more responsive to typhoons than GPP (average change levels were 160.4% and -41% for ER and GPP, respectively) (Figs. 2a-c). Nevertheless, the extent of metabolic changes and magnitude of AP and wind speed were not correlated (Fig. 2). Typhoons induced obvious interruptions for the time series of lake metabolism, surface DO and water temperature profiles. Water mixing during typhoons was evident when temperature data from 0.25 and 3.5 m depths were examined (Figs. 4a-d). The temporal trends of DO during and after disturbances were related to the water mixing regime and time series of GPP and ER (Figs. 4). DO level in YYL decreased (-16.7% to -58%) during medium and small typhoons (e.g., S2) but temporarily increased during large events and then quickly dropped to low levels after the typhoon (e.g., L1, +71%). Surface DO took 3-5 days to recover to pre-typhoon levels (Fig. 4e and f). The regular diel DO cycle (i.e., DO level increased at day and decreased at night) also weakened or even disappeared during typhoons but recovered within 1 or 2 days after a typhoon or storm. F_{atm} increased after small typhoons because decreased DO concentration enhanced the flux of atmospheric O_2 (Figs. 4g and h). All parameters took about 5-10 days to return to pre-disturbance levels.

Resistance and resilience of lake metabolism

Although changes in GPP, ER and NEP were not correlated with the intensity of typhoons (i.e., AP or wind speed), the *RS* of the three metabolic parameters showed a positive correlation with the intensity of AP (Figs. 5a-c). Surprisingly, more negative values of *RS* occurred with small typhoons (with average daily accumulated precipitation (ADAP) < ~200 $\mathrm{mm \cdot d^{-1}}$), which revealed that small events caused stronger effects on GPP, ER and NEP than medium (ADAP 200–350 $\mathrm{mm \cdot d^{-1}}$) and large-sized events (ADAP >350 $\mathrm{mm \cdot d^{-1}}$). Paired *t*-test results showed that the *RS* of GPP was significantly greater than ER, again indicating that ER is more responsive to typhoon disturbances than GPP. The *RL* of the three metabolic parameters was negatively correlated with AP (Figs. 5d-f), which indicated that ecosystem metabolism recovered faster after smaller disturbance events than after larger ones. Negative values of *RL* for ER and NEP were observed only in one large event (L1). *RL* did not significantly differ among the three metabolic parameters (p>0.05).

In addition to the direct effect of intensive precipitation and strong wind on the dynamics of lake metabolism, changes in limnological factors were also correlated with the reaction and recovery of lake metabolism to typhoons (Table 2 and 3). A positive correlation between changes in TP and *RS* of GPP (r=0.71, Fig. 6a) suggested that the lower resistance of GPP to small typhoons (Fig. 5a) may be mediated by decreased TP after most typhoons (Figs. 3d and e). Results of stepwise multiple regressions showed that Chl *a* and water color accounted for *RL* of GPP (p<0.05, Fig. 6d and Table 3), suggesting that the quicker GPP recovery rate after small typhoons (Fig. 5d) might result from increases in Chl *a* and color in the lake. Changes in

TN and DOC both showed a significant positive correlation with changes in water color, and these changes were all significantly driven by precipitation ($p<0.05$, Table 2). This correlation implied that both colored N- and C-rich compounds were affected by the increase in allochthonous organic matter after typhoons.

The *RS* of ER and NEP was negatively correlated with changes in TN (Table 2 and 3, Fig. 6c). Small typhoons tended to increase TN (Fig. 3c). This finding explained why ER and NEP were less resistant to smaller typhoons than large ones (Figs. 5b-c). Increases in the *RL* of ER and NEP were associated with the increase in water color, TN and DOC (Table 2 and 3). Changes in water color, TN and DOC were far less after typhoons with the least precipitation (Figs. 3a-c) which may explain the higher recovery of ER and NEP after these smaller events (Figs. 5d, e and f). Furthermore, changes in Chl *a* were correlated with *RS* and *RL* of ER and NEP (Figs. 6b, e and f). Such changes suggest that the observed GPP and ER reaction to typhoons may have been driven by autochthonous organic carbon. After typhoons, recovery rate (i.e. of *RL*) was not correlated with either daily water temperatures or light intensity. (Figs. 4c and d).

Discussion

One of the most interesting observations of this study was that YYL became temporarily heterotrophic after typhoons. The decreases in concentrations of TP and Chl *a* after typhoons accounted for reductions in GPP (Figs. 3d and e, Fig. 6a). In this lake, typhoons caused temporary partial or total mixing of water column and the water level to fluctuate (Figs. 4a-d). This finding suggests that lake water was moved out of the lake during typhoon events. The quick movement and renewal of lake water may reduce the concentration of Chl *a* and result in reduced GPP, which suggests that the rapid response of lake metabolism may be controlled simply by the change in hydrologic processes rather than by biological processes. This phenomenon has been observed in freshwater systems i.e. flood-prone rivers and alpine streams (Uehlinger et al. 2003; Acuña et al. 2004). Thus, bed-moving floods transiently reduce both GPP and NEP in stream ecosystems and shift ecosystem metabolism towards heterotrophy because of the reduction in primary producers (e.g., periphyton and diatoms). We found that DOC and water color increased after majority of typhoons (Fig. 3a and b). The increase in water color or DOC concentration might temporarily decrease light penetration within the water column and thus inhibit GPP. Karlsson et al. (2009) indicated that light availability is a strong limiting factor for ecosystem production in heterotrophic lakes and natural changes in colored dissolved organic matter (CDOM) override the effects of natural variations in nutrients (e.g., nitrogen and phosphorous) on ecosystem production. DOC of terrestrial origin would strongly absorb solar radiation and thus reduce the light availability for aquatic primary producers. Otherwise, the primary production of the phytoplankton community is affected by both instantaneous irradiance and the short-term light history (Obrien et al. 2009). Large quantities of algae were observed in the bottom layer of YYL during the stratification period between typhoons (Tsai et al. 2008). Large and medium typhoons destroyed the stratification that had characterized the water column between typhoon events and caused temporary mixing of the lake (Fig. 4b). These algae might be quickly released to the surface layer by the typhoon-induced vertical mixings and may have replaced the original algal species. Primary production of these dark-acclimated algae from hypolimnion may be more prone than the original light-acclimated species to photoinhibition by the high incident light after storms and typhoons (Figs. 4c and d), thus decreasing GPP. The change in phytoplankton community might also be responsible for the variation in GPP after typhoon, because a size-dependent change in Chl *a* and changes in photosynthesis efficiency were observed after typhoons (Frenette et al. 1996).

The major impact of typhoons on lake metabolism might be also mediated through the effect of weather conditions on the dynamics of limnological variables. ER and NEP were stimulated after typhoons (Fig. 2b), the *RS* of ER was negatively correlated to typhoon-induced changes in water color, Chl *a* and TN and the *RL* of ER and NEP were positively correlated to changes in water color, Chl *a*, TN, and DOC concentration (Table 2, Figs. 6b-c). Water color (light absorbance at 440 nm) is a good predictor of terrestrially produced dissolved organic matter in lakes (Carpenter et al. 2005). The increase in water color and DOC was widely reported as resulting from elevated precipitation, which increases loading of allochthnious carbon and affects ecosystem metabolism (Gergel et al. 1999, Pace and Cole 2002). Several lines of evidence support inputs of terrestrial organic material from landscapes substantially contributing to bacterial ER and resulting in reduced NEP in aquatic ecosystems (Beisner et al. 2003; Hanson et al. 2003; Karlsson et al. 2007). YYL is a persistently heterotrophic ecosystem (Tsai et al. 2008), which suggests that ER not only uses the organic compounds originally produced by photosynthesis but is also fueled by allochthonous carbon.

Temporary vertical mixing of the water column was prevalent during typhoons (Figs. 4a-d) and may have accelerated the release or re-suspension of essential nutrients from the sediment to the epilimnion, where they can be used by microbes, which results in increased ER (Robarts et al. 1998; Kirchman et al. 2004; Pérez and Sommaruga 2006). A negative correlation between the resistance of ER and change in Chl *a* (Fig. 6b) indicated that if typhoons cause a large decrease in chlorophyll, ER also changes less (i.e., high resistance). The decrease in Chl *a* after typhoons might provide a low autochthonous organic substrate for heterotrophic organisms (Aoki et al. 1996) and thus low rates of changes in ER. Our findings suggest that Chl *a* (i.e., the biomass of algal community) seems to be one of the key drivers for the response and recovery of ecosystem respiration to typhoons. Several lines of studies indicated that the release of nutrients from the autochthonous pool (e.g., sediment or littoral) after typhoons or floods, rather than just allochthonous sources, might be responsible for the change in lake metabolism because terrestrially derived carbon is often relatively refractory to biological use (Cole et al. 2002; Pérez and Sommaruga 2006; Colangelo 2007). Although we did not intend to assess the relative contribution of autochthonous and allochthonous carbon to post-storm responses, both autochthonous and allochthonous organic matter might play a key role in mediating the reaction of the lake metabolism to typhoon events.

DO concentrations decreased temporarily after typhoons. Two processes might account for the dynamic changes in DO level. First, the large increase in ER, and to a lesser extent the small decrease in GPP, after typhoons (Fig. 2b and Figs. 4g and h) can cause a steady decline in DO levels. Second, entrainment of low DO water from the hypolimnion during and after large typhoons could also account for the decrease in surface DO level after typhoons. Consequently, the recovery rate of ER and restratification would therefore be the key processes controlling the resilience of YYL metabolism.

*R*esults of resistance and resilience assessments indicated that small typhoons (with ADAP < 200 mm•d^{-1})) cause large changes (i.e., low resistance) in GPP, ER, and NEP as compared with medium- and large-sized events (Fig. 5). The differential response of lake metabolism to disturbance events of different intensity is an interesting observation. We found that small to moderate precipitations might flush available DOC and nutrients (TN) from the watershed, thus leading to increased concentrations of limnological drivers in the lake and resulting in rapid changes (i.e., low resistance) in lake metabolism. Additional precipitation associated with large typhoon events may merely serve to dilute the DOC (or nutrients) level would have been loaded in small to moderate events (Figs. 3a-d). This dilution would be manifested in a relatively higher resistance of lake metabolism to large typhoons (Fig. 5). The reduced resilience of the lake metabolism to large typhoon events may be mediated by the increased flushing, with massive precipitation substantially diluting the algal (Fig. 3d) and microbial population abundance. Lower recovery of ER and NEP after large typhoons (Figs.

5e and f) is associated with loss of Chl *a* (Figs. 6e and f), which might occur because of the decreasing nitrogen consumption due to the loss of Chl *a* after large typhoons.

Results of Pearson and stepwise multiple analyses indicated that frequency of typhoon (D_{SLT}) was not significantly correlated to the resistance and resilience of the lake metabolism (Table 2 and 3). Nevertheless, the interval and sequence of storms might affect how the lake reacts to the disturbance and determine the factors that affect the rate of metabolic recovery of the system. For example, larger typhoons may have a major "cleaning" effect, transporting DOC and/or other materials into the lake and thus reducing the amount of chemicals available for transport during the following small typhoon (e.g., the cases between L1 and S4, and between M3 and S6), resulting in smaller effects (i.e., higher resistance of the lake) compared to other small typhoons (e.g., S3, Fig. 5b and c). In contrast, if a small or medium typhoon following a sequence of typhoons with similar size, the resulting effects would be enhanced (i.e., lower resistance of the lake) (e.g., S2, S3, S8 and S10). The effect of the first small typhoon in each year is often large due to the abundance of materials accumulated since the last typhoon season (e.g., S1, Fig. 5b and c). Assessment of the frequency and cumulative effects of typhoons is in need of additional study, especially over multiple years.

In summary, this study revealed that episodic environmental events such as typhoons altered the daily dynamics of ecosystem metabolism in YYL. Typhoons tended to decrease GPP and stimulate ER, and thus the lake became more heterotrophic. Smaller typhoons caused stronger effects on lake metabolism than did medium- and large-sized typhoons; however, metabolism recovered more quickly after smaller typhoons than after medium or larger typhoons. Typhoon-induced changes in the quantity and quality of limnological drivers such as dissolved organic carbon and nutrients (TN and TP) and the biomass of primary producers (Chl *a*) mediated the response and recovery of lake metabolism to typhoons. Thus, patterns of typhoon intensity associated with corresponding changes in limnological drivers were key predictors of the daily dynamics of lake metabolism immediately after typhoons. Results of this study provide a scientific basis to predict how lakes might change as net sources or sinks of carbon from the atmosphere in subtropical or tropical regions if global warming leads to an increase in typhoon frequency.

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Table 1. The timing, total accumulated precipitation, mean wind speed, and strength of typhoons recorded in Yuang-Yang Lake (YYL) from May 2004 to October 2005.

Year	Date[a]	Code	Strength[b]	Accumulated precipitation[c] (mm)	Mean wind speed[c] (m•s^{-1})
2004	8-9 June	S1	Small	51.5 (51.5)	0.72 (5.3)
	1-4 July	S2	Small	160.0 (53.3)	1.35 (8.7)
	11-14 Aug.	S3	Small	205.0 (68.3)	2.19 (13.5)
	23-25 Aug.	L1	Large	816.5 (408.3)	3.25 (15.5)
	11-12 Sept.	S4	Small	115.5 (115.5)	1.29 (6.2)
	24-26 Oct.	S5	Small	256 (128.0)	2.13 (15.2)
	3-4 Dec.	M1	Medium	215.0 (215.5)	1.69 (5.7)
	Total			1741.0	
	Mean±SD			248.7±257.1	1.80±0.82
2005	17-19 July	M2	Medium	650.0 (325.0)	2.67 (11.9)
	3-5 Aug.	M3	Medium	620.0 (310.0)	3.45 (16.4)
	12-13 Aug.	S6	Small	118.0 (118.0)	2.21 (7.8)
	31 Aug.-1 Sept.	L2	Large	380.0 (380.0)	2.13 (11.3)
	10-13 Sept.	S7	Small	79.0 (26.3)	2.06 (6.0)
	21-23 Sept.	S8	Small	102.5 (51.3)	1.35 (6.7)
	1-3 Oct.	S9	Small	293.0 (146.5)	2.26 (20.5)
	7-9 Oct.	S10	Small	156.0 (78.0)	1.72(5.9)
	Total			2379.0	
	Mean±SD			297.4±228.8	2.2±0.63

[a] Typhoon events reported by the Central Weather Bureau in Taiwan (CWBT). Data adapted from the typhoon database of CWBT. Website: http://rdc28.cwb.gov.tw/. The duration of the typhoon event was adjusted by the measured timing of typhoon-induced precipitation in YYL.

[b] The strength of typhoon is determined based on the criterion for the precipitation classification of the Central Weather Bureau in Taiwan. Storms refer to small typhoon, if the averaged daily accumulated rainfall (ADAP) > 50 mm•d^{-1}; ADAP > 200mm•d^{-1}, referring to medium typhoon and large typhoon if 350 mm•d^{-1} or more. Website:

http://www.cwb.gov.tw/V6e/observe/rainfall/define.htm.

[c] Accumulated precipitation is the total amount of rainfall during each typhoon, where values in parentheses are the average daily precipitation of typhoon. Mean wind speed is expressed as 10-min mean value during each typhoon, where values in parentheses are the maximal measured wind speeds. Wind speed data and accumulated precipitation data were adapted from the lake metabolism database. Website: http://lakemetabolism.org/.

Table 2. Pearson correlation coefficients between resistance (*RS*) and resilience (*RL*) in gross primary production (GPP), ecosystem respiration (ER), net ecosystem production (NEP) and averaged wind speed (U_2), accumulated precipitation (AP), and changes in chlorophyll *a* (Chl *a*), dissolved organic carbon (DOC), water color (Color), total nitrogen (TN), and total phosphorus (TP) in the pre- and post-typhoon periods, and the interval between typhoons (D_{SLT}).

	RS.GPP	*RL*.GPP	*RS*.ER	*RL*.ER	*RS*.NEP	*RL*.NEP	U_2	AP	Color	Chl *a*	TP	TN	DOC	D_{SLT}
RS.GPP		-0.57	0.35	0.18	0.57	-0.12	0.13	0.02	0.08	0.31	0.71	-0.15	0.43	-0.52
RL.GPP			0.23	0.23	-0.70	0.46	-0.52	-0.19	0.48	-0.36	0.07	0.40	0.14	0.49
RS.ER				-0.22	0.27	-0.23	0.34	0.48	-0.11	-0.48	0.31	-0.43	0.08	-0.51
RL.ER					-0.69	**0.95****	**-0.90***	**-0.85***	**0.95****	**0.80***	0.66	**0.93****	**0.93****	0.20
RS. NEP						**-0.86***	**0.82***	0.61	**-0.78***	-0.33	-0.10	**-0.83***	-0.46	-0.44
RL.NEP							**-0.93****	**-0.86***	**0.95****	0.67	0.45	**0.97*****	**0.83***	-0.37
U_2								**0.88***	**-0.96****	-0.54	-0.50	**-0.97*****	**-0.78***	-0.57
AP									**-0.84***	**-0.79***	-0.35	**-0.92****	**-0.79***	-0.60
Color										0.59	0.67	**0.93*****	**0.89****	0.37
Chl *a*											0.37	0.69	**0.78***	0.006
TP												0.41	**0.79***	-0.20
TN													**0.79***	0.51
DOC														0.44

Correlations significant at least at $p<0.05$ are in bold. $^{*}p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$. $n = 78$ (6×13).

Table 3. Stepwise multiple linear regression analysis of effects of averaged wind speed (U_2), accumulated precipitation (AP), and changes in chlorophyll *a* (Chl *a*), dissolved organic carbon (DOC), water color (Color), total nitrogen (TN) and total phosphorus (TP) in the pre- and post-typhoon periods, and the interval between typhoons (D_{SLT}) on resistance (*RS*) and resilience (*RL*) in gross primary production (GPP), ecosystem respiration (ER), net ecosystem production (NEP). Only parameter with $P < 0.05$ are shown.

Dependent variable	Parameter	*n*	Overall r^2	Partial r^2	Coefficient	*p*
RS.GPP	rain	15	0.18	0.18	0.0004	0.033
RL.GPP	Chl *a*	6	0.64	0.58	-0.0235	0.040
	color			0.06	0.0392	0.047
RS.ER	DOC	6	0.44	0.44	0.0055	0.049
RL.ER	color	6	0.99	0.91	0.0049	0.003
	Chl *a*			0.08	0.0048	0.013
RS. NEP	TN	6	0.74	0.70	-0.0098	0.039
	color			0.04	-0.0060	0.047
RL.NEP	TN	6	0.94	0.94	0.0096	0.001

Figure legends

Fig. 1. Location and bathymetric map of Yuan-Yang Lake (YYL), showing the location of the buoy, water level sensor and meteorological station (solid square).

Fig. 2. Quantitative change in metabolic parameters, including (a) gross primary production (GPP), (b) ecosystem respiration (ER), and (c) net ecosystem production (NEP) between the 3-day mean value before and after typhoons and the corresponding total accumulated precipitation and mean wind speed of typhoons. Typhoon events are ranked from lowest to highest accumulated precipitation. Symbols: Solid bars, values of metabolic parameter before typhoon; gray bars, values of metabolic parameter after typhoons. *NS* indicates no significant changes (p>0.05).

Fig. 3. The percentage change in (a) water color, (b) dissolved organic carbon (DOC), (c) total nutrients (TN), (d) chlorophyll *a* (Chl *a*), and (e) total phosphorous (TP) near the mixed surface layer in the periods before and after typhoons of different magnitude. The instantaneous data collected within 3 days before and after typhoons were available for only 6 of the 15 recorded typhoons. Symbols: Solid bars, values of limnological variables before typhoon; gray bars, values of limnological variables after typhoons. The data below the graphs indicate the level of total accumulated precipitation.

Fig. 4. Daily changes in water level and mixing depth (a, b), and time series of high-frequency (10-min based) signals in (c, d) water temperature on 0 and 3.5 m depth and light intensity. (e, f) Dissolved oxygen (DO) at the surface layer and daily precipitation before, during and after selected typhoon disturbance scenarios (e.g. S2 and L1). The corresponding daily performance of gross primary production (GPP, solid squares), ecosystem respiration (ER, solid circles) and atmospheric flux (F_{atm}, open circles) are graphically summarized to describe the process accounting for the temporal variance of DO signals (g, h). Shade bars

represent the duration of typhoons.

Fig. 5. The calculated values of resistance (*RS*) and resilience (*RL*) for GPP, ER, and NEP as a function of the accumulated precipitation with a single typhoon. (n = 15)

Fig. 6. Scatter plots of *RS* and *RL* in metabolic parameters in relation to the percentage change in limnological drivers following typhoons in YYL in (a) GPP and TP, (b) ER and Chl *a*, (c) NEP and TN, (d) GPP and water color, (e) ER and Chl *a*, and (f) NEP and Chl *a*.