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Influence of typhoons on annual CO_2 flux from a subtropical, humic lake

STUART E. JONES*, TIMOTHY K. KRATZ†, CHIH-YU CHIU‡ and KATHERINE D. McMAHON§

**Limnology and Marine Sciences Program, University of Wisconsin–Madison, 1415 Engineering Drive, Madison, WI 53706, USA, †University of Wisconsin-Madison Trout Lake Station, 10810 County Hwy N, Boulder Junction, WI 54512, USA, ‡Research Center for Biodiversity, Academia Sinica, Nankang, 115 Taipei, Taiwan, ROC, §Department of Civil and Environmental Engineering, University of Wisconsin-Madison, 1415 Engineering Drive, Madison, WI 53706, USA*

Abstract

The Intergovernmental Panel on Climate Change predicts dramatic changes in precipitation patterns over the next century. One potential method for inferring how these changes in annual precipitation and intensity of storm events will influence aquatic ecosystems is to study and model present-day lakes that share climatic characteristics with future climate scenarios. A small lake in north-central Taiwan provided an excellent opportunity to explore the influence of intense meteorological events on CO_2 exchange between surface waters and the atmosphere. Each year Yuan Yang Lake (YYL) is influenced by multiple typhoons that pass near the island of Taiwan. This lake has been instrumented with a sensor network that monitors water column and meteorological parameters at a high temporal resolution (2–10 min intervals). Using this high-resolution data and manually collected CO_2 samples, a mass-balance model of CO_2 dynamics in YYL was developed. In addition, a generalized simulation model was used to explore how typhoon frequency, intensity, and timing impact CO_2 efflux to the atmosphere. Our findings suggest that increased annual precipitation and frequency of storm events results in greater epilimnetic interaction with the watershed and hypolimnion. These interactions resulted in elevated epilimetic CO_2 concentrations and therefore greater evasion of CO_2 to the atmosphere.

Keywords: atmospheric flux, carbon dioxide, frequency, intensity, lake, precipitation, subtropical, typhoon

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Introduction

Future climate scenarios developed by the Intergovernmental Panel on Climate Change (IPCC) predict global mean annual temperatures will rise 1.5–2 °C over the next 50 years, as a result of anthropogenic production of greenhouse gases (Meehl *et al.*, 2007). Warmer temperatures will result in more rapid drying of landmasses and increase the capacity of the atmosphere to hold water vapor (Trenberth *et al.*, 2003). These feedbacks will result in elevated precipitation in some areas of the globe and decreased precipitation in other areas (Meehl *et al.*, 2007). However, the intensity of precipitation events is likely to increase regardless of an increase or decrease in total precipitation (Groisman *et al.*, 1999; Trenberth *et al.*, 2003). Multiple studies have already observed trends in precipitation across the 20th century which agree with predicted scenarios for the 21st century (Karl & Trenberth, 2003; Gedney *et al.*, 2006). More precipitation results in increased runoff to streams and lakes. An increase in rainfall intensity may cause runoff from land surfaces to streams and lakes at the expense of soil moisture, suggesting that predicted changes in precipitation patterns will likely result in more runoff per millimeter of precipitation (Karl & Riebsame, 1989; Karl & Trenberth, 2003).

Future changes in precipitation and runoff amount and temporal pattern will influence recipient lakes and streams. Previous research has demonstrated a correlation between climatic drivers and CO_2 evasion to the atmosphere (Kelly *et al.*, 2001; Rantakari & Kortelainen,

Correspondence: Stuart E. Jones, fax +1 608 262 5199, e-mail: stuartjones@wisc.edu

2005). Year-to-year variation in the epilimnetic partial pressure of CO_2 of 11 boreal lakes was partially explained by interannual variation in weather patterns (Kelly *et al.*, 2001). Rantakari & Kortelainen (2005) linked annual CO_2 emission from large boreal lakes to precipitation during the open water period. Often chemical and biological drivers within the lake are considered when attempting to explain variation in CO_2 evasion from lakes, but factors external to the lake, such as meteorological and climatic variables, are also important to consider. This is especially true because such dramatic changes in climatic drivers are predicted over the next century (Meehl *et al.*, 2007).

One method for estimation of the influence of predicted climatic changes on epilimnetic CO_2 concentrations and CO_2 evasion to the atmosphere from lakes would be to use previously developed statistical relationships between precipitation and CO_2 concentration or flux (Kelly *et al.*, 2001; Rantakari & Kortelainen, 2005). However, these statistical relationships are based solely on data from the boreal region and extrapolation to warmer or wetter climates would be dubious. An alternative approach would be to study the influence of climatic variables on CO_2 evasion in a present-day system that experiences climate conditions similar to plausible future climates.

Numerous lakes in island and coastal regions of the West Pacific and West Atlantic experience typhoons or tropical storms annually, providing opportunities to explore lake responses to a warmer, wetter climate with infrequent, intense meteorological events. Studies related to tropical storms and lakes find that these disturbances have dramatic effects on the physical structure of limnetic systems (Yount, 1961; Weiping *et al.*, 1998). Typhoons weaken or completely destroy stratification, and this typhoon-induced physical change has been implicated in elevation of nutrient concentrations in the epilimnia of Asian lakes (Aoki *et al.*, 1996; Robarts *et al.*, 1998). To our knowledge, no published research has explored the influence of tropical storms on the carbon cycle of lakes. However, mixing liberates solutes normally sequestered in the hypolimnion, and in some cases the sediments (Aoki *et al.*, 1996; Robarts *et al.*, 1998). Because both CO_2 and organic carbon tend to accumulate in these strata, mixing, especially from large disturbances such as typhoons, may elevate the epilimnetic concentration of these carbon species following the disturbance and would subsequently influence lake CO_2 exchange with the atmosphere. Large precipitation and runoff events also increase connectivity between the watershed and the lake (Karl & Riebsame, 1989), which should influence CO_2 evasion to the atmosphere as well (Kelly *et al.*, 2001; Rantakari & Kortelainen, 2005).

Yuan Yang Lake (YYL) is a small lake located in north-central Taiwan. Each year typhoons impact Taiwan, dramatically influencing the physics, chemistry, and biology of the lake (Jones *et al.*, 2008). Large depressions in CO_2 concentrations (Fig. 1) and elevated lake volumes (increases over 1 m in a single day) occur following each typhoon. The draining stream, the atmosphere, and photosynthesis are the only potential routes for CO_2 to leave the lake. In order to quantify CO_2 efflux from YYL, we constructed a mass-balance model that simulated lake volume and CO_2 concentration dynamics in the epilimnion and hypolimnion of YYL. Based on these concentrations, CO_2 flux to the atmosphere and outlet stream was calculated during both stratified and mixed conditions. With this model we examined two questions regarding the influence of precipitation on CO_2 flux from a subtropical lake with an eye towards anticipated changes in precipitation patterns around the globe. (1) Can we estimate CO_2 flux from YYL using our mass-balance approach? (2) How do precipitation patterns (frequency, intensity, and temporal spacing) influence annual and individual event effluxes of CO_2 from a lake?

Materials and methods

Lake description and datasets used

YYL is located in north-central Taiwan. Because of its location in the mountainous central region of Taiwan, the lake (area = 3.6 ha, max depth = 4.5 m) and watershed (374 ha) are small. This subtropical, monomictic lake is slightly stained [mean epilimnetic dissolved organic carbon (DOC) = 6.3 mg L^{-1}] by organic matter

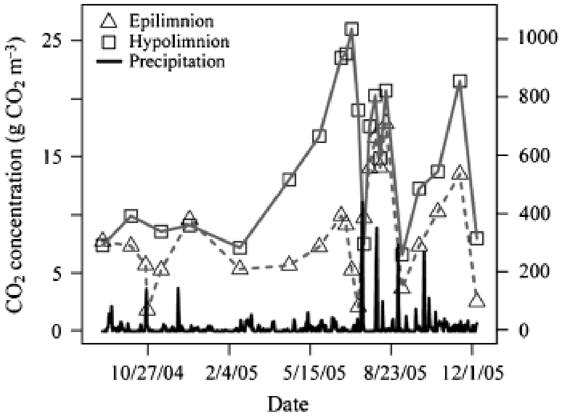

Fig. 1 Measured carbon dioxide concentrations in the epilimnion (△) and hypolimnion (□). Precipitation is plotted in black. Precipitation events above 120 mm result in complete mixing of the lake. Mean saturation concentration of CO_2 was ~ 500 mg CO_2 m^{-3} (range: 400–625 mg CO_2 m^{-3}).

input from the productive cloudforest watershed. The stained water results in strong stratification with an epilimnetic depth of approximately 0.75 m and pH ranging from 5 to 7. However, lake morphometry is such that approximately equal volumes occur in the epilimnion and hypolimnion ($\sim 28\,000$ and $\sim 25\,000\,\text{m}^3$, respectively). The lake is generally mixed from December to March and during typhoon events. A wireless sensor network installed at YYL provided high-resolution measurements of physical drivers used in our model (Porter *et al*., 2005). A buoy located at the deepest point of the lake measured water temperature through the water column at 0.5 m increments, water depth, and wind speed 2 m above the lake surface every 10 min. A meteorological station within 1 km of the lake collected precipitation, air temperature, and atmospheric pressure measurements at 10 min intervals.

Dissolved inorganic carbon (DIC) samples were taken from YYL approximately weekly during the typhoon season and monthly during winter from September 1, 2004 to December 6, 2005. Samples from 0, 0.5, 1, 2, and 3.5 m were collected at the deepest point in the lake and stored in the cold and dark for <3 days before being analyzed using a 1010 Total Organic Carbon Analyzer (O.I. Analytical, College station, TX, USA). A profile of pH was measured during each sampling using a Hydrolab sonde (Hach Environmental, Loveland, Co, USA) and was used to estimate CO_2 concentrations from DIC concentrations based on established carbonate equilibria relationships (Benjamin, 2002). Epilimnetic and hypolimnetic CO_2 concentrations were calculated as volume-weighted averages of concentrations measured at the discrete depths listed above.

Model approach and description

Our mass-balance model was a two-layer system, including the lake epilimnion and hypolimnion. Each layer was assumed to be completely and instantaneously mixed. The watersheds above and below the lake were considered only as a source and sink of water and CO_2 via bulk flow; the atmosphere was also considered as a sink of CO_2 via interfacial mass transfer from the lake epilimnion. The simulated variables in each layer of the model water column were CO_2 concentration (C_E and C_H, $\text{mg}\,CO_2\,\text{m}^{-3}$) and volume ($V_E$ and V_H, m^3). However, the hypolimnetic volume was held constant ($\sim 25\,000\,\text{m}^3$). Meteorological data (air and water temperature, atmospheric pressure, wind speed, and precipitation) collected by the sensor network installed at YYL were used to drive changes in lake volume and CO_2 concentrations.

Flux of water into the model epilimnion was simulated as a fraction of precipitation that fell on the watershed [Table 1, Eqn (4)]. Water movement out of the lake was simulated using two parameters, a constant outflow and a term dependent on precipitation during the current and previous time step [Table 1, Eqn (5)]. Although likely to be variable on an annual scale, the CO_2 concentration of water entering the lake from the watershed was held constant as we lacked sufficient data to describe seasonal trends in hydrologic inputs of CO_2 to the lake. The concentration of CO_2 in water entering the lake was estimated from maximum likelihood fits to lake CO_2 concentration time series data.

Net ecosystem production (NEP) was used to summarize all conversions between organic matter and CO_2 in both model lake layers. Because of the high organic matter content (mean DOC $\sim 6.3\,\text{mg}\,\text{L}^{-1}$), we expected respiration to outpace primary production in both layers of the lake (i.e. negative NEP; Hanson *et al*., 2003). NEP was modeled for both layers as a function of temperature using the Arrhenius equation [Table 1, Eqns (11) and (12)]. The Q_{10} term for both model lake layers was assumed to be 2 and the reference CO_2 production rate and reference temperature were estimated based on maximum likelihood fits to CO_2 time series data for each layer. Diffusion of CO_2 from the hypolimnion to the epilimnion was not considered, as this flux was determined to be extremely small and did not significantly influence annual flux of CO_2 across the atmosphere–water interface. A two-film layer transport model determined CO_2 efflux to the atmosphere from the lake epilimnion [Table 1, Eqn (9)] (Smith, 1985). Because CO_2 concentrations were supersaturated (Fig. 1), the lake was always a source of CO_2 to the atmosphere. Estimates of the water-to-atmosphere mass transfer coefficient, K_{600}, were made using the empirical relationship between wind and K_{600} for the inert tracer gas (SF_6), determined by Cole & Caraco (1998) [Table 1, Eqn (7)]. The mass transfer coefficient for CO_2 was determined from the K_{600} of SF_6 and an empirical relationship between the Schmidt number for CO_2 and temperature using data from Jahne *et al*. (1987). We used -0.5 for the exponent n based upon experimental measurement by Jahne *et al*. (1987) and Clark *et al*. (1995). Wind speed at 2 m was converted to wind speed at 10 m according to Smith (1985) for input into the two-film layer model (Cole & Caraco, 1998). For a complete review of interfacial mass transfer of gasses in lakes, see Smith (1985) and Cole & Caraco (1998).

Change in lake CO_2 concentrations and volume were simulated using differential equations (Table 1) that were numerically solved on an hourly time step in the R statistics package (R Development Core Team, 2005). Thresholds of precipitation and air temperature levels that resulted in lake mixis were graphically determined by inspecting time series of the thermal profile of the

Table 1 Model differential and intermediate equations

Differential equations (stratified conditions)

$$C_{\mathrm{E},t+1} = \frac{C_{\mathrm{E},t} \times V_{\mathrm{E},t} \times \mathrm{NEP}_{\mathrm{E},t} \times V_{\mathrm{E},t} + \mathrm{flux}_t + V_{\mathrm{in},t} \times C_{\mathrm{in}} - \mathrm{flush}_t}{V_{\mathrm{E},t+1}} \qquad (1)$$

$$C_{\mathrm{H},t+1} = \frac{C_{\mathrm{H},t} \times V_{\mathrm{H}} \times \mathrm{NEP}_{\mathrm{H},t} \times V_{\mathrm{H}}}{V_{\mathrm{H}}} \qquad (2)$$

Differential equation (mixed conditions)

$$C_{\mathrm{E},t+1} = C_{\mathrm{H},t+1} = \frac{V_{\mathrm{E},t} \times (C_{\mathrm{E},t} + \mathrm{NEP}_{\mathrm{E}}) + V_{\mathrm{H},t} \times (C_{\mathrm{H},t} + \mathrm{NEP}_{\mathrm{H}}) + V_{\mathrm{in}} \times C_{\mathrm{in}} + \mathrm{flux} - \mathrm{flush}}{V_{\mathrm{E},t+1} + V_{\mathrm{H}}} \qquad (3)$$

Intermediate equations

$$V_{\mathrm{in},t} = P_t \times \mathrm{WA} \times \mathit{rainin} \qquad (4)$$

$$V_{\mathrm{out},t} = (P_t + P_{t-1}) \times \mathrm{WA} \times \mathit{rainout} + \mathit{constout} \qquad (5)$$

$$V_{\mathrm{E},t+1} = V_{\mathrm{E},t} + V_{\mathrm{in},t} - V_{\mathrm{out},t} \qquad (6)$$

$$K_t = \frac{2.05 + 0.215 \times U_{10,t}^{1.7}}{100} \qquad (7)$$

$$C_{\mathrm{sat},t} = P_{\mathrm{CO_2},t} \times K_{\mathrm{H},\mathrm{WT}_{\mathrm{E},t}} \qquad (8)$$

$$\mathrm{flux}_t = K_t \times A_{\mathrm{E},t}(C_{\mathrm{sat},t} - C_{\mathrm{E},t}) \qquad (9)$$

$$\mathrm{flush}_t = V_{\mathrm{out},t} \times C_{\mathrm{E},t} \qquad (10)$$

$$\mathrm{NEP}_{\mathrm{E},t} = \mathrm{NEP}_{\mathrm{E}}^{\mathrm{o}} \times \mathrm{e}^{[Q_{10,\mathrm{E}} \times (\mathrm{WT}_{\mathrm{E},t} - T_{\mathrm{E}})/10]} \qquad (11)$$

$$\mathrm{NEP}_{\mathrm{H},t} = \mathrm{NEP}_{\mathrm{H}}^{\mathrm{o}} \times \mathrm{e}^{[Q_{10,\mathrm{H}} \times (\mathrm{WT}_{\mathrm{H},t} - T_{\mathrm{H}})/10]} \qquad (12)$$

Parameters definitions and units are presented in Table 2.

lake, air temperature, and wind speed. For precipitation, the threshold required $\geq 120\,\mathrm{mm\,day^{-1}}$ precipitation and was only seen during typhoon events. For temperature, the threshold was $\leq 6\,^{\circ}\mathrm{C}$ mean daily air temperature, and was only observed during winter mixis. When daily precipitation or mean daily air temperature exceeded these thresholds in the model, the epilimnion and hypolimnion masses of CO_2 were combined using a volume-weighted average and flux to the atmosphere and lake outlet were determined based upon the mixed concentration of CO_2 (Table 1). Simulated CO_2 efflux to the atmosphere and loss by bulk flow through the outlet stream were calculated daily and summed across the 365-day simulation to obtain annual estimates.

Parameter estimation, calibration, and sensitivity analysis

Large gaps in available lake depth data from the YYL sensor network necessitated a hydrologic model to relate precipitation and depth. We used continuous sections (>21 days) of lake depth and precipitation data from 2004 to 2005 (262 total days) and a hyposographic curve for YYL to parameterize the hydrologic portion of the model. Parameter values (Q_{in}, Q_{out}, $\mathit{const}Q_{\mathrm{out}}$) were calibrated using maximum likelihood fits (Table 2) with the nlm() function in the R statistics package (R Development Core Team, 2005) and the 262 days of precipitation and water depth measurements made by the YYL sensor network at 10 min intervals.

Table 2 Parameter values, state variables, and drivers with their associated units

Symbol	Name	Value	Unit	Source
Parameters				
Q_{in}	Proportion of precipitation entering lake	0.11	–	Fit to data
Q_{out}	Proportion outflow	0.054	–	Fit to data
$constQ_{\mathrm{out}}$	Constant outflow	140	m^3	Fit to data
C_{in}	Carbon dioxide concentration of inflow from watershed	11 286	$\mathrm{mg\,CO_2\,m^{-3}}$	Fit to data
$\mathrm{NEP}^{\mathrm{o}}_{\mathrm{E}}$	Reference epilimentic net ecosystem production	249.3	$\mathrm{mg\,CO_2\,m^{-3}\,day^{-1}}$	Fit to data
$\mathrm{NEP}^{\mathrm{o}}_{\mathrm{H}}$	Reference hypolimnetic net ecosystem production	40.7	$\mathrm{mg\,CO_2\,m^{-3}\,day^{-1}}$	Fit to data
T_{E}	Reference temperature for $\mathrm{NEP}^{\mathrm{o}}_{\mathrm{E}}$in the Arrhenius equation	1.14	°C	Fit to data
T_{H}	Reference temperature for $\mathrm{NEP}^{\mathrm{o}}_{\mathrm{H}}$ in the Arrhenius equation	5.63	°C	Fit to data
$Q_{10,\mathrm{E}}$, $Q_{10,\mathrm{H}}$	Q_{10} for Arrhenius equation	2	–	Hanson *et al.* (2004)
V_{H}	Hypolimnion volume	25 000	m^3	Bathymetry
N	Exponent for Schmidt number relationship	−0.5	–	Jahne *et al.* (1987)
$\mathrm{AT}_{\mathrm{critical}}$	Mean daily temperature; below results in lake mixing	6	°C	Data
P_{critical}	Daily precipitation; above results in lake mixing	120	mm	Data
State variables				
V_{E}	Epilimnion volume		m^3	Output
C	CO_2 concentration: E, epilimnion; H, hypolimnion; sat, saturation		$\mathrm{mg\,CO_2\,m^{-3}}$	Output
A_{E}	Epilimnion area		m^2	Output
V_{in}	Volume of water inflow from watershed		m^3	Output
V_{out}	Volume of water outflow to watershed		m^3	Output
K	Mass transfer coefficient for atmospheric exchange		$\mathrm{m\,day^{-1}}$	Output; Cole & Caraco (1998)
Drivers				
P	Precipitation		mm	Input
AT	Air temperature		°C	Input
U_{10}	Wind speed 10 m above lake surface		$\mathrm{m\,s^{-1}}$	Input
WT	Water temperature		°C	Input
AP	Atmospheric pressure		atm	Input

The hyposgraphic curve was also used throughout simulations to convert between lake volume, depth, and area. NEP parameter values ($\mathrm{NEP}^{\mathrm{o}}_{\mathrm{E}}, \mathrm{NEP}^{\mathrm{o}}_{\mathrm{H}}$) and reference temperatures (RT_{E}, RT_{H}) were determined for each layer of the lake (Table 2). These parameters and the concentration of CO_2 in the input water from the watershed (C_{in}) were estimated by iteratively simulating CO_2 dynamics in both model lake layers over the 461-day period for which CO_2 data were available, and minimizing the negative log-likelihood function using modeled CO_2 concentrations and measured CO_2 data. All negative log-likelihood minimizations were done with the R statistics package function nlm() (R Development Core Team, 2005).

We tested the sensitivity of the model to parameter estimates by increasing each parameter value by 10% and recording the percent change in annual CO_2 evasion to the atmosphere and efflux via the outlet stream. All sensitivity model runs were compared with a simulation using 2005 driver data and maximum likelihood point estimates of parameters. The model was considered sensitive to a parameter if a $>10\%$ change in annual CO_2 atmospheric flux resulted from the 10% increase of that parameter (Hamby, 1994). Sensitivity to hydrologic parameters was tested only when both the inlet and outlet parameters (Q_{in} and Q_{out}) were increased in tandem. If only one of the hydrologic parameters was modified, a dramatic imbalance in the water mass-balance occurred.

Impact of typhoon frequency, intensity, and spacing

In addition to estimating annual CO_2 efflux in 2004 and 2005, we used randomization of precipitation event pattern (*frequency, intensity,* and *spacing*) to develop hypotheses about the influence of typhoon regime on CO_2 flux out of YYL. A generalized version of the 2004–2005 YYL model based on distributions fit to the meteorological variables observed during 2004 and 2005 (Table 3) was used to explore the influence of meteorological patterns on CO_2 efflux to the atmosphere and to the catchment below the lake. We used two gamma

Table 3 Distributions, based on 2004 and 2005 data, of meteorological and physical drivers input to the model and their units

Variable	Unit	Distribution or function
Wind speed	$\mathrm{m\,s^{-1}}$	normal (1.15, 0.5); minimum of 0
Typhoon wind speed	$\mathrm{m\,s^{-1}}$	normal (4.2, 1); minimum of 0
Precipitation	mm	gamma (0.12, 55); maximum of 119
Typhoon precipitation	mm	gamma (8.7, 30.7); minimum of 121
Air temperature	°C	$0.18 \times t \times [1(t/366)] + \text{normal}\,(2, 3)$
Atmospheric pressure*	atm	normal (0.614, 0.0027)
Epilimnion water temperature*	°C	$10 - 0.17 \times \text{AT} + 0.04 \times \text{AT}^2 + \text{normal}\,(0, 3)$
Hypolimnion water temperature*	°C	$11.5 - 0.22 \times \text{AT} + 0.03 \times \text{AT}^2 + \text{normal}\,(0, 0.2)$

These distributions were used in generalized simulations to evaluate the impact of typhoon frequency, intensity, and spacing on carbon dioxide flux form the lake. AT, air temperature; *t*, simulation day number, and * indicates the simulated data was running median smoothed.

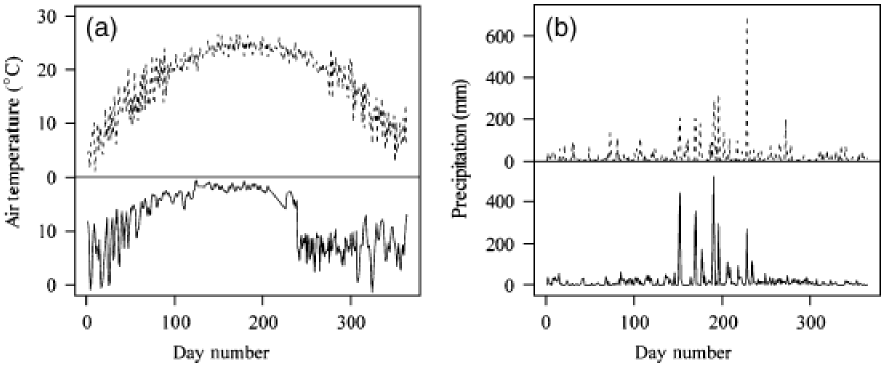

Fig. 2 Plots of (a) air temperature and (b) precipitation against day of simulation. Measured meteorological data from the 2005 time series are plotted with solid lines and simulated data based on distributions from 2005 are plotted with dashed lines.

distributions, typhoon and nontyphoon conditions, to simulate precipitation and two normal distributions for wind speed during nontyphoon and typhoon conditions. Atmospheric pressure was simulated using a single normal distribution. Air temperature was fit to a smoothed, stochastic autoregressive model, and water temperatures in the two layers of the lake were fit to normal distributions with means dependent on air temperature. Both simulated water temperature time series were smoothed using running median smoothing in the R statistics package (R Development Core Team, 2005) following simulation. The range and dynamics of simulated meteorological drivers were qualitatively compared with 2004–2005 meteorological data (Fig. 2).

The number of typhoons occurring in a year was defined as the *frequency* of typhoons and the time between the final winter mixing and first typhoon along with average time between storms was used to quantify typhoon *spacing* across a year. Finally, the amount of precipitation and wind accompanying each typhoon was used to describe *intensity* of individual events. Simulated change in CO_2 efflux from the water column to the atmosphere and to the catchment below the lake resulting from a change in typhoon pattern was used to evaluate the influence of storm event patterns. To explore the determinants of CO_2 efflux from a single disturbance event, we ran 1000 annual simulations with a single typhoon, lasting 2 days, randomly placed within the typhoon season. The typhoon season was defined as 16 March–5 October using a 95% confidence interval from typhoon records for 1996–2005 (A. Kitamoto, unpublished data). Mean daily wind speed and precipitation were also randomly assigned to the typhoon based on observed distributions from 2004 to 2005 meteorological data recorded at YYL (Table 3). A second set of 2000 simulations was run to explore the influence of climatic parameters on annual CO_2 loss from a lake. The simulation was run as above, but with the number of typhoons (again each lasting 2 days) also randomly assigned between 0 and 20. Zero to 10 typhoons represent a range slightly larger than that observed from 1996 to 2005 (A. Kitamoto, unpublished data), but a larger range was used to explore extreme levels of frequency. Linear regression was used to determine variables linking climatic pattern (frequency, intensity, and spacing of storm events) to simulated CO_2 efflux from YYL.

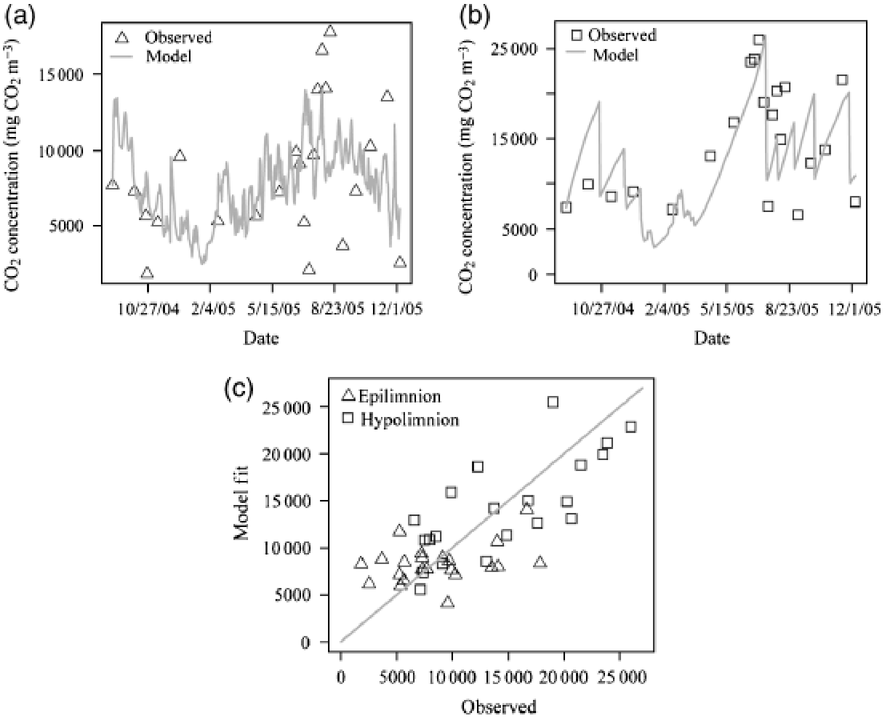

Fig. 3 2005 simulated time series of carbon dioxide concentration in the (a) epilimnion and (b) hypolimnion of Yuan Yang Lake (YYL). Lines represent maximum likelihood model fits and points are sampled concentrations (data). (c) A one-to-one plot of the observed and maximum likelihood-fit CO$_2$ concentrations of the epilimnion (△) and hypolimnion (□).

Results

Parameter estimation

The model produced CO$_2$ concentration dynamics that fit moderately well with the 2004–2005 data; the seasonal trend in epilimnion concentrations was evident, as well as the significant drops in hypolimnetic CO$_2$ concentration following typhoons (Fig. 3). The simple structure of the model probably precludes a tighter fit, but we attained our goal of capturing the major dynamics that are presumed to be driven by typhoon events. Modeled mean epilimnetic NEP ($4.5\,\mathrm{g\,CO_2\,m^{-3}\,day^{-1}}$) was at the high end of empirical and modeled estimates of NEP for north temperate lakes (Hanson *et al*., 2003, 2004). Hypolimnetic NEP rates (mean $= 0.17\,\mathrm{g\,CO_2\,m^{-3}\,day^{-1}}$, max $= 0.39\,\mathrm{g\,CO_2\,m^{-3}\,day^{-1}}$) also agreed with previous estimates available for north temperate lakes (Rich, 1980; Houser *et al*., 2003). The CO$_2$ concentration of influent water ($C_{\mathrm{in}} = 11\,\mathrm{g\,CO_2\,m^{-3}}$) fit to 2004–2005 data was similar to deeper hydrologic flowpaths or emergent groundwater observed by Johnson *et al*. (2006) in two Amazonian headwater catchments. Observed temperatures in headwater streams feeding YYL are suggestive of emergent groundwater (unpublished data). Also, the fitted value of C_{in} was only slightly higher than the average measured DIC in the two major inlets to YYL from November 2005 to January 2007 ($10.2\,\mathrm{g\,CO_2\,m^{-3}}$). This assumes that all DIC was in the form of CO$_2$, but extremely acidic soilwater (pH = 3.3–4.1) suggests that this may indeed be the case (Wu *et al*., 2001).

Annual estimates and contribution of typhoons

According to our model simulation, average daily loss of CO$_2$ to the atmosphere from September 2004 to December 2005 was estimated as $0.8\,\mathrm{g\,C\,m^{-2}\,day^{-1}}$. The two largest daily CO$_2$ fluxes to the atmosphere were estimated at 2.7 and $2.2\,\mathrm{g\,C\,m^{-2}\,day^{-1}}$ for a typhoon in October 2004 and the initial typhoon in 2005. The estimated average CO$_2$ flux during typhoon-induced mixis was $2.0\,\mathrm{g\,C\,m^{-2}\,day^{-1}}$. Approximately 57% of this flux was watershed-derived CO$_2$, the remaining portion was split between within-lake NEP (38%) and hypolimnetic CO$_2$ (5%). Based on our model, efflux of CO$_2$ during an average typhoon was ~2.5-fold greater than a nondisturbed day in 2004 and 2005. Typhoons occurred on 1.7% of the days between September 2004 and December 2005, but were responsible for 7% of the carbon dioxide release to the atmosphere during that time period. Annual CO$_2$ loss via the outlet stream was even more influenced by disturbance events. Typhoon-induced bulk flow of CO$_2$ represented 26% of annual bulk flow CO$_2$ loss. Over the entire time series, loss of CO$_2$ to the atmosphere was estimated to

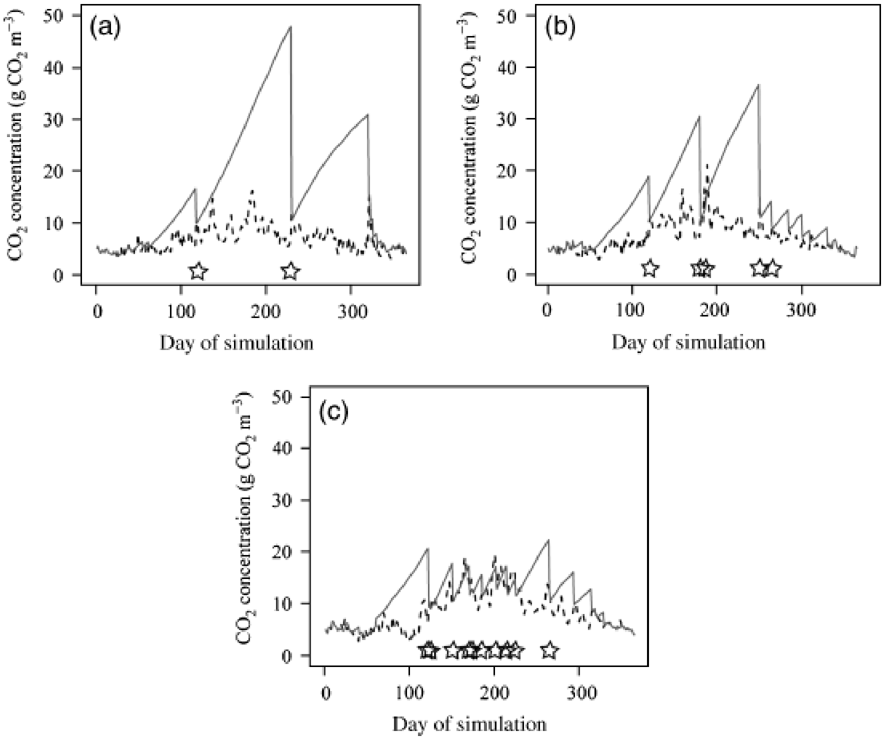

Fig. 4 Representative carbon dioxide dynamics in the epilimnion (black dashed) and hypolimnion (gray solid line) for model simulations with 2, 5, and 10 (a–c) typhoons. Stars indicate timing of simulated typhoons.

be twice the flux of CO_2 to the watershed below. However, during typhoon events, loss of CO_2 via the outlet stream was on average twofold greater than CO_2 flux to the atmosphere.

Based upon our hydrological model and sensor network data, typhoons have dramatic influence on the volume and flux of water into and out of the lake. We estimated that influx of water, and therefore CO_2, from the watershed increased by 30-fold during typhoon conditions. Accordingly, the theoretical hydraulic residence time decreased from ~13 days during nontyphoon conditions to a single day during the modeled typhoon events in 2004 and 2005.

Influence of typhoon frequency, intensity, and spacing

Typhoon frequency had a strong influence on simulated CO_2 concentrations in the model water column (Fig. 4). Using simulations with varied typhoon frequency, we observed a strong positive relationship between the number of typhoons in a year and annual CO_2 efflux (Fig. 5a). Approximately 100 simulations were run at each typhoon frequency ranging from 0 to 20; over this range, annual CO_2 efflux to the atmosphere increased from 11 000 to 34 000 kg C (Fig. 5a). A similar trend was observed for annual CO_2 loss via the outlet stream (4000–21 000 kg C for 0–20 typhoons). The incremental change in annual flux to the atmosphere (average = 1200 kg C typhoon^{-1}) when an additional typhoon was added to a simulation year was much greater than the flux that occurred during that typhoon event (~ 450 kg C). The majority of the annual increase in CO_2 flux to the atmosphere occurred during stratified conditions (63%). This was not the case for CO_2 loss via the outlet stream. The majority of annual increase in CO_2 lost to the outlet occurred during additional days of typhoon mixing (72%). Elevated atmospheric efflux during stratified conditions was likely driven by the observed increase in epilimnetic CO_2 concentrations as typhoon frequency increased (Fig. 5b; log typhoon frequency + 1, log mean C_E $R^2 = 0.75$, $P < 0.001$, $n = 2000$). The frequency of typhoons was highly related to total precipitation ($R^2 = 0.98$, $P < 0.001$, $n = 2000$), suggesting the watershed was a large source of the additional CO_2 to the atmosphere via the lake. A negative asymptotic relationship existed between the number of typhoons and the mean hypolimnion CO_2 concentration (Fig. 5b). This suggests that increased interaction between the epilimnion and hypolimnion also contributed to elevated epilimnion CO_2 concentration and CO_2 evasion to the atmosphere.

Total annual precipitation or typhoon frequency was always the strongest predictor of annual CO_2 efflux to the atmosphere and outlet stream ($R^2 = 0.92$ and 0.99,

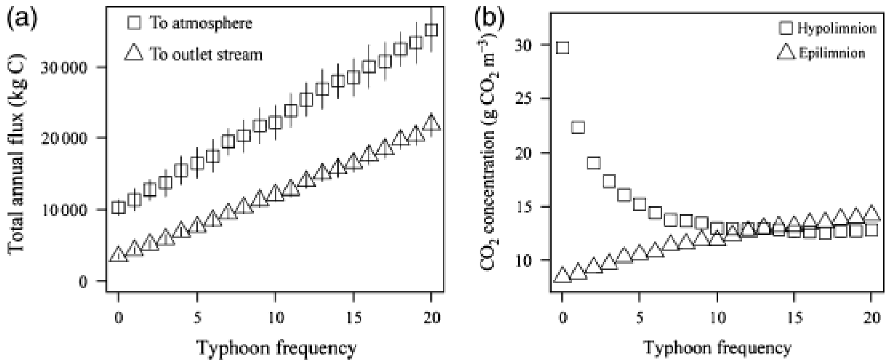

Fig. 5 (a) The effect of number of typhoons in a season on simulated total annual CO_2 efflux to the atmosphere (☐) and the outlet stream (△). Bars represent ± 1 SD. (b) The influence of number of typhoons in a season on simulated mean CO_2 concentration of the model epilimnion (△) and hypolimnion (☐).

respectively, $P<0.001$, $n=2000$, for both). We explored whether parameters in addition to typhoon frequency or total precipitation could be added to the model, such as days between the final spring mixing and the first typhoon, average separation between typhoon events, and average wind speed, but these parameters only marginally increased the amount of variance explained. Increase in precipitation with an increased typhoon frequency also altered the theoretical hydraulic residence time of the model system. The residence time with no typhoons was approximately 12 days, but as typhoon frequency increased the residence time asymptotically approached ~ 6 days.

To evaluate drivers of flux within a single typhoon event, we used simulations with a single event randomly placed during the season. Days since last mixis (DSM) was strongly related to the hypolimnetic concentration of CO_2 before typhoon-induced mixing ($R^2=0.98$, $P<0.001$, $n=1000$). Therefore, days since mixing always explained a moderate portion of variability in event flux of CO_2 to the atmosphere and outlet. However, the relationship was nonlinear and best described by a quadratic fit. Precipitation and DSM explained the most variance in CO_2 flux to the outlet ($R^2=0.84$, $P<0.001$, $n=1000$). Mean wind speed, DSM, and precipitation combined to explain the most variance in event CO_2 evasion to the atmosphere ($R^2=0.80$, $P<0.001$, $n=1000$).

Sensitivity analysis

We required a 10% change in total CO_2 flux to the atmosphere or outlet relative to fitted conditions to consider the model to be sensitive to parameter change (Hamby, 1994). Based on this definition, the model was sensitive only to hydrologic parameters. A 10% increase in both *rainin* and *rainout* resulted in an 11% decrease in atmospheric CO_2 flux and a 13% decrease in CO_2 flux to the outlet stream. The model was also slightly sensitive to the constant outflow term (*constout*), but only CO_2 evasion to the atmosphere was affected (14% increase). The model was not sensitive to the concentration of CO_2 in the water from the watershed above the lake or the NEP terms for either lake layer.

Discussion

We had two objectives for our modeling effort; first, we hoped to quantify rates of CO_2 evasion from YYL. For this purpose we chose to employ the commonly used film layer flux model. Empirical flux data were not available and, therefore, could not be used to verify the ability of the model to accurately predict CO_2 efflux, but our estimates are comparable with previous estimates during stratified and mixed conditions of temperate lakes (Riera *et al.*, 1999; Cole *et al.*, 2002; Hanson *et al.*, 2003). Our second aim was to evaluate the effect of typhoon frequency, intensity, and spacing on CO_2 efflux using a generalized version of a mass-balance model. Few empirical or theoretical studies have explored the influence of meteorological and climatic patterns on CO_2 evasion from lakes, especially in tropical regions.

Estimation of atmospheric CO_2 flux

Both measured and simulated YYL CO_2 surface water concentrations were always above saturation. Supersaturation of CO_2 in many lakes around the world has been described previously (Cole *et al.*, 1994; Sobek *et al.*, 2005). Large inputs of allochthonous material from the surrounding forest and subsequent microbially mediated decomposition probably cause the high CO_2 concentrations (Cole *et al.*, 2002, 2007; Sobek *et al.*, 2003). Overland and groundwater flow also likely serve as direct sources of CO_2 to YYL (Dillon & Molot, 1997; Striegl & Michmerhuizen, 1998). The large concentration gradient between the YYL epilimnion and the atmosphere resulted in high rates of CO_2 efflux to the atmosphere ($0.8\,g\,C\,m^{-2}\,day^{-1}$). This value is approximately fourfold greater than the majority of estimates made using surface water CO_2 measurements and film layer flux models in stratified lakes (Cole & Caraco, 1998; Riera *et al.*, 1999; Rantakari & Kortelainen, 2005). However, both elevated epilimnetic CO_2 concentrations and the resulting increased atmospheric release of CO_2 may be explained by high respiration rates (due to high organic matter concentrations and the subtropical climate), increased interaction between the hypolimnion and epilimnion as a result of typhoon-induced mixing, and large inputs of CO_2 from watershed runoff during typhoons.

Our mean estimate of water column net CO_2 production (assumed to result from heterotrophic activity and photochemical processes) was comparable with estimates at the high end of the range observed by Hanson *et al.* (2003) in temperate lakes. The lakes with comparable NEP in the Hanson *et al.* (2003) survey possessed much higher levels of DOC and total phosphorus (TP) ($DOC = 20–25\,mg\,L^{-1}$, $TP = 15–34\,\mu g\,L^{-1}$,) than YYL ($DOC = 6.0\,mg\,L^{-1}$, $TP = 6.4\,\mu g\,L^{-1}$). Again, the elevated interaction with the watershed and a warmer climate likely explain the comparatively elevated NEP. A bias of limnological research towards north temperate and boreal climates has resulted in a lack of information available in the literature considering gas concentration dynamics and flux to the atmosphere in tropical or subtropical lakes. However, a study of the Amazon basin suggested that tropical rivers release a higher percentage of their carbon load to the atmosphere than temperate rivers (Richey *et al.*, 2002).

Another potential context for our estimates of flux during typhoon-induced mixis is a small set of studies investigating flux of CO_2 from temperate, dimictic lakes to the atmosphere during seasonal mixing. Research on northern latitude lakes has indicated the potential importance of lake mixing on annual lake carbon budgets (Striegl & Michmerhuizen, 1998; Anderson *et al.*, 1999; Riera *et al.*, 1999). Temperate and boreal lakes are characterized by two periods of lake mixing, in the spring and fall; this mixing represents a period of rapid release of CO_2 that accumulated in the bottom waters of the lake during stratification, due to microbial respiration (Hesslein *et al.*, 1991; Cole *et al.*, 1994; Michmerhuizen *et al.*, 1996). Riera *et al.* (1999) estimated average daily CO_2 fluxes to the atmosphere to be $0.4–1.1\,g\,C\,m^{-2}\,day^{-1}$. The maximum daily flux was estimated as $2.8\,g\,C\,m^{-2}\,day^{-1}$ during autumn mixis of a humic lake in northern Wisconsin, USA. Similar average and maximal values have been observed in other north temperate lakes during seasonal mixing (Striegl & Michmerhuizen, 1998; Anderson *et al.*, 1999). Our estimates of CO_2 flux to the atmosphere from YYL during typhoon-induced mixing in 2004 and 2005 ($mean = 2\,g\,C\,m^{-2}\,day^{-1}$, $max = 2.7\,g\,C\,m^{-2}\,day^{-1}$) were similar, but again slightly elevated, when compared with the estimates presented above. Here, the slightly higher estimates for flux during typhoon-induced mixing relative to temperate seasonal mixing could be a result of greater input of CO_2 from the watershed or higher wind speeds during typhoons when compared with those observed during spring or autumn in the north temperate climate.

Influence of storm frequency, intensity, and spacing

We believe that the generalization of our model provides a useful framework for exploration of the relationship between meteorological events or climate regime and aquatic ecosystem processes, in this case carbon cycling. It is expected that total annual precipitation will increase 10–40% in Asia, Central Africa, and the boreal region (Meehl *et al.*, 2007). The IPCC (Meehl *et al.*, 2007) also predicts the intensity of meteorological events to increase in all areas regardless of expected changes in total precipitation. Our simulations reveal that storm frequency had the greatest impact on CO_2 flux from the system; increases of approximately $2200\,kg\,C\,yr^{-1}$ (60% atmospheric, 40% outlet stream) were observed per storm event. Somewhat surprisingly, the increased atmospheric flux was not completely caused by evasion during disturbance-induced mixis. Rather, typhoons appeared to elevate CO_2 concentrations in the epilimnion, creating a stronger concentration gradient between the surface water and the atmosphere resulting in increased flux to the atmosphere during the stratified conditions following the typhoon. The elevated epilimnetic CO_2 concentration following storm events resulted from the complete mixing of epilimnion with the hypolimnion, as well as inputs from the watershed. However, the increase in epilimnetic CO_2, and therefore, CO_2 evasion to the atmosphere, would not continue to increase at this rate indefinitely. As interaction with the watershed increases with increased storm frequency, the epilimnion concentration of CO_2 approached a steady state concentration determined by the amount of CO_2 in water entering the lake from the watershed and contributions from hypolimnetic and epilimnetic respiration. At a storm frequency above ~ 10, it appeared that the contribution of CO_2 from the hypolimnion to the epilimnion was at a maximum and the hypolimnion CO_2 concentration was at a minimum (Fig. 5b). In addition, the epilimnetic CO_2 concentration was leveling and approached $\sim 15\,g\,CO_2\,m^{-3}$ (Fig. 5b). Without any in-lake production of CO_2, one would expect the epilimnetic concentration to approach C_{in} ($11.3\,g\,CO_2\,m^{-3}$). However, NEP of CO_2 in the epilimnion and input of hypolimnetic CO_2 during typhoon-induced mixis resulted in a steady state epilimnetic CO_2 concentration above C_{in}.

Although typhoon temporal spacing and mean wind speed were important at an event scale, storm frequency and, therefore, total annual precipitation appeared to be the primary climatic feature impacting carbon flux in our model lake system on an interannual time scale. Previous research in boreal lakes has demonstrated a link between annual precipitation patterns and epilimnetic CO_2 concentrations or atmospheric CO_2 flux. Rantakari & Kortelainen (2005) linked precipitation between June and August to epilimnetic CO_2 concentration and open water season precipitation with annual CO_2 evasion. These authors argued that the linkage was likely driven by input of DOC from the watershed enhancing respiration in the sediments and water column. This is a likely hypothesis based on the extensive literature supporting allocthonous DOC respiration rates in lakes (e.g. Tranvik & Hofle, 1987), but Rantakari & Kortelainen (2005) did not consider CO_2 produced in the watershed as a contributor to the lake CO_2 standing stock or flux. A similar study of boreal lakes (Kelly *et al*., 2001) again found linkages between precipitation and epilimnetic CO_2 concentration, but did consider the potential influence of watershed runoff and groundwater for transport of CO_2 to the lake (e.g. Kling *et al*., 1991). The transport of CO_2 to a lake from groundwater has been especially high when the watershed contained peatlands (Hope *et al*., 1996; Kelly *et al*., 1997; Riera *et al*., 1999), as is the case in the YYL watershed (Wu *et al*., 2001).

Although not directly included in our model, the presence of terrestrial DOC in the water column of YYL is implicitly included by the NEP of CO_2. As a result the lake was always net heterotrophic. However, our model results emphasize the importance of hydrologic interaction between the lake water column and the watershed, as well as interaction between the CO_2-rich hypolimnion of lakes and the epilimnion as a result of lake mixis. Our model suggests that arctic lakes are not the only water bodies that can serve as 'gas conduits' for watershed-derived carbon (Kling *et al*., 1991), and that increased precipitation or changes in intensity of meteorological events can increase the flux of watershed-derived CO_2 to lakes. This will be particularly relevant for small lakes with short residence times (like YYL), but watershed influences may be weak in large lakes with long hydraulic residence times, as was highlighted by Kelly *et al*. (2001). If future climate predictions (Meehl *et al*., 2007) are correct, the connections between the watershed and lake water columns are likely to increase in importance.

Further empirical research similar to that conducted by Rantakari & Kortelainen (2005) and Kelly *et al*. (2001) in all regions of the globe would provide a rigorous test of hypotheses developed by our modeling exercise. Precipitation is a commonly measured parameter and technological developments in measurement of lake metabolism parameters (respiration, gross primary production, and NEP) will allow an unprecedented ability to link climatic variables with lake ecosystem processes.

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