

## Article

# Absence of winter and spring monsoon changes water level and rapidly shifts metabolism in a subtropical lake

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## Abstract

We investigated how the lack of usual winter and spring monsoons, effectively representing consecutive drought events, affected the dynamics of ecosystem metabolism in a shallow mesotrophic seepage lake in northeastern Taiwan. An instrumented buoy provided high-frequency free-water dissolved oxygen measurements, water temperature profiles, and meteorological data, which we used to estimate daily values of gross primary production (GPP), ecosystem respiration (R), and net ecosystem production (NEP). Results revealed that the disappearance of monsoons decreased lake level and volume, concentrated dissolved nutrients, stimulated the development of algal biomass, promoted stratification, and resulted in a major shift in lake metabolism. Offshore GPP and R were both initially stimulated but then decreased due to shallower mixing depths in the water column. The lake rapidly shifted from a heterotrophic state to a highly autotrophic status when the water level dropped to the lowest level. A return to autotrophy was caused by a greater decline in R than an increase in GPP. This study demonstrates the dramatic effect that drought events can have on lake ecosystem function and suggests that nutrient control may be important in mitigating the effects of a predicted warmer and drier climate and increased water withdrawal in this region.

**Key words:** autotrophy, drought, ecosystem metabolism, high-frequency measurement, subtropical lake, trophic status

## Introduction

The frequency of extreme weather events, such as prolonged droughts or intense rainstorms, is expected to increase globally with climate change (IPCC 2012). For example, summer rainstorms are predicted to be more intense, and winter and spring monsoons are expected to disappear in subtropical areas (Knutson et al. 2010, Chou et al. 2013). The increase in drought frequency and

duration and the alteration of the magnitude and timing of seasonal precipitation and subsequent runoff events are expected to affect biogeochemical cycles, food web structure, and ecosystem metabolism of subtropical freshwater ecosystems (Webster et al. 2005, Sadro and Melack 2012, Malone et al. 2013).

Ecosystem metabolism is a fundamental characteristic that provides a measure of trophic status and carbon balance as well as an indication of cross-ecosystem con-

nectivity to natural and human disturbances (Kortelainen et al. 2006, Jones et al. 2009a, Staehr et al. 2010). Worldwide, lentic freshwater ecosystems are active processors of carbon and are important contributors to regional carbon cycling and storage (Cole et al. 2007, Williamson et al. 2009, Malone et al. 2013), particularly in subtropical and tropical Asia where most lakes are small, shallow, and surrounded by terrain with high relief. Large quantities of terrestrially fixed organic materials and nutrients are rapidly delivered into adjacent aquatic ecosystems via intensive monsoons, typhoons, or frequent rain storms in these areas (Jones et al. 2006, 2009b, Buffam et al. 2011, Page et al. 2011). Subalpine lakes in Taiwan are mostly shallow (<5 m) and characterized by larger catchments than lake areas and highly variable natural perturbations, such as monsoon- and typhoon-induced rapid mixing and flushing (Tsai et al. 2008, 2011).

Studies of potential metabolic responses of lake to precipitation have been limited mostly to temperate or boreal areas (Tadonléké et al. 2012, Christensen et al. 2013, Vachon and del Giorgio 2014), and reported results have been inconsistent. For example, some studies indicated that droughts would increase water residence time and concentrate nutrients, which could eventually increase algal growth (Paerl and Huisman 2008, Romo et al. 2013, Cobbaert et al. 2014), whereas other studies indicated that net heterotrophy of ecosystems would increase during low water level periods. For example, ecosystem respiration was stimulated more than primary production by higher temperatures during droughts or by drought-induced vegetation dieback (Arle 2002, Staehr and Sand-Jensen 2006). Inorganic carbon limitation and elevated pH caused by initial increases in benthic photosynthesis or light-saturated photosynthesis of dense benthic vegetation also led to higher heterotrophy of lakes under prolonged droughts (Van et al. 1976, Christensen et al. 2013). Generally, these studies suggest that seasonal or annual droughts could be a catalyst that promotes reduction in lake volume and changes in nutrient levels, dominant vegetation and their photosynthetic physiology, underwater light availability, and other physical, chemical, and biological factors that shape site- or time-specific metabolic regimes in lakes.

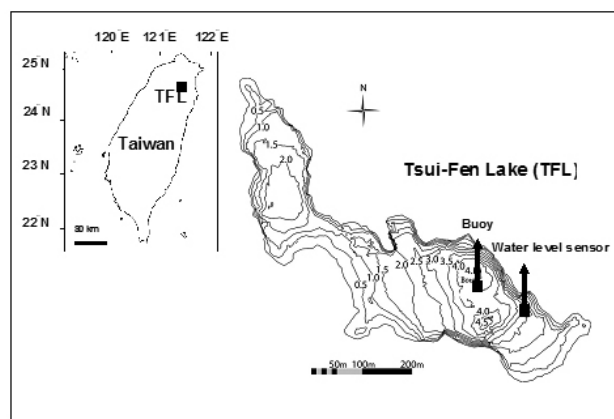
To date, effects of drier weather conditions on the ecosystem metabolism of subtropical lakes or inland waters have received relatively little attention (Molone et al. 2013). Understanding future changes in ecosystem metabolism and the role drought plays in regional carbon cycles of subtropical lakes is an important issue in global change ecology. The effects of episodic external disturbances on gross primary production (GPP) and respiration (R) can be explored through continuous monitoring of the

whole-lake metabolism by high-frequency *in situ* dissolved oxygen measurements (e.g., Tsai et al. 2008, 2011). Here we report the results of a nearly 2-year (Jan 2009–Sep 2011) investigation in a naturally mesotrophic, small shallow subtropical mountain lake. Our goal was to investigate how lake metabolism was affected by the unusual absence of winter and spring monsoons, and to unravel the importance of lake physical, chemical, and biological factors controlling ecosystem metabolism.

Our overall hypothesis was that primary production will be suppressed in the drier periods because the absence of storms associated with monsoon events will reduce input and resuspension of nutrients (Tsai et al. 2011). In addition, decreases in loading of allochthonous dissolved organic materials and primary production are expected to reduce ecosystem R. Although we expect both GPP and R to decline, it is difficult to predict whether they will do so in equal measure. Thus, the resulting effect on net ecosystem production (NEP) is unclear and will depend on the relative effect of the absence of monsoons on the relationship between GPP and R (Staehr et al. 2010, Christensen et al. 2013).

## Study site

Tsui-Fen Lake (TFL) is a 25 ha, dual-basin subalpine lake (1820 m a.s.l.; max. depth = 12 m, mean depth = 4.2 m) in northeastern Taiwan (24°30'N; 121°37'E), surrounded by cypress (*Chamaecyparis formosana*) forest (Fig. 1). TFL is in a deep valley open to southeast winds, in line with the lake's longest fetch. The lake has no surface outlet, but 9 stormwater inlets feed the lake during medium to heavy rainfall. TFL drains slowly by leaking into the underlying bedrock. It is naturally oligotrophic or



**Fig. 1.** Taiwan with enlarged bathymetric map of Tsui-Fen Lake (TFL) showing the buoy location.

mesotrophic, with total phosphorous and chlorophyll *a* ranges of 10–70 and 0.98–34.40  $\mu\text{g L}^{-1}$ , respectively. The lake is slightly humic with an average dissolved organic carbon (DOC) concentration of 6.1  $\text{mg L}^{-1}$ , slightly acidic with mean pH of 5.9, and has an extensive littoral zone (~30% of the total lake area). The mean annual temperature is ~13 °C (monthly average –5 to 15 °C). The average monthly precipitation in winter and spring (Nov–May) is about 450 mm; however, in the 2 years of this study, average monthly precipitation was only 247 mm (CWB 2006).

## Methods

### Instrumentation and data

Instrumented buoys were deployed at the deepest location in TFL (Fig. 1) to record pelagic dissolved oxygen (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). The membrane on the DO probe was changed monthly, and the sensor was calibrated in water-saturated air with a correction for barometric pressure before deployment. Additional calibration was made at monthly intervals by comparing the DO data measured by the sonde at 0, 0.25, 0.5, 1, 2, and 3.5 m with a portable water quality multiprobe (Hydrolab minisonde 4a, Hach Environmental, Loveland, CO, USA) to eliminate potential bias induced by drift of the *in situ* sonde. Vertical water temperature profiles were 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 an anemometer (model 03001, R.M. Young, Traverse, MI, USA). Variation in water level was measured using a submersible pressure transmitter (PS 9800(1), Instrumentation Northwest, Kirkland, WA, USA) deployed in the nearshore area (Fig. 1) to monitor changes in relative water levels. Precipitation, air temperature, and incoming photosynthetically active radiation (PAR) were collected at a land-based weather station ~1 km from the lake center using a tipping-bucket rain gauge, a temperature probe (41382VC; R.M. Young), and a PAR sensor (LI-190; Li-cor, Lincoln, NE, USA), respectively. High-frequency measurements of colored dissolved organic matter (CDOM) and chlorophyll *a* (Chl-*a*) were measured by a submersible fluorometer (C3; Turner Designs) at depth 0.25 m at the same site. The logging interval and maintenance schedule were the same as for the DO sonde.

Samples for water chemistry were collected manually at the buoy site at 4-week intervals across the entire study and analyzed according to standard methods (Tsai et al. 2008). Briefly, water samples from 0.25 m depth were collected for analysis of total phosphorus (TP) and total nitrogen (TN). Surface DOC samples were collected using a portable hand pump with in-line filters (47 mm GF/F, Whatman, Maidstone, Kent, UK) and analyzed with a total organic carbon (TOC) analyzer (Model 1010, O.I. Analytical, College Station, TX, USA). Chl-*a* was sampled to calibrate the sensor data by filtering lake water at depths of 0, 0.5, 1, 2, and 3.5 m. Filters with Chl-*a* samples were stored in the dark at 4 °C until Chl-*a* was extracted with methanol and then measured by a Portable Fluorometer 162 (10-AU-005-CE; Turner Designs, Sunnyvale, CA, USA; Hanson et al. 2003). Water color samples were also collected from the surface. Absorbance was measured with use of a spectrophotometer (Spectroquant, VEGA 400, Serial No:00060093, Merck, Whitehouse Station, NJ, USA), and color was expressed as wavelength-specific (440 nm) absorbance coefficient ( $a_{440}$ ,  $\text{m}^{-1}$ ):  $a_{440} = 2.303 \times$  (absorbance at 440 nm/0.1 m; Houser 2006).

### Light attenuation and euphotic zone

The vertical attenuation coefficient,  $k_d$ , was calculated from underwater light profiles measured at 0.5 m increments at 1200 h using a portable PAR sensor at a monthly interval (Licor LI-192). We defined the euphotic zone ( $Z_{\text{eu}}$ , m) as the depth at which 1% of the incident light occurred (i.e.,  $I(Z_{\text{eu}}) = 0.01 \times I_0$ ; Dodds 2002). The littoral zone was defined as the area shallower than the euphotic zone, where downward light was sufficient to allow the growth of benthic photosynthetic organisms (Dodds 2002).

### Calculation of ecosystem metabolism

The pelagic volumetric GPP and ecosystem R were calculated using free-water diel DO methods from DO measurements at 0.25 m depth. A metabolism model described by Cole et al. (2000), Hanson et al. (2003), and Staehr et al. (2010) was used to calculate GPP and R from recorded diel DO data. Briefly, R was calculated as the atmospheric diffusion-corrected changes ( $F_{\text{atm}}$ ) in DO during nighttime. External loading of DO by precipitation, surface inflow, and groundwater was assumed to be negligible, in keeping with previous work (Cole et al. 2000, Hanson et al. 2003, Tsai et al. 2008, 2011). GPP was estimated by assuming R was equal between day and night. Net ecosystem production ( $\text{NEP} = \text{GPP} - \text{R}$ ) was determined as the diffusion-corrected increase in surface-

layer DO during daytime. Diffusive fluxes of oxygen between the atmosphere and lake ( $F_{\text{atm}}$ ,  $\mu\text{mol m}^{-3} \text{h}^{-1}$ ) were estimated as:

$$F_{\text{atm}} = k (O_{2\text{sat}} - O_2)/Z, \quad (1)$$

where  $O_{2\text{sat}}$  and  $O_2$  are the saturation concentration of oxygen ( $\text{mg L}^{-1}$ ) and measured DO, respectively.  $O_{2\text{sat}}$  is a function of water temperature and altitude, estimated by the empirical equation given in Dodds (2002);  $Z$  refers to the depth of epilimnetic mixing layer (m) determined by continuously measuring water temperature profiles at assigned depths and is estimated as the depth at which the temperature gradient exceeded  $1 \text{ }^\circ\text{C m}^{-1}$  (Staeher et al. 2010);  $k$  is the gas transfer coefficient ( $\text{m h}^{-1}$ ) for oxygen, expressed as follows (Wanninkhof 1992):

$$k = k_{600} \times \left( \frac{SC_{\text{oxy}}}{600} \right)^{-0.67} \quad (2)$$

where  $k_{600}$  ( $k$  for a Schmidt number of 600,  $\text{m h}^{-1}$ ) is estimated as a function of wind speed at 10 m above the lake by the equation of Cole and Caraco (1998),

$$k_{600} = (2.07 + 0.215 U_{10}^{1.7})/100, \quad (3)$$

and  $SC_{\text{oxy}}$  is the Schmidt number for oxygen, calculated as follows (Wanninkhof 1992):

$$SC_{\text{oxy}} = 1800.6 - 120.1 \times t + 3.78 \times t^2 - 0.05 \times t^3, \quad (4)$$

where  $t$  is the water temperature ( $^\circ\text{C}$ ). Metabolic parameters were calculated for each day except for days with typhoons and rainstorms, when entraining of anoxic bottom waters during mixing events and potential DO loading from incoming waters may render the model invalid (Tsai et al. 2008, 2011, Jennings et al. 2012).

### Statistical analysis

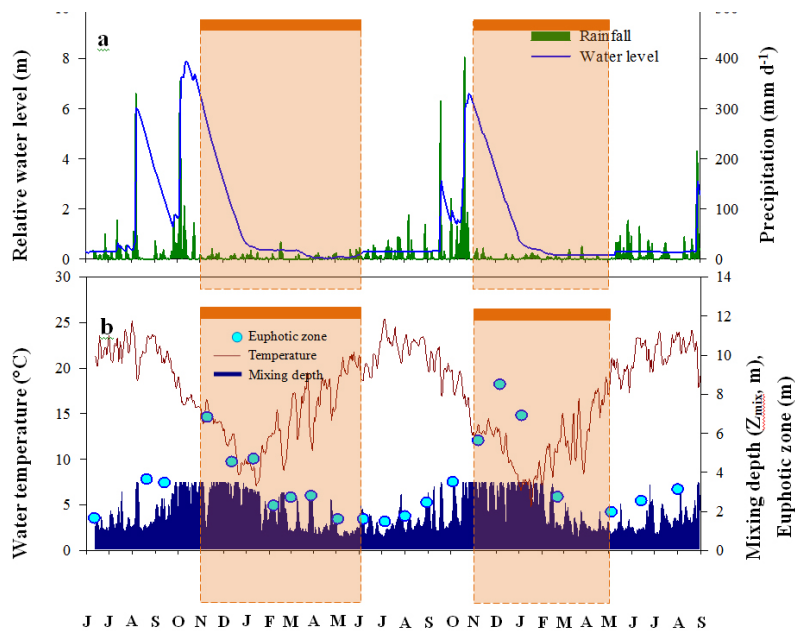
To evaluate the influence of missing winter and spring monsoons on ecosystem metabolism, we first divided the collected data of environmental, biological, and limnological variables as well as the 3 ecosystem metabolic parameters (GPP, R, and NEP) into 2 categories: the groups of abnormally dry periods (i.e., the absence of winter and spring monsoons from November to April or May) and periods of normal climatic conditions (from May or June to October), with no overlap between the 2 groups. Both periods were approximately equal. A Shapiro-Wilks test was applied to check the normality of the datasets, and variables were log-transformed to normalize data distribution, ensure homogeneity, and linearize relationship if necessary. We lumped the corresponding

datasets from the 2 study years and used Pearson correlation matrixes to evaluate the correlations among 3 metabolic parameters (state variables) and potential forcing variables in these 2 groups, removing highly correlated variables ( $-0.70 > r$  or  $r > 0.70$ ) in advance to avoid the covariance between potential forcing variables. Based on the results from this analysis, multiple linear regression analysis was then applied to determine key forcing variables for the variation GPP, R, and NEP in dry periods by evaluating all possible models and using Akaike's Information Criterion (AIC) to identify the most parsimonious solution. One-week averages of daily variables (e.g., 3 metabolic parameters, wind speeds, rainfall, and mixing depth) for the week during the monthly sampling date of water chemistry (e.g., TP, TN, DOC, water color, and Chl-*a*) were used in the regression analysis. Only environmental variables that showed significant relationships with metabolic variables ( $p < 0.05$ ) were included in the final regression model. The model with the lowest AIC value was considered the best model of those tested (Burnham and Anderson 2002, 2004). We used Statistica software (StatSoft, Tulsa, OK, USA) to perform all statistical analyses.

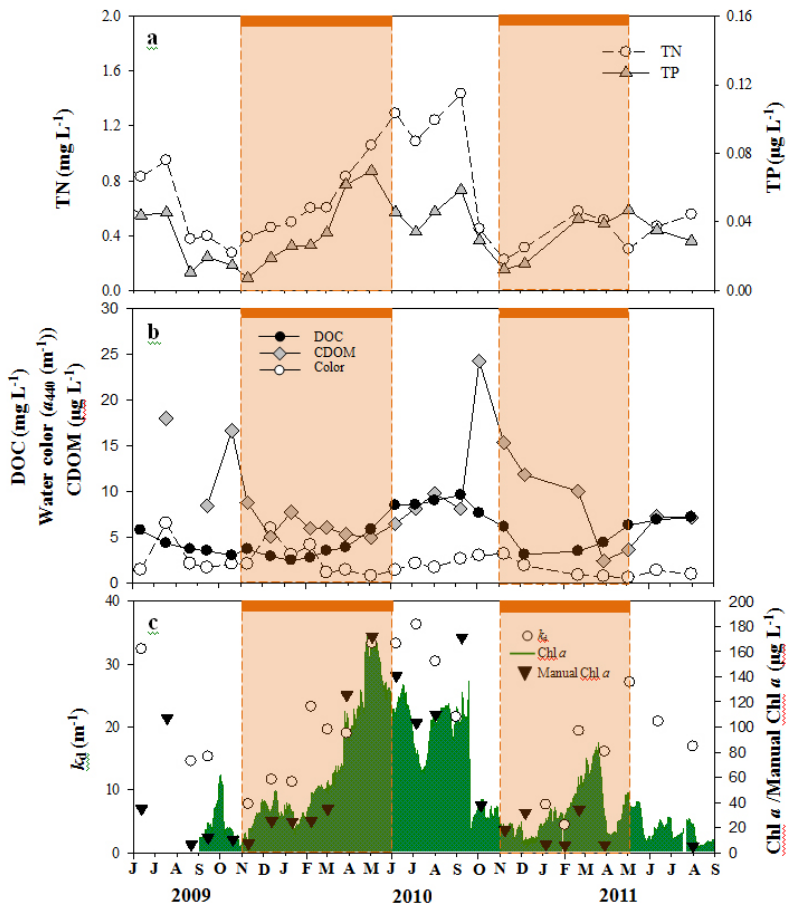
## Results

### Response of environmental and limnological attributes

Normal winter (Dec–Feb) and spring (Mar–May) monsoons did not occur during the 2 study years (Jan 2009–Sep 2011). Total precipitation values over winter and spring in these 2 years were 370 and 720 mm, respectively (Fig. 2a),  $\sim 50$ – $70\%$  lower than values in 2004–2008. Total precipitation values over summer and fall periods in 2009 and 2010 were 2358 and 2608 mm, respectively. Surface water temperatures (measured at 0.25 m depth) were  $7.1$ – $21.3 \text{ }^\circ\text{C}$  (mean =  $13.2 \text{ }^\circ\text{C}$ ) through winter and spring and  $2.7$ – $25.4 \text{ }^\circ\text{C}$  (mean =  $20.7 \text{ }^\circ\text{C}$ ) during summer and autumn (Fig. 2b). Seasonal whole-lake mixing ( $Z_{\text{mix}}$ , 3.5 m) began when surface temperature fell below  $\sim 17 \text{ }^\circ\text{C}$  in mid-autumn (Oct) and persisted until surface temperature exceeded  $\sim 9 \text{ }^\circ\text{C}$  in late winter (Feb). Episodic lake mixings were recorded over spring droughts, with the occurrence of cold fronts and strong winds (Fig. 2b). Lake water level fluctuated with precipitation events (Fig. 2a), rising 6–8 m during typhoons or rainstorms during wet periods (summer and autumn). Water levels took 2–3 months to return to previous levels during drier periods (Mar 2010 and Feb 2011) and remained low until the beginning of the next wetter period (Fig. 2a). Changes in precipitation altered the water level, determined the lake volume (Fig. 2a), and therefore



**Fig. 2.** Temporal variations in (a) daily precipitation and relative water level changes, and (b) the water temperature and mixing depth and euphotic zone in TFL from Jan 2009 to Sep 2011. Horizontal shading represents the duration of the absence of winter and spring monsoons (dry periods) in the plot.



**Fig. 3.** Time trends of limnological drivers measured in lake surface water, including (a) TN and TP; and (b) DOC, CDOM, and water color; and (c) light attenuation coefficient ( $k_a$ ), manual spectrophotometric measurements of Chl-*a*, and automated sonde-based measurements of Chl-*a*. Samples were collected at monthly intervals. Vertical shading represents the dry periods in the plots.

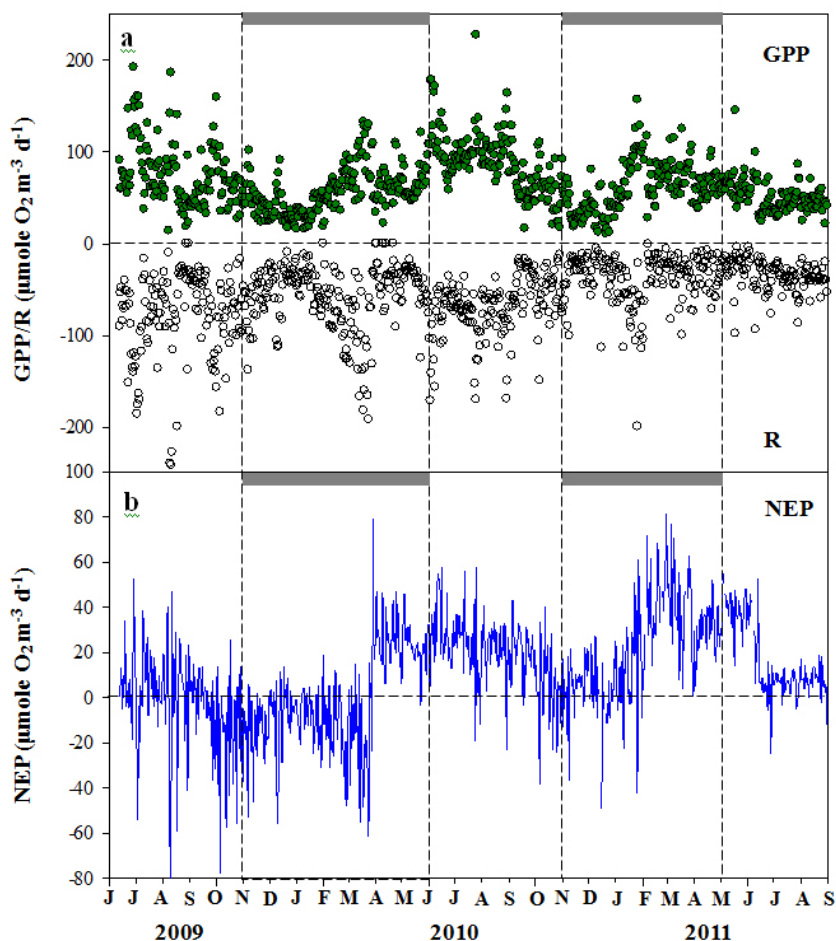
shaped the temporal variation of lake chemical variables, such as nutrient concentrations (TP and TN), CDOM, and DOC.

DOC was positively related to Chl-*a* concentration during both dry and wet periods (Fig. 3b and c, Table 1), implying that the lake DOC pool was primarily endogenously produced. Temporal patterns of TP, TN, DOC, and Chl-*a* concentrations were similar (Fig. 3a–c), increasing with the lowering water level from early winter and peaking in late spring (Apr–May) when the relative water level dropped to the lowest level (0.03–0.11 m; Fig. 2a and 3a–c). Nutrient concentrations and algal biomass (Chl-*a*) increased with lowered water level; however, indices of terrestrial organic carbon, such as water color and CDOM, generally decreased (Fig. 3b) during dry periods. Light attenuation ( $k_d$ ) increased rather than decreased with increasing Chl-*a* concentrations (Fig. 3c, Table 1) due to the lower inputs of colored organic matter during dry periods.

### Response of ecosystem metabolism and trophic status

GPP and R were tightly coupled and showed similar temporal trajectories throughout the study period (Fig. 4a). GPP and R progressively increased as water level dropped, and nutrient concentration increased with the beginning of the dry weather season (Fig. 2a, 3a, and 4a). GPP and R both peaked at the lowest recorded water level (Mar 2010 and Feb 2011, respectively; Fig. 2a and 4a). After this initial increase, both GPP and R abruptly decreased and then remained at low levels until the end of dry periods (Apr 2010 and May 2011, respectively; Fig. 4a). Peaks of GPP and R occurred occasionally during dry periods, when the lake mixed due to strong winds or a decrease in air temperature (Fig. 2b and 4a).

TFL tended to be heterotrophic (NEP < 0) or in metabolic balance (NEP = 0) at the start of the dry period (Fig. 4b); however, the lake shifted to net autotrophy



**Fig. 4.** Time series of daily estimates of (a) gross primary production (GPP), ecosystem respiration (R), and (b) net ecosystem production (NEP). Rates of R are shown as negative values. Horizontal shading represents the dry periods in the plots.

**Table 1.** Pearson correlation coefficients between metabolic variables (GPP, R, NEP) and potential drivers, including mixing depth ( $Z_{\text{mix}}$ ), water temperature ( $W_{\text{temp}}$ ), wind speed ( $W_{\text{speed}}$ ), TP, TN, Chl- $a$ , water color (WC), DOC, CDOM, light attenuation ( $k_d$ ), water level (WL) and daily rainfall in Tsuei-Feng Lake (TFL). The analysis was performed on all available data in drier and wet periods, respectively.

	Variables	R	NEP	$Z_{\text{mix}}$	$W_{\text{temp}}$	$W_{\text{speed}}$	TP	TN	Chl- $a$	WC	DOC	CDOM	$k_d$	WL	Rain	
Dry periods	GPP	<b>-0.70**</b>	0.23	-0.27	0.59	<b>0.66*</b>	0.45	<b>0.79*</b>	0.52	-0.26	<b>0.83*</b>	-0.33	0.60	-0.21	<b>-0.63*</b>	
	R		0.11	0.28	-0.57	-0.24	0.20	-0.39	0.02	-0.08	-0.64	-0.06	-0.30	-0.13	0.36	
	NEP			-0.07	0.20	<b>0.65*</b>	<b>0.86*</b>	0.67	<b>0.76*</b>	-0.45	0.47	-0.53	0.51	-0.43	-0.44	
	$Z_{\text{mix}}$				<b>-0.86**</b>	-0.34	-0.36	-0.44	-0.54	-0.58	-0.53	0.28	-0.57	0.07	0.58	
	$W_{\text{temp}}$					0.66	0.32	0.64	0.55	-0.53	<b>0.82*</b>	-0.11	0.66	0.09	0.62	
	$W_{\text{speed}}$						0.60	<b>0.76*</b>	<b>0.70*</b>	-0.47	<b>0.73*</b>	-0.19	<b>0.73*</b>	-0.13	-0.32	
	TP								<b>0.79*</b>	<b>0.95***</b>	-0.61	0.52	-0.64	<b>0.76*</b>	-0.72*	-0.29
	TN									<b>0.87**</b>	-0.57	<b>0.91**</b>	-0.39	<b>0.91**</b>	-0.56	-0.32
	Chl- $a$										-0.60	<b>0.85*</b>	-0.61	<b>0.87**</b>	-0.60	-0.36
	WC											-0.55	-0.05	-0.49	0.21	0.38
	DOC												-0.12	<b>0.78*</b>	-0.21	-0.48
	CDOM													-0.53	0.67	0.26
	$k_d$														-0.64	-0.16
	WL															-0.24
	Wet periods	GPP	<b>-0.94**</b>	-0.86	0.65	-0.82	0.50	-0.19	-0.46	-0.31	<b>-0.93**</b>	-0.54	0.80	-0.80	0.61	0.61
R			<b>0.92**</b>	-0.88	<b>0.94**</b>	-0.77	0.52	0.74	0.62	<b>0.90*</b>	0.80	-0.54	<b>0.96*</b>	-0.84	-0.84	
NEP				<b>-0.94*</b>	<b>0.91**</b>	-0.87	0.66	0.85	0.74	0.81	0.89	-0.38	0.79	-0.92	<b>-0.93*</b>	
$Z_{\text{mix}}$					<b>-0.96**</b>	<b>0.98***</b>	<b>-0.86*</b>	-0.77	<b>-0.91**</b>	-0.59	0.74	0.07	-0.88	0.83	<b>0.91**</b>	
$W_{\text{temp}}$						-0.72	0.71	<b>0.88*</b>	0.78	0.78	-0.69	-0.33	0.89	<b>-0.95**</b>	<b>-0.95**</b>	
$W_{\text{speed}}$							-0.84	0.68	<b>-0.98**</b>	-0.42	0.92	-0.12	-0.92	<b>0.95**</b>	<b>0.95*</b>	
TP									<b>0.76*</b>	<b>0.99***</b>	0.10	<b>-0.87*</b>	0.44	0.74	-0.90	-0.90
TN										0.99	0.38	<b>0.92**</b>	0.17	0.90	-0.98	<b>-0.98**</b>
Chl- $a$											0.22	<b>0.96**</b>	0.33	0.82	-0.95	<b>-0.95**</b>
WC												0.47	-0.85	0.74	-0.53	-0.53
DOC													0.07	<b>0.94*</b>	1.00*	<b>0.92*</b>
CDOM														-0.28	0.01	0.01
$k_d$															-0.86	-0.76
WL																<b>0.90**</b>

Correlations significant at least at  $p < 0.05$  are in bold, \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ .

(mean  $\pm$  standard error =  $25.2 \pm 1.49$  and  $35.6 \pm 1.89$  during the 2010 and 2011 dry periods, respectively) when the lowest water level was observed (Fig. 2a, 4b, and 5). Autotrophy of TFL occurred because the decrease in ecosystem respiration was greater than the decrease in GPP (Figs. 4a and b). R had 68.8% and 75.8% declines from spring peaks in 2010 and 2011, respectively, compared to 38.5% and 25.8 % decreases in GPP in 2010 and 2011, respectively.

### Drivers of metabolic response

Environmental factors such as rainfall and wind speed showed significant correlations with the GPP during dry periods (Table 1). Wind speed was positively related to GPP whereas precipitation was negatively related to GPP (Table 1). Stepwise regression analysis revealed that rainfall, nutrient concentrations (TN and TP), and algal biomass (Chl- $a$ ) were the primary forcing variables of GPP during dry periods (Table 2, Fig. 6a). R during dry periods was highly correlated with the production of

autochthonous organic matter (i.e., GPP; Table 1 and 2); however, R during wet seasons was also related to the input of allochthonous organic matter (i.e., water color; Table 1). During dry periods, the relationships (slope and variance explained) between R and GPP were lower than during wet periods. The slope and  $r^2$  of the simple linear regression models decreased from 0.99 and 0.72 during wet periods to 0.81 and 0.48 during dry periods (Fig. 7a and b), implying a somewhat different relationship between these metabolic parameters and a weaker dependence of ecosystem R on autochthonous production under dry weather conditions.

### Discussion

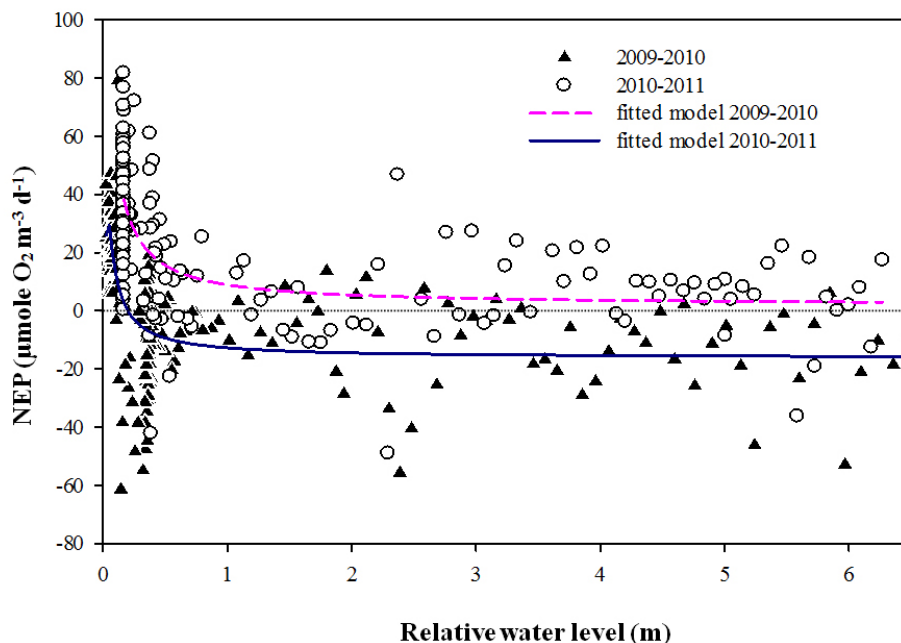
The temporal variation of water level is particularly sensitive to altered precipitation patterns and seems to be a primary driver influencing limnological processes such as thermal regime, DO, nutrient concentrations, and algal dynamics. These influences of changing water levels seem to be especially prevalent in shallow and small inland

**Table 2.** Results of stepwise multiple linear regression analysis of effects of mixing depth ( $Z_{mix}$ ), water temperature ( $W_{temp}$ ), wind speed ( $W_{speed}$ ), TP, TN, Chl-*a*, water color (WC), DOC, CDOM, photosynthetically active radiation (PAR), light attenuation ( $k_d$ ), water level (WL), and daily rainfall on gross primary production (GPP), ecosystem respiration (R), and net ecosystem production (NEP) in TFL during dry periods. Only the models with lowest AIC value are shown.

State variable	Regression model	Forcing variable	Partial correlation coefficient	Partial	Overall $r^2$	$p$	AIC	
GPP	$1.31 \times TN - 1.0 \times \text{Chl-}a - 0.51 \times \text{Rainfall}$				0.997	0.041	52.605	
		Total Nitrogen	0.999	0.806				0.024
		Algal biomass	-0.998	0.868				0.035
		Daily rainfall	-0.998	0.382				0.037
R	$-1.09 \times GPP$	Gross primary production	-0.815	0.479	0.458	0.162	62.194	
NEP	$1.16 \times \text{Chl-}a - 0.62 \times k_d - 0.45 \times \text{PAR} + 0.45 \times GPP$				0.951	0.008	21.981	
		Algal biomass	0.973	0.724				
		Light attenuation	-0.924	0.684				0.025
		Photosynthetically active radiation	-0.937	0.252				0.019
		Gross primary production	-0.897	0.564				0.039

lakes worldwide (López-Archilla et al. 2004, Tsai et al. 2008, Alfonso et al. 2014, Gaeta et al. 2014) because of their higher surface area to volume ratio compared to larger lakes (Schindler et al. 1990, Adrian et al. 2009). Our research in a shallow subtropical mesotrophic lake

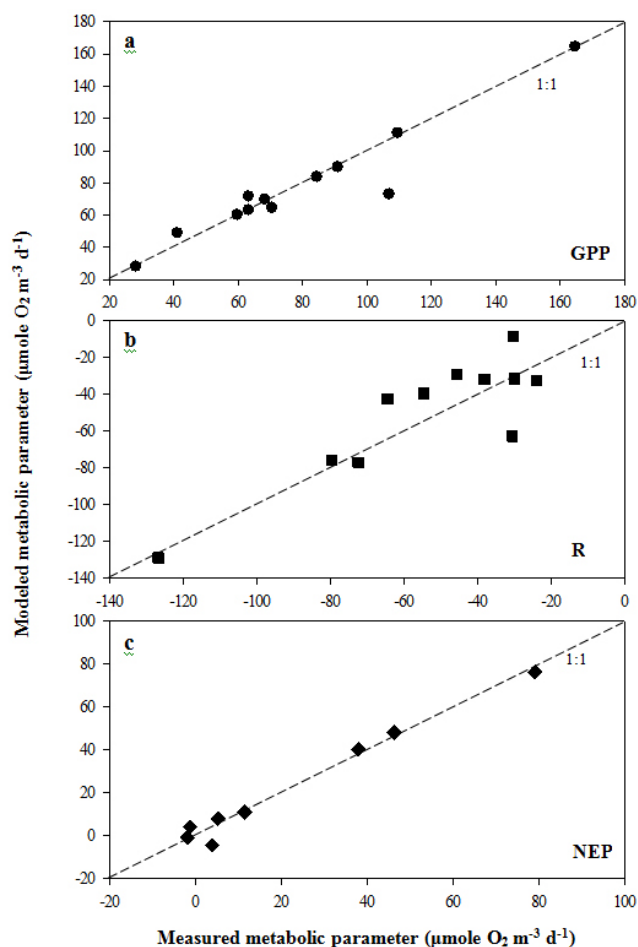
indicated that decreases in water level due to lack of winter and spring monsoons concentrated waterborne nutrients, reduced the depth of upper mixed layer, and stimulated algal biomass, thus playing a key role in the rapid alteration of the metabolic status of the lake.



**Fig. 5.** Relationship between daily NEP ( $\mu\text{mole O}_2 \text{ m}^{-3} \text{ d}^{-1}$ ) and the relative water level (m) during dry periods in the 2 study years (Nov 2009–May 2010 and Nov 2010–April 2011). The lines show the fits of the polynomial, inverse second-order model. Data number ( $n$ ) and coefficient of determination ( $r^2$ ) are 212 and 0.43, and 173 and 0.44 in these 2 study years, respectively.



To our knowledge, this is the first daily-scale report of an alternation of ecosystem metabolism and trophic status caused by drought-induced decreases in water levels. Although data for normal monsoon years were not available, our previous studies in nearby oligotrophic Yuan-Yang Lake (YYL) showed that, in normal monsoon years (2004–2007), seasonal trends of GPP and R dropped from autumn peaks, remained low in winter, and then rapidly built up in spring. (Tsai et al. 2008; 2011). TFL and YYL share similar geographical and morphological attributes, such as latitude and altitude, spatial scales, watershed vegetation, and meteorological conditions. TFL and YYL showed similar metabolic trends in summer and autumn; however, under drought conditions, GPP and R in TFL were both stimulated in winter but then declined quickly and remained low in the spring, contrary to the patterns observed in a normal year at YYL (Fig. 4a). Our data are consistent with the following potential processes underlying these shifts.



**Fig. 6.** Scatter plots of measured pelagic GPP, R, NEP and their corresponding estimations predicted by the stepwise regression models (Table 2).

## Nutrients as a driver of altered metabolism

The stimulation of autotrophy in TFL (Fig. 2a and 4b) in the absence of monsoons seems to be driven by concentrations of dissolved nutrients during drier periods, causing extensive algal growth and increased GPP and R at the outset (Fig. 3a and 4a). Abrupt collapses of GPP and R occurred, coincident with shallower mixing depths and massive algal biomass development (Chl-*a*) when the water level dropped to the lowest point (~0.03–0.12 m total; Fig. 2a and b, 3c, and 4a). Results of correlation matrix and regression analyses suggested that increased nutrient concentrations during this time are primary drivers of massive algal blooms and increased GPP more than other factors such as warming temperature (Table 1 and 2), although both clearly play a role in bloom development (Rigosi et al. 2015). Brookes and Carey (2011) demonstrated that increased nutrients could strengthen thermal stratification without directly increasing water temperature. Increases in algal biomass induced by higher nutrients enhanced surface absorption of solar radiation, leading to stronger lake stratification, thus facilitating the growth of certain algal species (e.g., cyanobacteria) favored by increased temperature and stronger thermal stratification. Such effects are more apparent in warmer than in colder lakes (Jones et al. 2005).

## Stratification as a driver of altered metabolism

Lake autotrophy occurred (Mar 2010 and Feb 2011), accompanied by the rapid shrinking of mixing depth (Fig. 2b and 4b), suggesting that the water levels and the mixing regime of the lake could play a key role for the autotrophy of TFL (Fig. 2b and 5). Primary production and respiration of lakes tend to increase with depth during periods of stronger stratification in shallow lakes because of development of a deep chlorophyll maximum, sinking of particulate organic matter, and generally higher nutrients found in deeper layers (Sadro et al. 2011). For shallow lakes with clear water like TFL (water color 0.53–5.95; mean  $\pm$  standard error =  $2.12 \pm 0.29$  [ $a_{400}$  in  $\text{m}^{-1}$ ]; Fig. 3b), the euphotic zone often extends below the epilimnion (i.e., the mixing depth; Fig. 2b), implying that light penetration is sufficient to support benthic primary production (Obrador et al. 2014). Those benthic zones are often shallow enough to support a major part of the total primary production in the lake (Vadeboncoeur et al. 2008, Van de Bogert et al. 2012). In this case, a significant fraction of gross primary production of the lake may be unaccounted for by focusing solely on epilimnetic layer, which might be another explanation for the collapse of measured offshore GPP when the water level was lowest during the middle of those unpredicted dry periods.

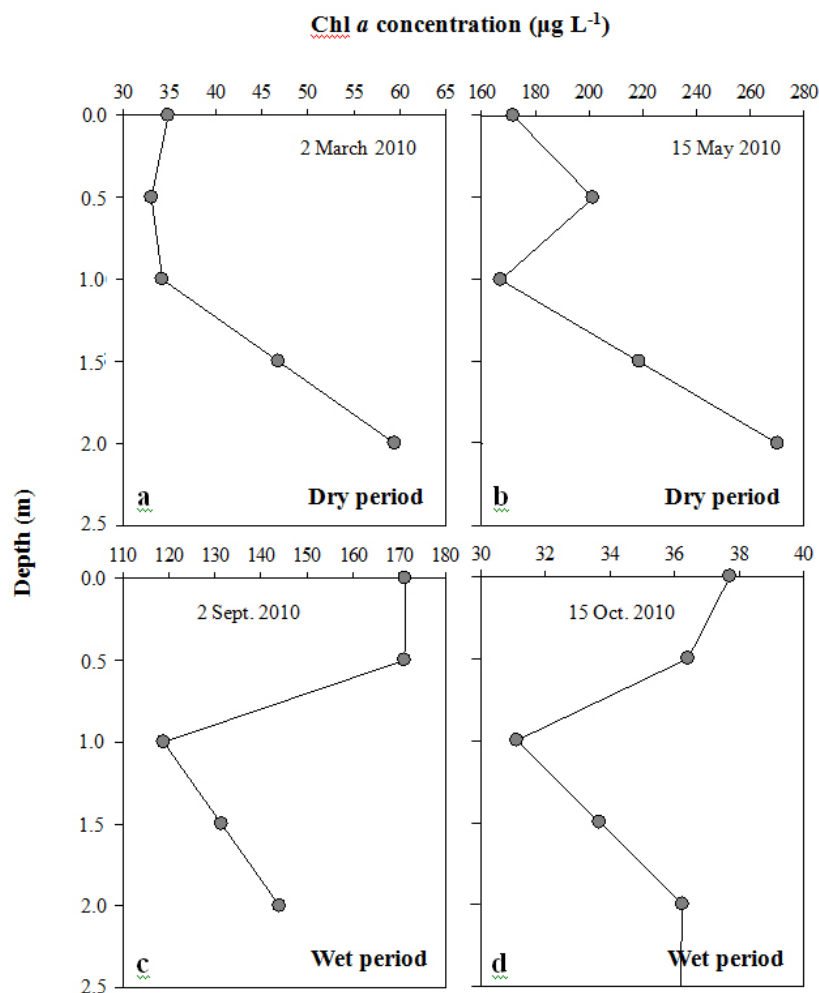
Abundant algal biomass (as Chl-*a*) in TFL was trapped in the hypolimnion during the drier period due to stronger stratification than during the wet period (Fig. 7a and b). We found that wind speed played a key role for temporally increasing the pelagic nutrients (TN) and algal biomass (Chl-*a*) and stimulated the GPP and NEP in dry conditions (Fig. 2b and 4, Table 1). Windy conditions likely changed stratification patterns, favoring internal nutrient loading and suspension of benthic microalgae, which contributed to epilimnetic algal biomass and lake primary production (Jones et al. 2006, 2009b, van der Molen and Perissinotto 2011). These conditions would also explain the higher rates of GPP and R observed when temporary lake mixing occurred during dry periods with strong winds (Fig. 2b and 4a).

Although the assessment of spatial metabolic differences between habitats was beyond the scope of this study, we suggest that horizontal and vertical spatial variability in ecosystem metabolism should be assessed in future studies. For example, the relative contribution of

littoral/pelagic zones, and/or epilimnion/hypolimnion, habitats to whole-lake metabolism is understudied, particularly in clear, small, and shallow lakes with larger littoral zones like TFL (Van de Bogart et al. 2007, Staehr et al. 2010, Sadro et al. 2011).

### R–GPP relationship during the absence of monsoons

We found a lower strength and pattern of the coupling between R and GPP during dry periods ( $r^2 = 0.48$ , slope = 0.81) than during wet periods ( $r^2 = 0.72$ , slope = 0.99, Fig. 8a and b). Ecosystem respiration was generally tightly coupled to GPP because allochthonous material was usually refractory to biological uptake within lakes (McKnight et al. 2001), and autotrophic and heterotrophic communities cannot collectively respire more autochthonous organic materials than the autotrophic organisms produce (Solomon et al. 2013). More than 80% of GPP can typically immediately be respired by heterotrophic



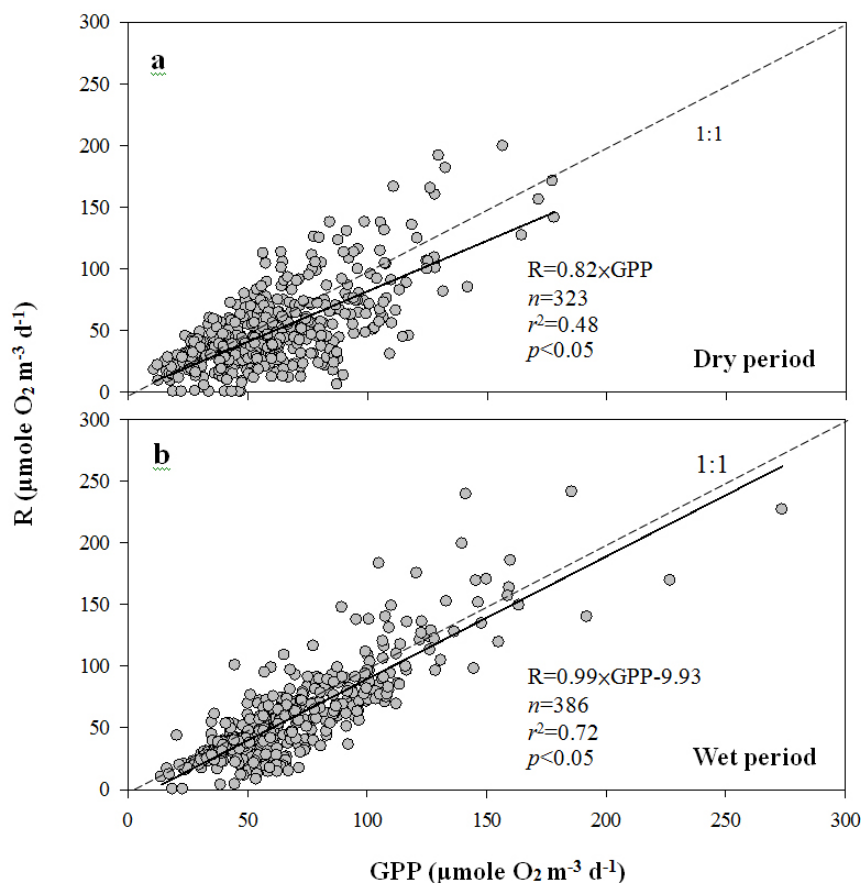
**Fig. 7.** Vertical profiles of Chl-*a* concentration at TFL selected from typical dates in the (a and b) dry and (c and d) wet periods.

processes (Toming et al. 2013), and the slope of the R–GPP relationship is generally high (slope of R on GPP = 0.8–1.0) in oligotrophic and dystrophic lakes (TP concentrations = 20–40  $\mu\text{g L}^{-1}$ ; Solomon et al. 2013). The dependence between R and GPP, however, decreases substantially with increasing productivity in lakes because substantial primary production can quickly outpace respiratory processing and lead to increased sedimentation or export to adjacent ecosystems (Caraco and Cole 2004, Solomon et al. 2013). We found that the absence of winter and spring monsoons pushed the study lake (TFL) from an oligotrophic or mesotrophic lake (TP = 7.3–12.2  $\mu\text{g L}^{-1}$ ) at the end of wet periods toward a highly eutrophic ecosystem (TP up to 69.8  $\mu\text{g L}^{-1}$ ) due to the concentration of dissolved nutrients during drier periods (Fig. 2a and 3a). Lower  $r^2$  values during dry periods (Fig. 7a) provide further evidence of a decoupling of R and GPP, implying that ecosystem respiration might also be supported by inputs of other organic materials, such as stored autochthonous organic matter in the sediments or allochthonous terrestrial organic material, instead of autochthonous production (Lovett et al. 2006). We found that the

autotrophic nature of TFL resulted from a greater decline in rates of ecosystem respiration instead of increased GPP during the dry period. Generally, covariance in R–GPP was high (slope of R on GPP = 0.82–0.99) throughout this study (Fig. 8a and b). Thus, the decrease in primary production accompanied by lower loads of allochthonous terrestrial materials in the middle of droughts should decrease heterotrophy or increase autotrophy via suppression of R.

## Conclusions

Our study provides insights into the metabolic response of lakes to abrupt changes in meteorological forcing. TFL rapidly shifted from a heterotrophic to a highly autotrophic ecosystem in the absence of spring and summer monsoons. The metabolic response of this lake was primarily triggered by water level decline, which induced changes in nutrient concentrations and lake physics (shallower mixing layer). This abrupt shift in trophic status may occur more frequently with a changing climate because of the predicted increase in extreme events and



**Fig. 8.** Scatter plots of gross primary production (GPP) to corresponding ecosystem respiration (R) in (a) dry periods and (b) wet periods. Data analyzed were performed on all available data (data number,  $n$ ). Bold solid lines represent the regression models; dash lines are the 1:1 lines

the potential for stronger lake stratification under higher air temperatures (Winder and Schindler 2004). Controlling nutrient inputs could play a critical role in increasing the resilience of aquatic ecosystem metabolism to climate changes. Future studies might profitably focus on experimental manipulations to more explicitly test the mechanisms driving the rapid shift in trophic status in response to predictions of drier and warmer climatic conditions in this region (Chou et al. 2013).

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