附件一

行政院國家科學委員會補助專題研究計畫

■ 成 果 報 告
□期中進度報告

氣候變遷對亞熱帶高山湖泊藻類群落動態及生態系統代謝之影響（第 2 年）

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(二) 中英文摘要及關鍵詞

摘要

淡水生態系統(例如，湖泊、溪流、水庫及溼地等)面積僅佔陸地生態系約3~5%，然而，淡水生態系統，卻在生物圈(bioaphere)裡面的生物地質化學循環過程中扮演著極重要的「導管」(conduit)角色，就全球的碳循環過程而言，陸域生態系中的有機態碳約5~50%是藉由溪流或湖泊生態系內的生物地球化學作用轉化後，再以無機態碳的型態輸送回大氣中。因此，在全球暖化的浪潮下，探討淡水生態系在區域性碳循環的角色，為近年來生態學家極為關注的研究議題，在第一年中，我們利用高頻率的溶氧監測系統及Odum代謝模式解析亞熱帶高山湖泊生態系(鴛鴦湖)代謝的季節性動態變化，研究結果顯示總初級生產量(gross primary production, GPP)及生態系呼吸量(ecosystem respiration, ER)在初夏及秋末時會達到峰值，而在颱風季節與冬季時會相對較低，以年的時間尺度來看此二湖泊為異營生態系。與夏初時期的峰值比較，颱風季節期間GPP及R分別下降約50%及25%，ER對颱風季節擾動的抵抗力較GPP高並呈現出較明顯的每日變化。湖水中陸源溶解性有機態碳(dissolved organic carbon, DOC)質及量上的變化為湖泊代謝調控與時間變化的主要控制因子，水色及allochthony (水體中有機態碳庫中，由陸地輸入者所佔的比例)為主要連結外界環境變動(例如，颱風、降雨或光強度)與生態系代謝的關鍵因子。我們的研究結果亦顯示降雨強度為影響湖泊生態系中DOC與代謝動態變化的主要環境作用力。同時，颱風侵襲會造成水體短暫的垂直混合，並促使累積在底層水中的大量無機態碳釋放回大氣層，因此，颱風將強化湖泊成為大氣中CO_2輸出源的角色。

在第二年中，利用高頻率間測儀器(每 10 分鐘一筆)紀錄颱風前後 7 天的溶氧變化量及相關氣象因子，我們可以評估在以「日」計的時間尺度下，生態系代謝對颱風侵擾的反應。研究結果顯示颱風過後 GPP 會因為初級生產者生物量被稀釋而下降，而 ER 則因大量陸源有機態碳的輸入而上升。湖泊代謝對颱風干擾的容忍力及恢復力則與降雨強度有關，我們發現湖泊代謝對小型颱風(總累積雨量<200mm)的容忍力較弱，而湖泊代謝在經歷中型以及大型颱風 (200mm<總累積雨量<600mm) 後的恢復力較差。研究發現颱風對鴛鴦湖生態代謝的影響與湖水中溶解性有機態碳在質與量上的變化以及初級生產者的生物量變動有關。

關鍵字：氣候變遷、湖泊代謝、颱風、碳循環、藻類

Abstract

Global warming is expected to increase the number and frequency of intense typhoon events in subtropical and tropical regimes. These changes may modify the dynamics of lake metabolism and ecosystem stability to external disturbances. However, few studies have investigated how typhoons affect lake metabolic processes. Our previous study reported how a typhoon altered the seasonal dynamics of limnological variables and lake metabolism in a subtropical lake in Taiwan. In this study, we further explored how typhoon strength affects the daily dynamics of ecosystem metabolism. We also clarified the potential mechanisms causing these effects and assessed the stability (i.e., resistance and resilience) of lake metabolism during typhoon disturbances. Surprisingly, as compared with medium- and large-sized typhoons, small typhoons caused stronger effects on lake metabolism, and the metabolism recovered more rapidly. The daily response of the ecosystem metabolism in our lake to typhoons is likely linked to typhoon-induced changes in lake physics (e.g., the mixing regime and dissolved oxygen level), quantity and quality of dissolved organic carbon and nutrients (especially nitrogen) and the biomass of primary producers in different disturbance scenarios. Results of this study provide a unique basis to predict how lakes tend to be net sources or sinks of carbon from the atmosphere under the circumstance of global warming and an increase in typhoons.

Keyword: climate change, lake metabolism, typhoon, carbon cycling, algae

(三) 報告內容

3.1 前言

The factors influencing lake metabolism, defined here as the collection of processes that determine the gross primary production (GPP), ecosystem respiration (ER), and net ecosystem production (NEP), have been the subject of current research, because lake metabolism indicates the trophic status and the extent to which lakes are net sources or sinks of carbon from the atmosphere (Hanson et al. 2003; Kortelainen et al. 2006). Worldwide, lakes and reservoirs are thought to be both a net source of carbon to the atmosphere and to sequester an amount of carbon in their sediments similar in magnitude to the amount of carbon reaching the world's oceans from streams and rivers (Dean 1999).

Global warming is expected to change the spatial distribution of precipitation patterns, potentially causing large functional changes in local ecosystems (Kerr 2007; Zhang et al. 2007). 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 disturbance frequency may increase surface runoff from watersheds to recipient aquatic ecosystems, thus changing their biochemical cycling, food web structures, ecosystem metabolism, and, potentially, ecosystem stability under external disturbances.

3.2 研究目的

YYL is a small, shallow, subtropical, subalpine lake located in north-central Taiwan. The lake experiences multiple typhoon events each year. A single typhoon can drop more than a meter of precipitation on the 4.5-m-deep lake, which results in rapid flushing (Tsai et al. 2008). We present the results of 2 years 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 lake metabolic dynamics are altered as a result of changes in physical, chemical and biological processes due to typhoons on a daily scale.

We hypothesized that small- and medium-sized typhoons cause stronger effects on lake metabolism and metabolism recovers more quickly than with large typhoons because small to moderate precipitation may flush terrestrial nutrients or chemicals from the watershed and lead to obvious changes in the lake's metabolic process. By contrast, additional precipitation associated with large typhoons may merely add additional chemical-free water and serve to dilute the chemicals that would have been loaded during small to moderate events. The recovery of lake metabolism after large typhoons would be slower than that after small to moderate events because of the increased flushing out of the primary producer and heterotrophic population abundances caused by 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 stability (i.e., resistance and resistance) of lake metabolism to typhoon disturbances.

3.3 文獻探討

Subtropical alpine lakes are usually characterized by highly variable environmental perturbations such as typhoon-induced rapid flushing, high diel variation in irradiation, and large temperature changes, all of which might be expected to affect physical and biogeochemical processes and, thus, the metabolism of these lake ecosystems (Frenette et al. 1996; Dodds 2002). Because most studies of lake metabolism are from temperate dimictic or cold monomictic lakes, the 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). Our previous study 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, as compared with summer peaks during the typhoon periods (July to October) (Tsai et al. 2008). Nevertheless, the response to and recovery of lake metabolism from typhoon disturbances in daily scales and the inherent mechanistic processes are still little known. Because typhoons are associated with strong winds and large amounts of precipitation, they are likely to cause vertical mixing of the water column and loading of nutrients and dissolved organic carbon (DOC). The resulting effects on lake metabolism are difficult to predict *a priori* because nutrient loading would tend to push the lake toward autotrophy and DOC loading would push the lake toward heterotrophy (Hanson et al. 2004).

Typhoons and tropical storms may have a strong impact on lake metabolism, especially in subtropical and tropical regions, with their high disturbance frequencies but unpredictable timing and strength of storms. Limited information about the impact of typhoons on lake metabolism results from difficulties in access to study sites and research facilities. 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). Understanding an ecosystem's stability (i.e., resistance and resilience) in natural or anthropological disturbances can help determine its ability to continue functioning under different disturbance scenarios. The GPP and ER of freshwater ecosystems provide a fundamental matrix of cross-ecosystem connectivity responding to natural and human disturbances. They are useful parameters for evaluating aquatic ecosystem stability because both processes integrate energy and material flows through the components of an ecosystem (Uehlinger 2000; Williamson et al. 2008).

3.4 研究方法

High-frequency data collection

An instrumented buoy was deployed in April 2004 at the deepest spot in YYL to record surface DO concentration, water temperature and wind speed every 10 min. 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). 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 downwelling photosynthetically active radiation (PAR) were measured at a land-based meteorological station approximately 1 km away from the lake (Tsai et al. 2008). Over the entire period of observation (May 2004 to October 2005), data were successfully recorded on 446 days.

Limnological sample

Associated limnological samples were collected manually at the surface of YYL at weekly intervals during the typhoon season (June or July to October). Additional samplings were conducted before the onset of typhoons and immediately after typhoons if it was possible to access the lake. DOC samples were collected by use of a portable hand pump with inline filters (Whatman, 47 mm GF/F, Maidstone, Kent, UK). The vials were stored on ice until analysis with an O.I. TOC analyzer (Model 1010, O.I. Analytical, College Station, TX, USA) with persulfate digestion. Samples of chlorophyll *a* (Chl *a*) were collected by filtering surface lake water with use of GF/F filters. Filters were stored at 4^{o}C and in the dark until Chl *a* was extracted with use of methanol. Nutrient concentrations were measured from unfiltered surface water samples. Total phosphorus (TP) and total nitrogen (TN) were estimated as per the American Public Health Association (1998). Water color samples were collected from the surface, passed though GF/F filters, 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 external loading of DO by precipitation, 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; Uehlinger 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 day by 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 were checked hourly 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} s^{-1} (Lauster et al. 2006). Exchange of oxygen between water column and atmosphere (F_{atm}) was estimated as $F_{atm}= k(O_{2sat}–O_2)/Z$ (μmol m^{-3} h^{-1}) (Cole et al. 2000, 2002), where Z is the depth of mixing layer (m) and k is the transfer coefficient (m h^{-1}) for oxygen and is estimated by using the empirical relation between k_{600} (k for a Schmidt number of 600), wind speed, water temperature and Schmidt number of oxygen (Wanninkholf 1992; Cole and Caraco 1998; Tsai et al. 2008). $O_2(t)$ 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

The inherent assumption of the metabolism model is that the external loading of DO is negligible**.** This assumption likely is violated during typhoon or storm events; therefore, we adopted the difference between 3-day means of GPP, ER, and NEP before and immediately after a typhoon event to quantify the metabolic change. Stability of ecosystem metabolism includes the magnitude of response (i.e., resistance) and rate of recovery after a disturbance (i.e., resilience). The index for resistance (*RS*) was calculated as follows (Orwin and Wardle 2004):

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

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:

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

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 (maximal resistance) and full recovery (maximal resilience). An *RS* value of 0 indicates a 100% reduction or enhancement and an *RL* value of 0 represents no recovery (i.e., $D_0 = D_X$). 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 1-way ANOVA 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 3 ecosystem metabolic parameters (i.e., GPP, ER and NEP). We used Statistica® software (StatSoft, Tulsa, OK, USA) to calculate the coefficient of determination (R^2). A $p < 0.05$ was considered statistically significant.

3.5 結果與討論

Typhoon disturbance regimes

Typhoon and storm disturbances were prevalent in YYL, with 7 typhoon events in 2004 and 8 events in 2005. The accumulated precipitation (AP) of a single typhoon ranged from 51.5 to 816.5 mm, and the 10-min averaged wind speed ranged from 0.72 to 3.45 m s^{-1}. The AP was positively correlated with the corresponding wind speed of typhoons (r=0.88, p<0.05, n=15). 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 the limnological variables of the lake. Most of the typhoons immediately increased the water color and the concentration of DOC and TN in the lake but decreased the Chl *a* and TP concentration. 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 medium and large typhoons.

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 increased ER (7.1%–827.7% increase), and thus the lake became more heterotrophic after typhoon events (27.6%–852.4% increase in heterotrophy) (p<0.05). The daily changes in NEP were mainly controlled by the dynamics of ER, because ER was more responsive to typhoons than was GPP (average change levels were 160.4% and -41% for ER and GPP, respectively). Nevertheless, the extent of metabolic changes and magnitude of AP and wind speed were not correlated. Figure 1 shows the time series of GPP, ER, atmospheric flux (F_{atm}), surface DO concentration, water temperature at the surface (0.25 m) and bottom (3.5 m) of the lake, and daily precipitation for periods of 5 days before and 7 days after typhoons with different AP intensities (e.g., T2 [AP=160 mm] and T4 [AP=816.5 mm]). The temporal trends of temperature and DO during disturbances were related to the water mixing regime of the lake. DO level in YYL decreased (-16.7% to -58%) during medium and small typhoons but increased during large events (e.g., T4, +71%) and then progressively recovered thereafter (Figs. 1C and D). 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 the decreased DO concentration enhanced the flux of oxygen from the atmosphere to the lake (Figs. 1E and F). All of these parameters recovered gradually after typhoons, and it took about 5-10 days to recover 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 3 metabolic parameters showed a positive correlation with the intensity of AP (Figs. 2A-C). Surprisingly, more negative values of *RS* occurred with small typhoons (with AP < ~200 mm), which revealed that small events caused stronger effects on GPP, ER, and NEP as compared with medium-sized events (AP 200–600 mm) and large-sized events (AP >600 mm). Results of paired *t* test showed that the *RS* of GPP was significantly greater than that of ER (p<0.05), which again indicated that the ER is more responsive to typhoon disturbances than is GPP. The *RL* of the 3 metabolic parameters was negatively correlated with AP (Figs. 2D-F), which indicated that the ecosystem metabolism recovered faster after small disturbances than after larger events. Negative values of *RL* for ER and NEP were observed only in large events. *RL* did not significantly differ among the 3 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 the lake metabolism to typhoons. A positive correlation between changes in TP and Chl *a*, and *RS* of GPP (r=0.31-0.71) suggested that the lower resistance of GPP to small typhoons (Fig. 2A) may be mediated by decreased Chl *a* and TP after most typhoons. Increases in water color and TN were correlated with *RL* of GPP (r=0.40-0.48, p>0.05), which suggests that the quicker recovery rate (i.e., high resilience) of the GPP after small typhoons (Fig. 2D) might result from increases in color and TN 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 (or wind speed) ($p<0.05$), which implied that both colored N- and C-rich compounds were affected by the increase in allochthonous organic matter in the lake after typhoons.

The *RS* of ER and NEP was negatively correlated with changes in TN. Small typhoons tended to increase TN. This finding explained why ER and NEP were less resistant to smaller typhoons than large ones (Figs. 2B-C). Increases in the *RL* of ER and NEP were associated with the increase in water color, TN and DOC. The magnitude of the change in water color, TN and DOC after typhoons decreasing with the rainfall intensity of typhoons explained the higher recovery rate of ER and NEP after small typhoons (Figs. 2E and F). Furthermore, changes in Chl *a* (and TP) were correlated with *RS* and *RL* of ER and NEP (Figs. 2E and F). In this case, the autochthonous organic carbon was suggested to be the driver accounting for the reaction of both GPP and ER to typhoons. The recovery rate (i.e., the *RL*) of the 3 metabolic parameters was not correlated with the daily dynamics of water temperature and light intensity after 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 during and after typhoons.

Discussion

In general, with typhoon disturbances, YYL was temporarily more heterotrophic, by reducing GPP and increasing ER. The decreases in concentrations of TP and Chl *a* after typhoons accounted for the decrease in GPP. In this lake, typhoons caused the water column to mix temporarily and the water level to fluctuate (Figs. 1A and B, Tsai et al. 2008). This finding suggests that YYL was flushed during typhoon events. The quick flushing 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 turnover rather than by biological processes. A similar phenomenon was observed in freshwater ecosystems such as flood-prone rivers and alpine streams (Uehlinger 2003; Acuna et al. 2004). Thus, bed-moving floods transiently reduce both GPP and NEP in stream ecosystems because of the loss of primary producers (e.g., periphyton and diatoms) and shift ecosystem metabolism towards heterotrophy. The primary production of the phytoplankton community is affected by both instantaneous irradiance and the short-term light history (Obrien et al. 2009). Typhoons destroyed the stratification that had characterized the water column between typhoon events and caused resuspension of algae into the overlying water. Large quantities of algae were observed in the bottom layer of YYL during the stratification period between typhoons and were quickly released to the surface layer by the typhoon-induced vertical mixings and may have replaced the original algal species (Tsai et al. 2008). Primary production of these dark-acclimated algae from hypolimnion may be more prone than the original light-acclimated species to photoinhibition by the high light conditions after storms and typhoons (Figs. 1A and B), thus decreasing GPP. The change in phytoplankton community might also be responsible for the variation in GPP during typhoons, because a size-dependent change in Chl *a* and changes in photosynthesis efficiency were observed in reacting to the typhoon-induced change in light and nutrient conditions in the lake (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, and their *RS* and *RL* were significantly correlated with the typhoon-induced change in water color, TN and DOC. Water color (light absorbance at 440 nm) is a good predictor of terrestrially produced dissolved organic matter in lakes (Hessen and Tranvik 1998). 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 and 2004; 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. 1 and B) 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 *RS* of ER and change in Chl *a* revealed that if typhoons cause a large decrease in chlorophyll, ER also increases less (i.e., low 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 metabolism 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 responsible for the change in lake metabolism because terrestrially derived carbon is often relatively refractory to biological use (Baines and Pace 1991; 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 played a key role in mediating the reaction of the lake metabolism to typhoon events.

We found DO concentration temporally decreased after typhoons. The lake metabolism model describes the change in DO level as a result of dynamic balances between GPP, ER and F_{atm}. Two processes might account for the dynamic changes in DO level. First, the tremendous increase in ER after typhoons can cause a steady decline in DO level. GPP played only a minor role in controlling the DO concentration as compared with ER (Figs. 1E and F). Second, the decrease in DO level in the surface layer and increase in the deep layer during typhoons was related to the mixing regime of the lake (Figs. 1A and C, B and E), which suggests that the entrainment of water with low DO concentration from the hypolimnion between typhoons might be the other key process accounting for the decrease in surface DO level. Consequently, the recovery rate of ER and water stratification would therefore be the key processes controlling the resilience of YYL metabolism.

Results of stability assessments (i.e., *RS* and *RL*) indicated that small typhoons (with AP < 200 mm) cause large effects (i.e., low resistance) on GPP, ER, and NEP as compared with medium- and large-sized events (Fig. 2). The differential response of lake metabolism to disturbance events of different intensity is an interesting observation. We found that small to moderate precipitations flushed 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 add additional DOC (or nutrients)-free water and serve to dilute the DOC (or nutrients) level that would have been loaded in small to moderate events. This dilution in level of limnological drivers would be manifested in a relatively higher resistance of lake metabolism to large typhoons (Fig. 2). 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 and microbial population abundance. Lower recovery of ER and NEP after large typhoons (Figs. 2E and F) is associated with loss of Chl *a*, which might occur because of the decreasing nitrogen consumption due to the loss of Chl *a* after large typhoons.

In summary, this study revealed that episodic environmental events such as typhoons altered the daily dynamics of the ecosystem metabolism in YYL. Typhoons tended to weaken 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, the metabolism recovered quicker after smaller typhoons than after medium or larger typhoons. Results of this study provide a scientific basis to predict how lakes tend to be net sources or sinks of carbon from the atmosphere in subtropical or tropical regions under the circumstance of global warming with its increase in typhoons.

(四) 參考文獻

Acuña, V., Giorgi, A., Muñoz, I., Uehlinger, U., and Sabater, S. 2004. Flow extremes and benthic organic matter shape the metabolism of a headwater Mediterranean stream. Freshw. Biol. **49**(7): 960-971. doi: 10.1111/j.1365-2427.2004.01239.x.

Aoki, T., Hayami, Y., Fujiwara, T., Mukai, H., and Tanaka, Y. 1996. Nutrient dynamics in the North Basin of Lake Biwa: I. Changes in the vertical distribution of nutrients due to an internal surge induced by a strong typhoon. J. Gt. Lakes Res. **22**(2): 331-340. doi:10.1016/S0380-1330(96)70959-0.

American Public Health Association (APHA). 1998. Standard methods for the examination of water and wastewater. American Publication Health Association, Washington, D.C.

Baines, S.B., and Pace, M.L. 1991. The production of dissolved organic matter by phytoplankton and its importance to bacteria: patterns across marine and freshwater systems. Limnol. Oceanogr. **36**(6): 1078-1090.

Beisner, B.E., Dent, C.L., and Carpenter, S.R. 2003. Variability of lakes on the landscape: Roles of phosphorus, food webs, and dissolved organic carbon. Ecology **84**(6): 1563-1575. doi:10.1890/0012-9658(2003)084[1563:VOLOTL]2.0.CO;2.

Colangelo, D.J. 2007. Response of river metabolism to restoration of flow in the Kissimmee River, Florida, U.S.A. Freshw. Biol. **52**(3): 459-470. dol:10.1111/j.1365-2427.2006.01707.x.

Cole, J.J., Caraco, N.F., Kling, G.W., and Kratz, T.K. 1994. Carbon Dioxide Supersaturation in the Surface Waters of Lakes. Science **265**(5178): 1568-1570. doi:10.1126/science.265.5178.1568.

Cole, J.J., Carpenter, S.R., Kitchell, J.F., and Pace, M.L. 2002. Pathways of organic carbon utilization in small lakes: Results from a whole-lake 13C addition and couple model. Limnol. Oceanogr. **47**(6): 1664-1675.

Cole, J.J., Pace, M.L., Carpenter, S.R., and Kitchell, J.F. 2000. Persistence of net heterotrophy in lakes during nutrient addition and food web manipulations. Limnol. Oceanogr. **45**(8): 1718-1730.

Dean, W.E. 1999. The carbon cycle and biogeochemical dynamics in lake sediments. J. Paleolimn. **21**(4): 375-393. doi:10.1023/A:1008066118210.

Dodds, W. K. 2002. Freshwater ecology. Academic Press, San Diego, CA. pp. 212-213.

Frenette, J.J., Vincent, W.F., Legendre, L., and Nagata, T. 1996. Size-dependent phytoplankton responses to atmospheric forcing in Lake Biwa. J. Plankton Res. **18**(3): 371-391. doi:10.1093/plankt/18.3.371.

Gergel, S.E., Turner, M.G., and Kratz, T.K. 1999. Dissolved organic carbon as an indicator of the scale of watershed influence on lakes and rivers. Ecol. Appl. **9**(4): 1377-1390. doi:10.1890/1051-0761(1999)009[1377:DOCAAI]2.0.CO;2.

Hanson, P.,C., Bade, D.L., Carpenter, S.R., and Kratz, T.K. 2003. Lake Metabolism: Relationships with Dissolved Organic Carbon and Phosphorus. Limnol. Oceanogr. **48**(3): 1112-1119.

Hanson, P.C., Pollard, A.I., Bade, D.L., Predick, K., Carpenter, S.R., and Foley, J.A. 2004. A model of carbon evasion and sedimentation in temperate lakes. Glob. Change Biol. **10**(8): 1285-1298. doi: 10.1111/j.1365-2486.2004.00805.x.

Houser, J.N. 2006. Water color affects the stratification, surface temperature, heat content, and mean epilimnetic irradiance of small lakes. Can. J. Fish. Aquat. Sci. **63**(11): 2447–2455. doi:10.1139/F06-131.

Jones, S.E., Kratz, T.K., Chiu, C.Y., and McMahon, K.D. 2009. Influence of typhoons on annual CO_2 flux from a subtropical, humic lake. Glob. Change Biol. **15**(1): 243-254. doi: 10.1111/j.1365-2486.2008.01723.x.

Karlsson, J., Jonsson, M., and Jansson, A. 2007. Respiration of allochthonous organic carbon in unproductive forest lakes determined by the Keeling plot method. Limnol. Oceanogr. **52**(5): 603-608.

Kirchman, D.L., Dittel, A.I., Findlay, S.E.G., and Fischer, D. 2004. Changes in bacterial activity and community structure in response to dissolved organic matter in the Hudson River, New York. Aquat. Microb. Ecol. **35**(3): 243-257.

Kortelainen, P., Rantakari, M., Huttunen, J.T., Mattsson, T., Alm, J., Juutinen, S., Larmola, T., Silvola, J., Pertti, J., and Martikainen, P.J. 2006. Sediment respiration and lake trophic state are important predictors of large CO_2 evasion from small boreal lakes. Glob. Change Biol. **12**: 1554-1567. doi: 10.1111/j.1365-2486.2006.01167.x.

Kerr R.A. 2007. Global warming is changing the world. Science **316**: 188-190. Available from http://www.sciencemag.org/cgi/reprint/316/5822/188.pdf

Lauster, G.H., Hanson, P.C., and Kratz, T.K. 2006. Gross primary production and respiration differences among littoral and pelagic habitats in northern Wisconsin lakes. Can. J. Fish. Aquat. Sci. **63**(5): 1130-1141. doi:10.1139/F06-018.

O'Brien, K.R., Burford, M.A., and Brookes, J.D. 2009. Effects of light history on primary productivity in a phytoplankton community dominated by the toxic cyanobacterium *Cylindrospermopsis raciborskii*. Freshw. Biol. **54**(2): 272-282. doi:10.1111/j.1365-2427.2008.02106.x.

Orwin, K.H., and Wardle, D.A. 2004. New indices for quantifying the resistance and resilience of soil biota to exogenous disturbances. Soil Biol. Biochem. **36**(11): 1907-1912. doi:10.1016/j.soilbio.2004.04.036

Pace, M.L., and Jonathan, J.C. 2002. Synchronous variation of disolved organic carbon and color in lakes.

Limnol. Oceanogr. **47**(2): 333-342.

Prez, M.T., and Sommaruga, R. 2006. Differential effect of algal- and soil-derived dissolved organic matter on alpine lake bacterial community composition and activity. Limnol. Oceanogr. **51**(6): 2527-2537.

Porter J.H., Peter A., Braun H.W., Bryant P., Gage S., Hansen T., Hanson P.C., Lin C.C., Lin F.P., Kratz T.K., Michener W., Shapiro S., and Williams T. 2005. Wireless Sensor Networks for Ecology. BioScience **55**(7): 561-572. doi:10.1641/0006-3568(2005)055[0561:WSNFE]2.0.CO;2.

Porter, J.H., Nagy, E., Kratz, T.K., Hanson, P.C., Collins, S.L., and Arzberger, P. 2009. New Eyes on the World: Advanced Sensors for Ecology. BioScience **59**(5): 385-397. doi:10.1525/bio.2009.59.5.6.

Robarts, R.D., Waiser, M.J., Hadas, O., Zohary, T., and S., M. 1998. Relaxation of phosphorus limitation due to typhoon-induced mixing in two morphologically distinct basin of Lake Biwa, Japan. Limnol. Oceanogr. **43**(6): 1023-1036.

Tsai J.W., Kratz T.K., Hanson P.C., Wu J.T., Chang W.Y.B., Arzberger P.W., Lin B.S., Lin F.P., Chou H.M. and Chiu C.Y. 2008. Seasonal dynamics, typhoons and the regulation of lake metabolism in a subtropical humic lake. Freshw. Biol. **53**(10): 1929-1941. doi:10.1111/j.1365-2427.2008.02017.x.

Uehlinger, U. 2000. Resistance and resilience of ecosystem metabolism in a flood-prone river system. Freshw. Biol. **45**(3): 319-332. doi: 10.1111/j.1365-2427.2000.00620.x.

Uehlinger, U., Kawecka, B., and Robinson, C.T. 2003. Effects of experimental floods on periphyton and stream metabolism below a high dam in the Swiss Alps (River Spöl). Aquat. Sci. **65**(3): 199-209. doi:10.1007/s00027-003-0664-7.

Wanninkhof, R. 1992. Relationship between wind speed and gas exchange over the sea. J. Geophys. Res. **97**(C5): 7373-7382.

Williamson, C.E., Dodds, W., Kratz, T.K., and Palmer, M.A. 2008. Lakes and streams as sentinels of environmental change in terrestrial and atmospheric processes. Front. Ecol. Environ. **6**(5): 247-254. doi: 10.1890/070140.

Zhang, X., Zwiers, F.W., Hegerl, G.C., Lambert, F.H., Gillett, N.P., Solomon, S., Stott, P.A., and Nozawa, T. 2007. Detection of human influence on twentieth-century precipitation trends. Nature **448**(7152): 461-465. doi:10.1038/nature06025.

(五) 附圖與附表

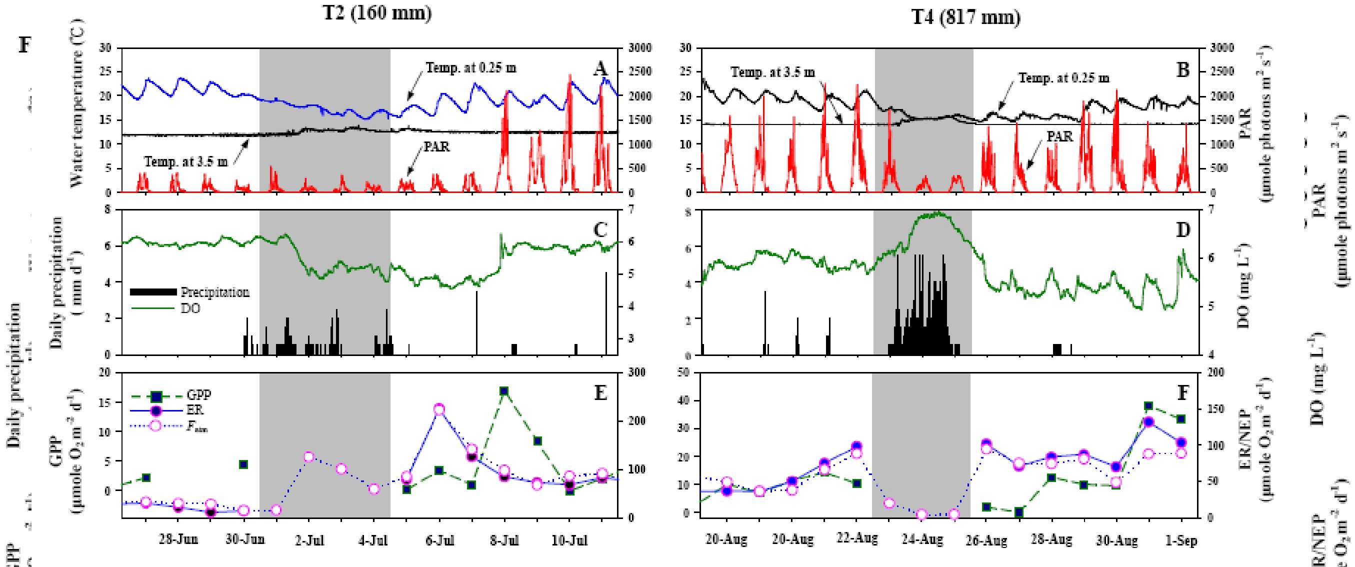

Fig. 1. Time series of high-frequency (10-min based) signals in (A, B) water temperature on 0 and 3.5 m depth and light intensity. (C, D) Dissolved oxygen (DO) at the surface layer and daily precipitation before, during and after selected typhoon disturbance scenarios (e.g. T2 and T4). The corresponding daily performance of gross primary production (GPP), ecosystem respiration (ER) and atmospheric flux (F_{atm}) are graphically summarized to describe the process accounting for the temporal variance of DO signals (E, F). Shade bar represents the duration of typhoons.

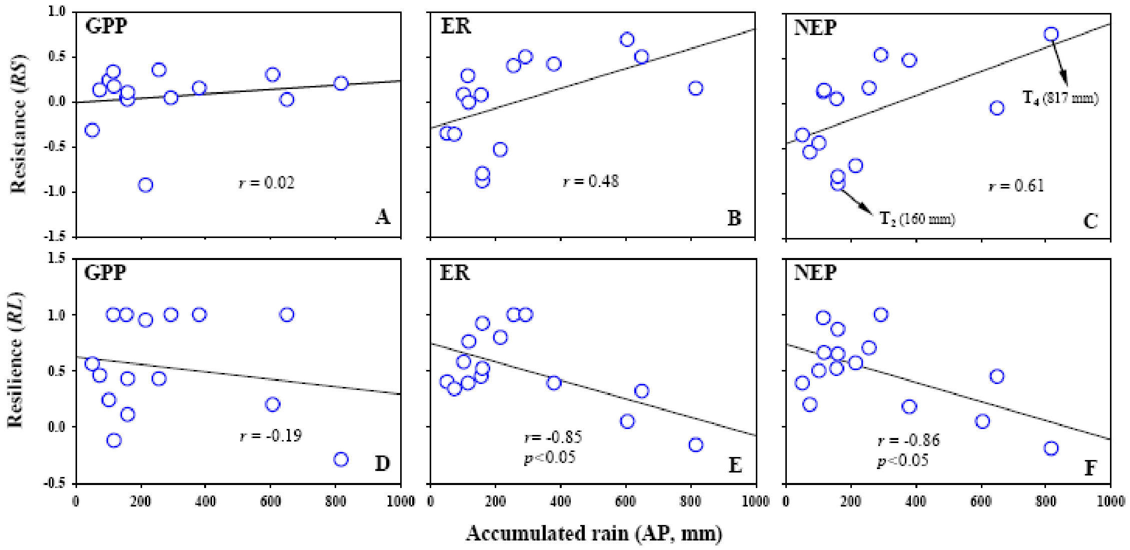

Fig. 2. The calculated values of resistance (*RS*) and resilience (*RL*) for GPP, ER, and NEP as a function of the accumulated precipitation with a single typhoon. ($n = 15$)

(六) 計畫成果自評

附件二

國科會補助專題研究計畫成果報告自評表

請就研究內容與原計畫相符程度、達成預期目標情況、研究成果之學術或應用價值（簡要敘述成果所代表之意義、價值、影響或進一步發展之可能性）、是否適合在學術期刊發表或申請專利、主要發現或其他有關價值等，作一綜合評估。

1. 請就研究內容與原計畫相符程度、達成預期目標情況作一綜合評估

■達成目標

□ 未達成目標（請說明，以 100 字為限）

  □ 實驗失敗

  □ 因故實驗中斷

  □ 其他原因

說明：

2. 研究成果在學術期刊發表或申請專利等情形：

論文：■已發表■未發表之文稿 □撰寫中 □無

專利：□已獲得 □申請中 □無

技轉：□已技轉 □洽談中 □無

其他：（以 100 字為限）

3. 請依學術成就、技術創新、社會影響等方面，評估研究成果之學術或應用價值（簡要敘述成果所代表之意義、價值、影響或進一步發展之可能性）（以 500 字為限）

淡水生態系統(例如，湖泊、溪流、水庫及溼地等)因面積僅佔陸地生態系不到 3%，加上經濟產量遠不及海洋及河口生態系統。然而，淡水生態系統，卻在生物圈(bioaphere)裡面的生物地質化學循環過程中扮演著極重要的「導管」(conduit)角色，例如，湖泊及水庫等內陸水體為陸域生態系中碳元素循環過程中最重要的匯池(sink)之一，就全球的碳循環過程而言，陸域生態系中的有機態碳約 5~50%是藉由溪流或湖泊生態系內的生物地球化學作用轉化後，再以無機態碳的型態輸送回大氣中。因此，在全球暖化的浪潮下，探討淡水生態系在區域性碳循環的角色，為近年來生態學家極為關注的研究議題，台灣的湖泊或淡水濕地不多且面積不大，然而台灣地區山高水急、乾溼季分明加上每年定期的颱風季節等大型環境干擾特性，反而為水域生態的研究提供的極佳的現場即時研究機會，因此吸引了世界最頂尖的淡水生生態研究團隊，美國威斯康辛大學麥迪遜分校湖沼學研究中心的科學家的注意。在本二年期研究計畫中，我們利用高頻率生態監測網絡提供即時及不同時間尺度的湖泊代謝訊號紀錄，收集到傳統採樣方式無法提供的新資料類型。我們利用數學生態模式解析所收集到的高頻率生態與環境資料，主要目的為探討氣候變遷情況下，颱風或暴雨對亞熱帶地區淡水生態系代謝及藻類族群動態變化之影響。目前我們已經量化颱風降雨強度與湖泊代謝能力在時間與空間上的關係，並已初步探明支配影響過程的生物及非生物學機制，我們的研究結果可提供未來政府在因應氣候變遷的條件下，在執行水域生態系保育、集水區土地使用或水資源開發利用之管理策略制定作為參考。相關研究結果已被「*Freshwater Biology*」及「*Canadian Journal of Fisheries and Aquatic Sciences*」等高排名國際期刊刊登與接受。後續相關研究亦正持續進行中。

(七) 附錄

本研究計畫相關成果發表:

SCI 原始論文

1. **Tsai JW**, Kratz TK, Hanson PC, Wu JT, Lin FP, Chou HM, Chiu CY. 2010. Metabolic changes and the stability of a subtropical alpine lake ecosystem to typhoon disturbance. Submitted to *Canadian Journal of Fisheries and Aquatic Sciences*. (IF=1.95, 14% in FISHERIES).

2. **Tsai JW**, Kratz TK, Hanson PC, Wu JT, Chang WYB, Arzberger PW, Lin BS, Chao YL, Lin FP, Chou HM, Chiu CY. 2008. Seasonal dynamics, typhoons and the regulation of lake metabolism in a subtropical humic lake. *Freshwater Biology* 53, 1929–1941. (IF=2.86, 7% in MARINE & FRESHWATER BIOLOGY)

非SCI 原始論文

1. 薛郁欣，藍煜翔，蔡正偉，吳俊宗，柳文成，林芳邦，周秀美，邱志郁。2009。棲蘭山鴛鴦湖水體的分層與混合現象。中華林學季刊(審查中)

2. 蔡正偉、周雅嵐、林秉石、吳俊宗、邱志郁。2009。鴛鴦湖湖泊代謝之季節性變化。中華林學季刊(Quarterly Journal of Chinese Forestry) 42(3):335-345。

3. **Tsai JW** , Kratz TK, Hanson PC,Wu JT, ChangWYB, Arzberger PW, Lin BS, Chao YL, Lin FP, Chou HM, Chiu CY. 2008. Seasonal dynamics of lake metabolism in a sub-tropical alpine lake. *Verhandlungen Internationale Vereinigung für theoretische und angewandte Limnologie* 30(3)**:** 381–385.

研討會論文與發表

1. **Tsai JW**, Liao CM, Chen CT, Huang YH. An ecophysiologically-based modeling approach for chronic metal exposure risk assessment in aquatic ecosystems. Proceeding of International Conference on Mathematical Biology and Ecology. Tokyo, Japan, May 26-28, 2010. *(Oral presentation)*

2. **Tsai JW** , Kratz TK, Hanson PC, Lin FP, Chou HM, Chiu CY. Resistance and resilience of a subtropical alpine lake metabolism to typhoon disturbance. The Global Lake Ecological Observatory Network 9th Workshop. Boulder Junction, Wisconsin, USA, October 12-15, 2009. *(Oral presentation)*

3. **Tsai JW** , Kratz TK, Hanson PC, Lin FP, Chou HM, Chiu CY. Typhoons enhance lake acting as carbon conduits to atmosphere. Darwin 200: International Symposium on Global Biodiversity, Human Health and Well-being. China Medical University, Taichung, Taiwan, December 3-5, 2009 *(Invited speaker)*

4. **Tsai JW** , Kratz TK, Hanson PC,Wu JT, Chang.WYB, Arzberger PW, Lin FP, Chou HM, Chiu CY. 2008. Temporal response and stability of lake metabolism to typhoon in a subtrophic lake. The Global Lake Ecological Observatory Network 7thWorkshop. Norrtälje, Sweden, September 28-October 2. (Oral presentation)

5. **Tsai JW** , Kratz TK, Hanson PC, Lin FP, Chiu CY. 2008. Response of Ecosystem Metabolism in a Subalpine Lake to Climate Changes. International Symposium on Global Mountain Biodiversity Scientific Programme. Taichung , Taiwan , June 7-10. (Oral presentation)

6. **Tsai JW** , Kratz TK, Hanson PC,Wu JT, ChangWYB, Arzberger PW, Lin BS, Chao YL, Lin FP, Chou HM, Chiu CY. 2007. Seasonal dynamics of lake metabolism in a sub-tropical alpine lake. 30 th Congress of the International Association of Theoretical and Applied Limnology. Montreal , Canada , August 12-18. (Oral presentation)

附件四

國科會補助專題研究計畫項下出席國際學術會議心得報告

日期 99 年 9 月 10 日

計畫編號	NSC 97-2621-B-039-001-MY2		
計畫名稱	氣候變遷對亞熱帶高山湖泊藻類群落動態及生態系統代謝之影響（第 2 年）		
出國人員姓名	蔡正偉	服務機構及職稱	中國醫藥大學生態暨演化生物學研究所
會議時間	99 年 5 月 26 日至 99 年 5 月 28	會議地點	日本東京都
會議名稱	（中文）2010 年國際數學生物與生態研討會 （英文）International Conference on Mathematical Biology and Ecology 2010		
發表論文題目	（中文）發展以生態生理為基礎之模式以評估金屬污染物對湖泊生態系代謝之影響 （英文）An ecophysiologically-based modeling approach for chronic metal exposure risk assessment in aquatic ecosystems		

一、參加會議經過

本研討會是由「世界科學、工程與科技學會」(World Academy of Science, engineering and technology)所主辦的綜合性研討會，會議時間為 2010 年 5 月 26 日至 28 日，地點在日本東京都假日飯店(Holiday Inn)的會議中心。這項研討會涵蓋許多主題，包括人類與社會科學、生物與生命科學，以及自然與應用科學等，是比較偏重於技術應用的一個研討會。過去一年來，本研究室剛建立了一個評估受重金屬污染水域生態系中暴露風險預測模式，因此便計畫藉由此次大會中關於「數學生物與生態」這個主題進行投稿，初稿經過研討會審查委員審查通過接受後，再進行報名註冊與繳費的動作。

本人於研討會第一天即抵達現場進行報到，因為第一天的議程多為醫學相關研究成果的發表，與我所從事的生態環境相關研究的主題較無直接相關，因此我僅選擇性的聽了幾位歐美學者關於環境毒物暴露風險的研究發表進行聆聽，我對於因為全球暖化造成病媒蚊或是動物媒介(如禽流感居後候鳥遷徙散播病毒)的趨勢預測方式感到十分有趣，並私下與一位德國科學家討論如何將資料不確定性整合到模式模擬上的方式。第二天，我被排到上午 11 點進行論文發表，我的發表引起了一位南京地理與湖泊研究所研究員的注意，會後也討會到他們正著力於解決太湖污染的問題，雙方也談及未來在研究合作上的可能性。第三天議程僅有半天，我選擇應用科學和工程技術為主的

部門聆聽，了解了一些水文學者利用數理模型模擬河口、海灣或水庫中的流場行為與溫室氣體或汙染物傳輸的動態模擬方式。

二、與會心得

本次研討會中比較可惜的是本人報名的 International Conference on Mathematical Biology and Ecology 這個部分因為投稿的文章不多，因此被合併到生命科學的部份進行，因為利用數學模式我研究方法進行生態研究的國內學者不多，因此，原本想藉由此研討會跟其他同行進行討論的期望有些不如預期。加上此次研討會在日本舉辦，出席者以亞洲國家學者居多，歐美研究者人數相對少了許多，部分有興趣文章的作者亦未出席。不過，此次會議卻讓我有機會與大陸學者進行接觸，除了對大陸研究生的專業能力、思考及英文簡報能力感到印象深刻外，對於大陸學生與學者對知識探求的熱情與自信心感到印象深刻、由他們口中的知大陸對科研投入的資源與對研究人員的資助感到羨慕。此外，我對歐美研究者也開始試圖利用科技設施，如設置教育網站或軟體及與社區民眾與幹部結合的方式，走出象牙塔落實研究成果於保育實務上的做法感到敬佩，學術研究的成果不應只供學術界人士研究使用，研究人員更應有責任與熱誠將研究成果以非專業的形式向一般社會大眾說明，並進而藉由社區參與的形式喚醒民眾對生態保育的意識，真正做到化知識為行動的目的。

三、考察參觀活動(無是項活動者略）

無

四、建議

我認為國際會議還是應該參加由歐美名校或有公信力學會舉辦的國際研討會，不論發表的研究素質或學者出席的餐與程度會比較踴躍。參加研討會除了磨練自己的報告技巧、增廣見聞之外，獲取相關領域研究的最新動態與資訊亦為重點，此次研討會，多數歐美著名學校或研究單位作者未出席，不免讓藉由參加研討會以增加與好研究機構或學者交流與合作的機會，此為較可惜的地方。

五、攜回資料名稱及內容

本次帶回的資料包括研討會的論文集與 CD 及出席證明。

六、其他

無