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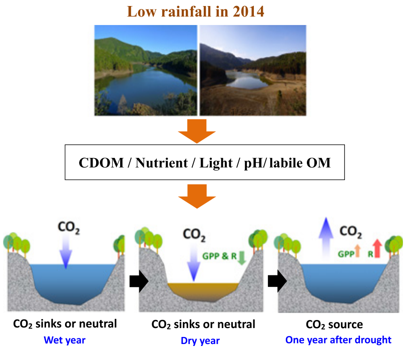
HIGHLIGHTS

- Effects of droughts on inter-annual C fluxes were studied in subtropical lakes.
- Multi-parameter probes were deployed to record key parameters over five years.
- Lakes shifted from a C sink in dry year to C source in subsequent normal year.
- C fluxes were more responsive to droughts in the mesotrophic colored lake.
- Terrestrial DOM serves as a driver for the response of lakes to droughts.

GRAPHICAL ABSTRACT



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ABSTRACT

Lentic ecosystems are important agents of local and global carbon cycling, but their contribution varies along gradients of dissolved organic matter (DOM) and productivity. We investigated how contrasting summer and autumn precipitation can shape annual and inter-annual variation in ecosystem carbon (C) flux (gross primary production (GPP), ecosystem respiration (ER), and CO_2 efflux) in two subtropical lakes differing substantially in trophic state and water color. Instrumented buoys recorded time series of free-water DO, terrestrial DOM (tDOM), chlorophyll *a*, water temperature profiles, and meteorological measurements over five years (2009–2011 and 2014–2015). Reduced precipitation caused immediate and prolonged effects on C flux in both lakes. During the drought year (2014) GPP and ER declined by 60 to 80% and both lakes were either CO_2 sinks or neutral. In the subsequent wet year (2015), GPP and ER increased by 40 to 110%, and both lakes shifted to strong net CO_2 emitters. Higher ecosystem R resulted from larger GPP while higher tDOM contributed to a dramatic increase in dissolved inorganic carbon, which intensified CO_2 emission in both lakes. C flux was more responsive in the clear mesotrophic lake, declining by approximately 40% in the cumulative GPP and ER, and

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Trophic status

increasing by >400% in CO_2 efflux whereas changes in the oligotrophic colored lake were more modest (approximately 30% and 300% for metabolic declines and efflux increases, respectively). Temporal variation and magnitude of C flux were governed by tDOM-mediated changes in epilimnetic nutrient levels and hypolimnetic light availability. This study demonstrated terrestrial loads of DOM strongly influence the inter-annual response and sensitivity of ecosystem C flux to variation in inter-annual precipitation. Our findings have important implications for predicting the trend, magnitude, duration, and sensitivity of the response of C flux in subtropical lakes/reservoirs to future changes in precipitation patterns under altered climatic conditions.

1. Introduction

Freshwater ecosystems are considered sentinels of climate/environmental change because of rapid response to alterations in precipitation, solar irradiance, temperature, hydrology, and organic matter input (Malone et al., 2013; Williamson et al., 2008, 2009). Most lakes across the globe receive substantial loads of terrestrial organic material and are important contributors to local and global carbon cycling, processing, emission and storage (Brett et al., 2017; Hanson et al., 2015; Solomon et al., 2015). Small lakes, because of generally shallower depths, higher sediment loads, larger shoreline to water volume ratios and frequent mixing, often show higher CO_2 and CH_4 emissions than large lakes (Duarte and Prairie, 2005; Holgerson and Raymond, 2016). The small lakes typical of subtropical areas experience monsoons or typhoons that deliver intense rain events and thus promote mixing as well (Page et al., 2011; Tsai et al., 2008, 2011). Subtropical ecosystems will likely experience alterations in the intensity and frequency of precipitation with climate change (Burls and Fedorov, 2017; Eccles et al., 2019). Altered precipitation will change both surface runoff, and inputs of terrestrial dissolved organic matter (tDOM) to these ecosystems, thereby modifying their hydrology, temperature profiles, light regimes, and biochemical processes (Houser, 2006; Paerl and Huisman, 2008; Sowerby et al., 2010). Potentially these modifications will modify the role of freshwater ecosystems in global and regional carbon cycling (Hanson et al., 2015; Kerr, 2007; Solomon et al., 2015).

The dynamics of carbon (C) flux within a lake ecosystem is often described by gross primary production (GPP), and ecosystem respiration (ER) as well as external carbon inputs, especially after rain events. GPP and ER are fundamental ecosystem processes, which describe organic carbon fixation by autotrophs and consumption by higher trophic levels within an ecosystem, respectively. Their balance (i.e., net ecosystem production, NEP) provides a measure of trophic status as well as an indication of cross-ecosystem connectivity to natural and human disturbances (Kortelainen et al., 2006; S.E. Jones et al., 2009; Staehr et al., 2010; Hamdan et al., 2018). In addition, NEP determines whether the ecosystem is a net source or sink of atmospheric carbon (Bortolotti et al., 2016; Christensen et al., 2013; Hanson et al., 2003; Jane and Rose, 2018; Kortelainen et al., 2006). Being the lowest point in the landscape, lakes receive substantial organic material input from terrestrial sources by precipitation runoff, which controls organic matter turnover and carbon cycling (Kayler et al., 2019; Mehner et al., 2016). The chromophoric component of external dissolved organic matter (CDOM) is mostly lignin material from vascular plants, and is used as a proxy for tDOM inputs to aquatic systems (Fichot et al., 2016). These materials can influence the availability of underwater light, nutrients, primary production/respiration, oxygen and water column thermal structure in aquatic systems (Gu and Wyatt, 2016; Thrane et al., 2014; Williamson et al., 2009). Consequently, tDOM may interact with variable precipitation to influence structure and function of lakes (Brett et al., 2017; Williamson et al., 1999).

Previous studies conducted in temperate or boreal lakes indicate that the effects of tDOM loading on aquatic ecosystem C flux are complex. Evidence shows that moderate increases in tDOM can enhance whole lake primary production by releasing bound nutrients (Frey and Smith, 2005; Pagano et al., 2014). This response is expected in clear oligotrophic lakes (Kissman et al., 2013; Klug, 2002; Meili, 1992; Seekell et al., 2015) where greater DOM promotes pelagic production (Brett et al., 2017; Jansson et al., 2012; Lapierre et al., 2013; Nydahl et al., 2019; Seekell et al., 2015; Williamson et al., 1999). Across all lakes, however, it is difficult to predict the response of C flux to precipitation by relying only on tDOM loading as an indicator of nutrient, organic matter and light regimes. Contrasting effects of tDOM loads on C flux may show lake-specific patterns influenced by trophic state and other features, including water color (Jones et al., 2016; Seekell et al., 2015; Williamson et al., 1999).

Compared with their temperate counterparts, subtropical lakes in East Asia are relatively small, shallow, and often surrounded by steep mountainous terrain. Hydrological conditions including precipitation, water level/volume, mixing regime and residence time display clear seasonal variation and large inter-annual differences as a result of the Asian monsoons and typhoons (Tsai et al., 2008, 2016; Wang et al., 2011). Previously, few studies have investigated C flux in subtropical lakes in response to variation in annual precipitation (Tsai et al., 2008, 2011, 2016; Wang et al., 2011; Xing et al., 2005), especially over timescales of seasons and years where differential responses to climatic events and watershed characteristics can occur. Such insight is needed to assess and predict long-term change and the sensitivity of subtropical lakes to climatic and other anthropogenic disturbances (Brighenti et al., 2015; Staehr et al., 2012).

Herein, we investigate whether the effect of altered precipitation on annual and inter-annual lake C flux is mediated by tDOM input, via changes in epilimnetic nutrients (total phosphorus, TP and total nitrogen, TN), light availability and labile organic carbon, or their interaction, in two contrasting natural subalpine lakes that differ substantially in trophic status and water color. Our primary goals were: (1) to investigate the response of annual and inter-annual C flux (GPP, ER, net ecosystem production -NEP- and CO_2 efflux) to differing patterns of annual rainfall in both lakes; (2) to compare the response sensitivities of C flux between these lakes; and (3) to test the hypothesis that tDOM measurably influences observed annual and inter-annual patterns of C flux and determines underlying mechanisms in these lakes.

2. Materials and methods

2.1. Study site

Yuan Yang Lake (YYL) is a small (3.6 ha), shallow (maximum depth = 4.5 m, mean depth = 1.5 m) lake located in the north-central mountains of Taiwan (24°35′N, 15121°24′E, elevation 1730 m a.s.l.; Fig. 1). YYL has one defined inlet and one outlet, and is a colored oligotrophic lake with an average dissolved organic carbon (DOC) concentration of 6.1 mg L^{-1}, mean pH of 5.9, and total phosphorus (TP) ranged from 3.4 to 6.7 μg L^{-1} (Tsai et al., 2008). Tsui-Fen Lake (TFL) is a 25 ha subalpine lake (elevation 1820 m a.s.l., maximum depth = 12 m, mean depth = 4.2 m) in northeastern Taiwan (24°30′N, 121°37′E; Fig. 1). TFL is a natural mesotrophic to eutrophic lake (TP ranged from 10 to 70 μg L^{-1}; mean DOC = 2.9 mg L^{-1}; mean pH = 5.9) with one major inlet and no surface outlet. Several storm water inlets feed these lakes during medium to heavy rainfall but are not active during dry periods.

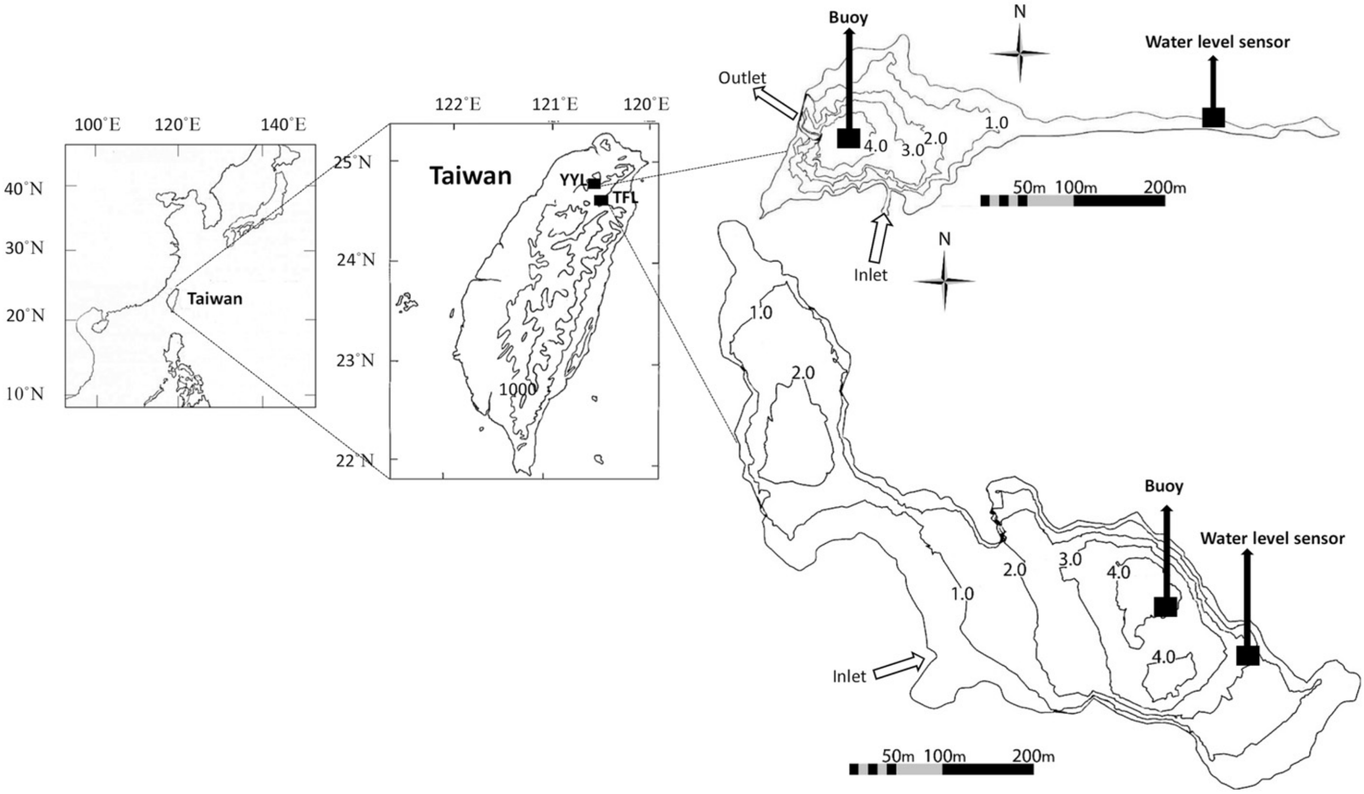

Fig. 1. Location map of Taiwan with an enlarged bathymetric map of Tsui-Fen Lake (TFL) and Yuan-Yang Lake (YYL) drawn with 1, 2, 3, and 4 m water depth contour lines. Buoy and water level sensor deployment sites in the two study lakes are shown.

YYL and TFL have similar geology and climate and are located within about 14 km. Annual mean temperature is approximately 13.4 °C (monthly averages range from 4.0 to 21.8 °C), and annual precipitation exceeds 4 m in wet years. The lakes experience frequent monsoon rainstorms and one to seven typhoons each year in spring, summer and during an autumn rainy season, when >50% of annual precipitation may occur. Watershed characteristics, however, differ: YYL is surrounded by pristine old-growth cypress forest, while TFL is surrounded by secondary cypress forest that was replanted five decades ago after selective logging. In addition, drainage patterns differ. A creek regulates water level and surface outflow in YYL, but TFL mostly relies on permeation or leakage from bedrock drainage, which effects limnological processes. Both YYL and TFL were designated long-term ecological study sites by the Ministry of Science and Technology, Taiwan, in 1990, and each joined the Global Lake Ecological Observatory Network (GLEON) as site members in 2004 and 2009, respectively.

2.2. Data collection and field measurements

The study was conducted from 2009 to 2015 (excluding years 2012 and 2013). This period was characterized by inter-annual differences in precipitation. In 2014 (the dry year) total annual precipitation was <40% of the average of the other four wet years, because of no typhoon, or major summer and autumn rainstorms occurred. The four wet years: 2009, 2010, 2011 and 2015, had typical seasonal precipitation patterns dominated by prevalent summer and autumn typhoons or rainstorms.

2.3. Environmental and limnological data

We deployed buoys equipped with multiple sondes over the deepest point of each lake to collect limnological and meteorological data, including surface pelagic dissolved oxygen (DO) concentration, water temperature, pH, Chlorophyll *a* (Chl-*a*), CDOM, and wind speed (Fig. 1). These data were recorded every hour over the entire course of the study. Daily values were computed as the mean of hourly data, and weekly means and standard deviations were calculated from daily values, respectively. Surface DO concentrations were measured at 0.25 m by a sonde (600-XLM, YSI, Yellow Springs, OH, USA) fitted with a rapid pulse oxygen temperature electrode (6562 Rapid Pulse Dissolved Oxygen Sensor, YSI, Yellow Springs, OH, USA). Oxygen probes were calibrated in air-saturated water, and the membrane was changed monthly. Additional calibration was performed by measuring DO concentration and pH at 0, 0.25, 0.5, 1, 2, 3.5 m with a portable water-quality multiprobe (Hydrolab DS5, Hach Environmental, Loveland, CO, USA) to eliminate the potential bias induced by drift of in situ sonde between each monthly visit. A thermistor chain (Templine, Apprise Technologies, Duluth, MN, USA) recorded vertical water temperature profiles at 0.5 m increments. A submersible fluorometer (C3, Turner Designs, San Jose, CA, USA) was used to measure CDOM and Chl-*a* levels at a depth of 0.25 m near the buoy site, using the same logging interval and maintenance schedule as the DO sonde. The excitation and emission wavelength of the C3 submersible fluorometer represents to the content of terrestrial humic-like substances in the water column (Lee et al., 2015; Mladenov et al., 2018). Raw CDOM measurements were corrected by using temperature readings from the sonde according to Watras et al. (2011). Wind speed was measured 2 m above the lake by an anemometer (Model 03001, R.M. Young, Traverse, MI, USA). Relative water level variation was characterized using a submersible pressure transmitter (PS 9800(1), Instrumentation Northwest, Kirkland, WA, USA) set in the lakeshore (Fig. 1). Weather stations located approximately 1 km from the lakeshore measured daily precipitation, air temperature, and photosynthetically active radiation (PAR) using a tipping bucket rain gauge, temperature probe (41382VC; R.M. Young), and a PAR sensor (LI-190, LI-COR, Lincoln, NE, U.S.A.), respectively.

2.4. Limnological samples

Three to five replicate water samples were collected at 0.25 m near the buoy site at noon during monthly visits; these collections were scheduled during calm conditions at least 7 days following rainstorm events (Tsai et al., 2011). A portable hand pump with inline filters (Whatman, 47 mm GF/F, nominal pore size 0.7 μm, Maidstone, Kent, UK) was used to collect DOC and dissolved inorganic carbon (DIC) samples. Samples were stored in precombusted amber borosilicate vials with Teflon-coated septa. Sample vials were chilled on ice no longer than 3 days after collection until phosphoric acid and persulfate digestion, which was followed by analysis with a Total Organic Carbon analyzer (Model 1030W, O.I. Analytical, College Station, TX, USA). Samples of Chl-*a* were used to calibrate sensor data and were collected by filtering 200 mL of surface lake water through filters (Whatman, 47 mm GF/F, nominal pore size 0.7 μm, Maidstone, Kent, UK). Filters were stored in the dark at 4 °C until Chl-*a* was extracted with methanol and measured using a Portable Fluorometer (10-AU-005-CE; Turner Designs, Sunnyvale). The lower limit of detection for Chl-*a* was 0.05 μg L^{-1}. Total phosphorus (TP) and total nitrogen (TN) concentrations were analyzed in unfiltered surface water samples and were quantified according to the American Public Health Association (1998).

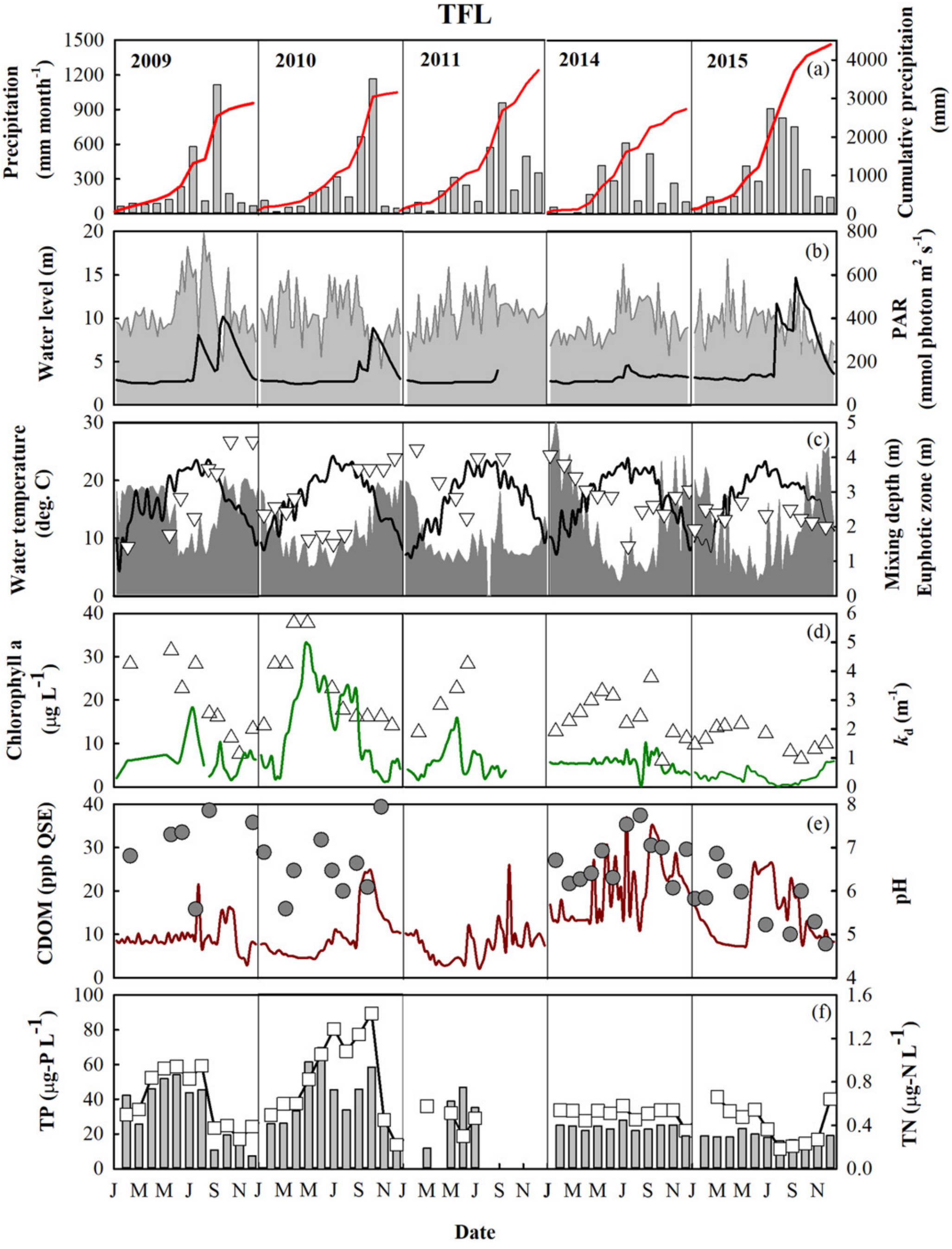

Fig. 2. Temporal variation in (a) monthly precipitation (bars) and cumulative precipitation, (b) relative water level (black line) and photosynthetically active radiation (PAR), (c) water temperature (solid black line), euphotic depth (open inverse triangle) and mixing depth, (d) chlorophyll *a* and light attenuation rate (k_d, open triangle), (e) colored dissolved organic matter (CDOM - red line) and pH, and (f) total phosphorous (TP - bars), and total nitrogen in Tsui-Fen Lake (TFL). Data of euphotic depth, k_d, pH, TP and TN are shown as monthly means, while all other data are expressed as weekly means.

2.5. Data processing and analysis

2.5.1. Metabolic parameters and CO_2 flux

Diurnal DO variation in aquatic ecosystems was dominated by both biological flux (GPP and ER) and water-atmospheric diffusion (F_{atm}) (Hoellein et al., 2013; Odum, 1956). We used open-water diel DO curves measured by sensors to quantify annual and inter-annual dynamics of GPP and ER (Staehr et al., 2010, 2012). Daily values of epilimnetic GPP and ER were estimated using the metabolism model of Cole et al. (2000) and Staehr et al. (2010, 2012) as dO_2/dt = GPP-ER + F_{atm}. R was estimated as the atmospheric diffusion-corrected changes in hourly DO concentrations during nighttime, while GPP was estimated from the hourly increase in DO during daytime, with flux corrected by assuming equal ER during day and night (Cole et al., 2000; Hanson et al., 2003). NEP was the difference between the daily values of GPP and ER. Changes in DO resulting from other abiotic processes (photochemical) and the entrainment of anoxic water from the hypolimnetic layer during high-wind and heavy-rainfall conditions were not included (Cole et al., 2000; Tsai et al., 2008). Oxygen flux between the lake and the atmosphere (F_{atm}) was calculated as $F_{\text{atm}} = k(O_{2\text{sat}}–O_2)/Z$ (μmol m^{-3} h^{-1})

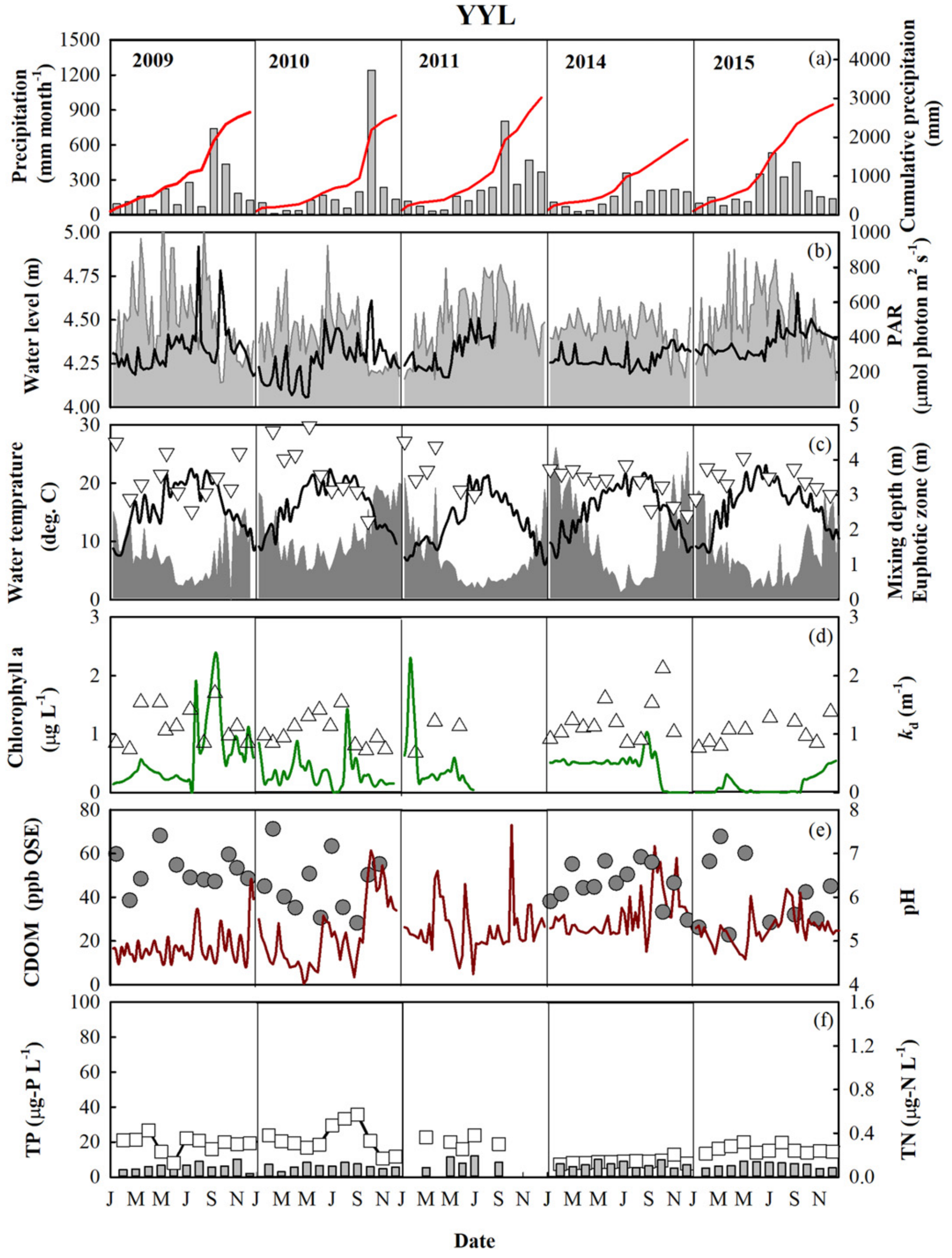

Fig. 3. Temporal variation in (a) monthly precipitation (bars) and cumulative precipitation, (b) relative water level (black line) and photosynthetically active radiation (PAR), (c) water temperature (solid black line), euphotic depth (open inverse triangle) and mixing depth, (d) chlorophyll *a* and light attenuation rate (k_d, open triangle), (e) colored dissolved organic matter (CDOM - red line) and pH, and (f) total phosphorous (TP - bars), and total nitrogen in Yuan Yang Lake (YYL).

(Cole et al., 2000), where Z is the depth of the epilimnetic mixing layer (m) as determined by continuous measurement of water temperature profiles. Daily values of Z were estimated as the depth at which the temperature gradient exceeded 1 °C m^{-1} (Staehr et al., 2010, 2012). *k* is the transfer coefficient (m h^{-1}) for oxygen. *k* was estimated from the empirical model that describes the correlation between the gas transfer velocity (*k*600, *k* for a Schmidt number of 600), wind speed, water temperature and the Schmidt number of oxygen (Wanninkholf, 1992). *k*600 was calculated as a function of wind speed (Cole and Caraco, 1998). $O_2(t)$ and $O_{2sat}(t)$ refer to the measured DO concentration and the saturation concentration of oxygen (mg L^{-1}) at *t* °C, respectively. O_{2sat} was determined by water temperature and altitude using the empirical equation given by Dodds (2002).

2.5.2. DIC and CO_2 efflux

CO_2 concentration in water samples was estimated from monthly measurements of DIC and pH, corrected for water temperature (Tonetta et al., 2017; Wetzel and Likens, 2000). Waterborne CO_2 was estimated from daytime samples (noon) to avoid overestimating CO_2 efflux because of CO_2 reduction due to primary production. Saturation concentrations were calculated from the partial pressure of CO_2 in the atmosphere (P_{CO2}, atm) and Henry's constant of CO_2 transfer between the atmosphere and water (K_H, mole L^{-1} atm^{-1}), with appropriate adjustments made for effects of temperature and altitude (Davidson et al., 2010). Daily net flux of CO_2 between the atmosphere and lakes can reflect the influx or efflux of under-saturated and over-saturated water respectively. The flux estimate was calculated according to Fick's law, with the effect of local wind speed and air temperature factored in (Ojala et al., 2011).

2.5.3. Light attenuation

Vertical light attenuation (k_d) was estimated by optimal fitting of the exponential light attenuation model to underwater profiles, which were measured monthly at 0.5 m increments at noon using a portable PAR sensor (LI-COR, LI-192). The euphotic zone (Z_{eu}, m) was defined as the depth of 1% of the incident light ($I(Z_{eu}) = 0.01 \times I_0$, where I_0 is surface PAR, Dodds, 2002).

2.6. Statistical analysis

Weekly averages of environmental and limnological data were calculated from daily instrument measurements (e.g. GPP/ER/NEP, CDOM, Chl-*a*, wind speeds, rainfall, and mixing depth) for the week of the monthly water sampling (e.g. TP, TN, DOC, DIC, Chl-*a* and water color). We used the Shapiro-Wilks test to measure normality; if necessary, variables were log-transformed to normalize data distribution, ensure homogeneity, and linearize relationships. One-way analysis of variance (ANOVA) with a Tukey's post hoc test was used to evaluate

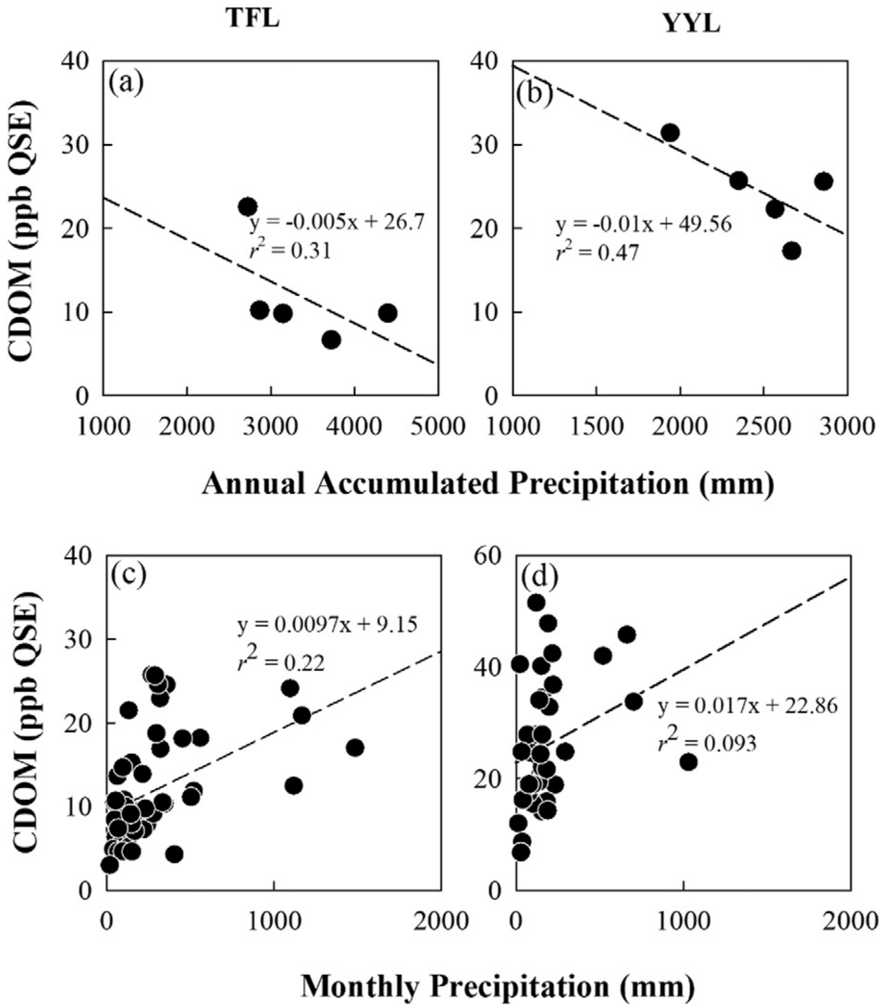

Fig. 4. The linear relationships between (a, b) annual accumulated precipitation and mean annual colored dissolved organic matter (CDOM) concentration, and (c, d) monthly means of CDOM and monthly precipitation through the entire study period (July 2009 to December 2015) in the two study lakes. QSE stands for the quinine sulfate equivalent.

differences in environmental, limnological and C-flux variables (GPP, ER, NEP, and CO_2 efflux) between seasons and years in the two study lakes. Pearson correlation matrices were employed to evaluate the relationships between the four C flux variables and potential environmental and limnological variables. Correlations were used to develop empirical models for the effects of lower annual precipitation on annual and inter-annual changes in C flux. Strongly correlated forcing variables ($r < -0.70$ or $r > 0.70$) were removed in advance to avoid co-variance. Forward stepwise multiple linear regression analysis was then applied to determine key forcing variables for the inter-annual variation in CO_2 flux, and the seasonal dynamics of GPP, ER, and CO_2 flux in the dry year (January 2014–December 2015) in TFL and YYL, respectively. Only variables showing significant relationships ($p < 0.05$) with C-flux variables were included in the candidate regression models. All possible models were evaluated by using Akaike's Information Criterion (AIC) to identify the most parsimonious solution (Burnham and Anderson, 2004). Statistical analyses were performed using Statistica® software (StatSoft, Tulsa, OK, USA).

3. Results

3.1. Meteorological conditions, CDOM, and limnological variables

Inter-annual variation in precipitation between lakes was large, ranging from 2700 to 4500 mm in TFL and 1800–3000 mm in YYL (Figs. 2a, 3a). Only one small typhoon passed by the study site during the dry year (2014), hence the total accumulated precipitation in the rainy season (June–October) was roughly 38% and 31% lower in TFL and YYL, respectively, relative to the rainy season of other years (2009, 2010, 2011, and 2015). Seasonal cumulative precipitation in winter and spring (November–May) did not differ between dry and wet years (YYL: $F = 62.93$, $p < 0.01$; TFL: $F = 9.76$, $p = 0.45$). Lake water levels indicate rapid seasonal and inter-annual variation in intensity and frequency of precipitation in the two study lakes (Figs. 2b, 3b). Weekly relative water levels ranged between 2.45 and 14.67 m in TFL and 4.05–4.98 m in YYL in wet years. In the dry year, the range was 3.21–4.49 m in TFL and 4.16–4.35 m in YYL (Figs. 2b, 3b).

Seasonal and inter-annual trends in water temperature (W_{temp}) and PAR were similar, with no significant differences between lakes ($p > 0.05$, Figs. 2b–c, 3b–c). The difference between the maximum and minimum water temperature were 7 and 13 °C in YYL and 18 and 23 °C, respectively in TFL (Figs. 2c, 3c). Weekly mean mixing depths (Z_{mix}) were 0.27/1.78 m in summer, 0.83/2.78 m in autumn, 0.94/4.33 m in winter, and 2.05/5.07 m in spring for YYL/TFL respectively (Figs. 2c, 3c), and showed typical temporal patterns corresponding to seasonal water temperatures. Monthly and inter-annual variation of CDOM (shown in weekly value) was assessed to determine how values relate to precipitation patterns, and are related with conspicuous variation in seasonal and inter-annual GPP, ER, NEP, and CO_2 efflux. At a monthly scale, CDOM levels generally increased concomitantly with precipitation in both rainy (May–October or November) and dry seasons (January–May), especially in TFL (Fig. 4c–d and Table 1).

Results show negative regression slopes between annual cumulative precipitation and mean annual CDOM (slope $= -0.005$-0.01, $r^2 = 0.31$–0.47) (Fig. 4a–b). TP was negatively correlated with CDOM in both lakes (Fig. 5a–b; $r = -0.43$ and -0.5, Table 1). Nutrient levels were lower in the dry year than the wet years. Inter-annual dynamics of Chl-*a* were positively correlated with TP ($r = 0.92$, $p < 0.01$, Table 1) and negatively correlated with CDOM ($r = -0.42$ and -0.45, $p = 0.05$–0.1, Table 1) in both lakes. Compared to the wet years (2009, 2010 and 2011), Chl-*a* levels were lower during and after the dry year (2014–2015). Consistent with expectations, k_d values were correlated with CDOM in both lakes (Fig. 5c–d). As a result, the amount of light available to support hypolimnetic primary production (i.e. Z_{eu}/

Table 1
Correlation matrix among GPP, ER, NEP, CO_2 efflux (ef), and relative environmental and limnological variables: weekly rainfall, wind speed (W_{speed}), mixing depth (Z_{mix}), water temperature (W_{temp}), water level (WL), light attenuation (k_d), CDOM, pH, TP, TN, Chl-*a*, and DOC, for the entire study duration (January 2009–December 2015) in TFL and YYL. Green, yellow, and orange represents $p = 0.05$–0.1, $p = 0.01$–0.05, and $p < 0.01$, respectively.

Lake	Variables	**ER**	**NEP**	**CO_2 ef**	**Rain**	**W_{speed}**	**Z_{mix}**	**W_{temp}**	**WL**	**k_d**	**CDOM**	**pH**	**TP**	**TN**	**Chl-*a***	**DOC**	**DIC**
TFL	**GPP**	-0.86	0.04	−0.01	0.25	0.02	−0.45	0.52	−0.38	−0.49	−0.14	0.04	0.51	0.53	0.52	0.08	−0.09
	ER		0.47	−0.05	−0.09	0.05	0.39	−0.29	0.30	0.30	0.05	−0.02	−0.24	−0.24	−0.17	0.06	−0.05
	NEP			−0.27	0.25	0.14	−0.02	0.33	−0.05	−0.26	−0.14	0.04	0.41	0.50	0.56	0.26	−0.25
	CO_2 ef				−0.06	−0.54	−0.26	0.31	0.66	−0.11	0.53	−0.50	−0.35	−0.40	−0.29	0.52	0.88
	Rain					−0.06	−0.06	0.50	0.05	−0.32	0.41	−0.34	−0.11	−0.02	0.00	0.12	0.08
	W_{speed}						0.19	−0.06	−0.34	0.34	−0.07	0.34	0.17	0.32	0.16	0.05	−0.28
	Z_{mix}							−0.66	0.19	0.24	0.43	−0.10	−0.36	−0.32	−0.28	−0.21	0.21
	W_{temp}								0.12	−0.41	0.24	−0.20	0.24	0.36	0.35	0.62	0.37
	WL									−0.16	0.44	−0.50	−0.56	-0.53	−0.40	0.64	0.51
	k_d										0.45	0.18	−0.12	−0.16	−0.30	−0.26	0.01
	CDOM											−0.45	−0.43	−0.49	−0.42	0.37	0.66
	pH												0.42	0.32	0.33	−0.22	−0.34
	TP													0.84	0.92	−0.03	−0.35
	TN														0.86	0.12	−0.43
	Chl *a*															0.18	−0.31
	DOC																0.55
YYL	**GPP**	−0.61	0.09	0.03	0.27	−0.05	0.10	0.52	0.01	−0.20	−0.27	−0.25	0.29	−0.15	0.45	0.15	0.01
	ER		0.73	0.06	−0.54	0.13	−0.33	−0.09	0.08	0.05	0.11	0.26	−0.03	0.19	−0.59	−0.17	0.25
	NEP			0.10	−0.45	0.12	−0.33	0.33	0.10	−0.11	−0.09	0.11	0.21	0.11	−0.35	−0.09	0.33
	CO_2 ef				0.00	0.19	−0.30	0.29	0.38	−0.33	0.70	−0.55	0.14	−0.16	−0.15	0.49	0.88
	Rain					0.01	0.08	0.06	0.55	0.02	0.28	−0.27	0.19	−0.25	−0.11	0.44	−0.31
	W_{speed}						−0.17	0.02	0.20	−0.26	0.39	−0.06	0.35	−0.38	−0.44	0.09	0.10
	Z_{mix}							-0.51	−0.27	0.56	−0.42	0.39	−0.55	−0.27	0.40	−0.54	−0.12
	W_{temp}								0.21	−0.51	0.08	−0.51	0.45	0.36	0.07	0.63	0.21
	WL									-0.32	0.68	−0.10	0.43	-0.25	−0.28	0.33	0.26
	k_d										−0.41	0.29	−0.67	−0.24	0.21	−0.49	−0.23
	CDOM											−0.23	−0.50	−0.14	−0.45	0.49	0.56
	pH												−0.09	−0.13	−0.00	−0.70	−0.24
	TP													0.06	−0.32	0.38	−0.06
	TN														0.02	0.40	−0.13
	Chl *a*															−0.30	−0.01
	DOC																0.18

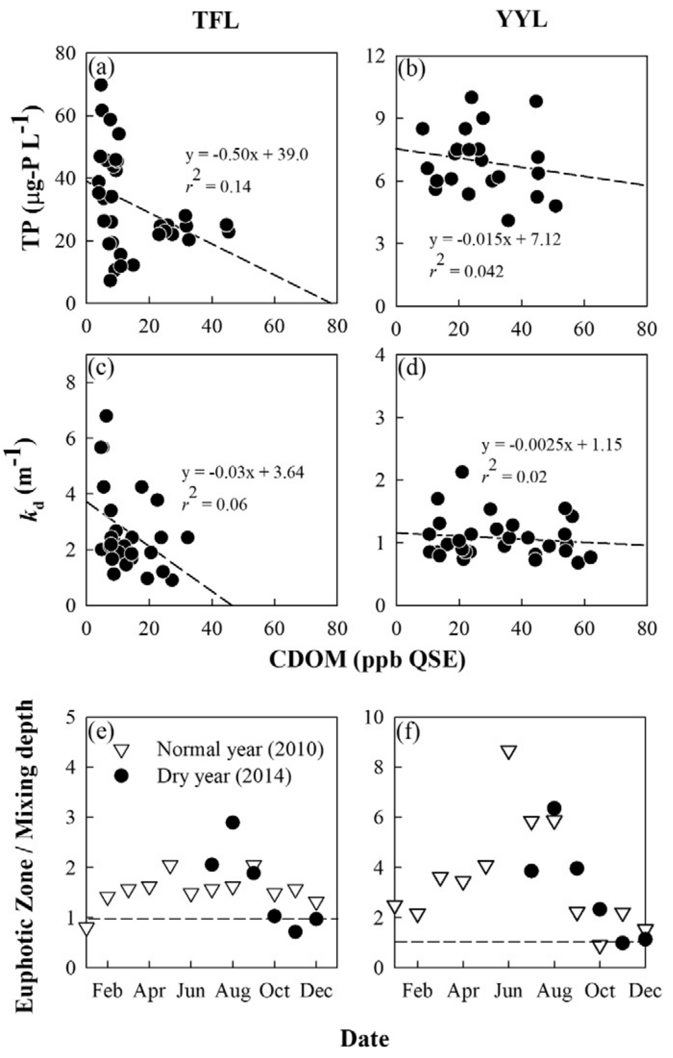

Fig. 5. The linear relationships between (a, b) monthly mean colored dissolved organic matter (CDOM) and total phosphorous (TP) concentrations, (c, d) monthly mean light attenuation (k_d) and CDOM through the entire study period (July 2009 to December 2015), and (e, f) the time series of the ratio of euphotic zone to mixing depth between a typical normal (2010) and the dry (2014) year in the two study lakes. Dotted lines indicate a non-significant slope.

Z_{mix}) was reduced during summer and autumn (Sept–Dec) in the dry year in TFL (euphotic zone/mixing depth < 1), but did not undergo an obvious change in YYL (Fig. 5e–f).

3.2. Responses in C flux

To examine how annual and inter-annual C flux responded to precipitation, we compared data from two sets of two sequential years that differed in inter-annual precipitation patterns. The first data set consisted of two years characterized with normal annual precipitation (January 2009–December 2010, wet years), and the second featured one dry year (2014) and the following wet year (2015).

In the wet years (2009–2010, 2015), GPP and ER showed similar seasonal trends, which increased from the end of winter (January), peaked in summer (July or August), then declined to the lowest level in winter (December). In contrast, temporal variation in GPP and ER was less distinct during the summer and autumn in the dry year (2014; Fig. 6a–d). Mean summer and autumn GPP in 2014 were approximately 60% lower in TFL and 21% lower in YYL compared to the same period in 2009 and 2010 (Fig. 6a–b). Similarly, mean summer and autumn ER in 2014 was 79% lower in TFL and 28% lower in YYL compared to 2009 and 2010 (Fig. 6c–d). In wet years (2009–2010), both lakes tended to autotrophy (NEP > 0) during summer and autumn (June–October), especially in 2010. However, in the dry year (2014), the two lakes also tended to autotrophy (NEP > 0), but shifted towards heterotrophy (NEP < 0) in the subsequent wet year (2015; Fig. 6e–f).

During wet years (2009–2010), CO_2 efflux was persistently negative (-1.1 to -919.1 mmol m^{-2}d^{-1}) in TFL and positive (0.7 to 958.8 mmol m^{-2}d^{-1}) in YYL, indicating that TFL acted as a strong atmospheric CO_2 sink seasonally, while YYL was carbon neutral or a weak CO_2 source (Fig. 7a–b). CO_2 efflux reached a maximum of 616 in TFL and 959 mmol m^{-2}d^{-1} in YYL in summer/autumn 2015. Temporal dynamics of CO_2 efflux in 2015 saw an increase in both GPP and ER, and higher CDOM levels (Figs. 2e, 3e and 6a–d). Carbon efflux in the rainy season differed between wet and dry years. Low precipitation in 2014 did not alter the direction of CO_2 flux; however, TFL and YYL were both strong CO_2 sources in the subsequent wet year (2015; Fig. 7a–b). Results suggest that lower summer typhoon or storm precipitation not only affects the current carbon cycles, but that the effects persist into the subsequent year (inter-annual dynamics), despite normal precipitation patterns (Figs. 6 and 7).

3.3. Drought sensitivity and control

The response of C flux to lower annual precipitation was lake-specific. Compared to a wet year (2009–2010), the clear meso- to eutrophic lake (TFL) showed a 42% and 37% decline, and a 4.2-fold increase in the annual cumulative value of GPP, ER, and CO_2 efflux, respectively during the dryer years (2014–2015); in YYL the same variables showed a 18%, 40%, and 3.3-fold increment, respectively (Fig. 8a–f). Annual cumulative carbon efflux increased in both lakes, and the meso- to eutrophic clear lake (TFL) was more responsive to precipitation change (4.2-fold, increased from -3147 to -768 mmol CO_2 m^{-2} d^{-1}, Fig. 8e). Multiple linear regression showed CDOM, DIC, and GPP were the primary forcing variables; together, they explained 96% of variation in whole-lake CO_2 efflux (partial correlation = -0.62–0.94, Table 2) during the dry year (2014–2015) in TFL. In YYL, 87% of the variation in CO_2 efflux was explained by both DIC and pH (partial correlation = 0.91 and -0.80, respectively, $p < 0.01$, Table 2), where DIC positively co-varied with CDOM ($p < 0.05$, Table 1).

4. Discussion

This study suggests, at annual and inter-annual scales, variation in lake C flux was mediated by changes in the loading of terrestrial DOM derived from precipitation. Consistent with previous studies, changes in solute loading from the watershed lead to the qualitative and quantitative changes in lake DOM characteristics, as well as lake GPP, R, pH and DIC level at seasonal and annual scales, (Jane et al., 2017; Langman et al., 2010; Nydahl et al., 2019).

4.1. Precipitation, CDOM and nutrient levels

Compared with wet years, results show that annual CDOM levels were higher in the dry year (2014) and in the subsequent wet year (2015) in both lakes (Figs. 2e, 3e). The watersheds of both lakes contain subtropical perhumid forests. These strongly acidic soils (pH values ranged from 3.3 to 4.5) are high in moisture because of year-round precipitation (Shiau et al., 2018). Moisture slows decomposition of organic matter, thereby increasing its accumulation in the watershed (Chen and Chiu, 2000; Shiau et al., 2018). Conversely, lower soil moisture in drier years would facilitate the production and export of terrestrial organic material to recipient aquatic ecosystems (Clark et al., 2005; Eimers et al., 2008; Freeman et al., 2001, 2004; Szkokan-Emilson et al., 2017). When the soil is then re-wetted following a prolonged dry period, a dramatic increase in CDOM has been observed, which may persist for

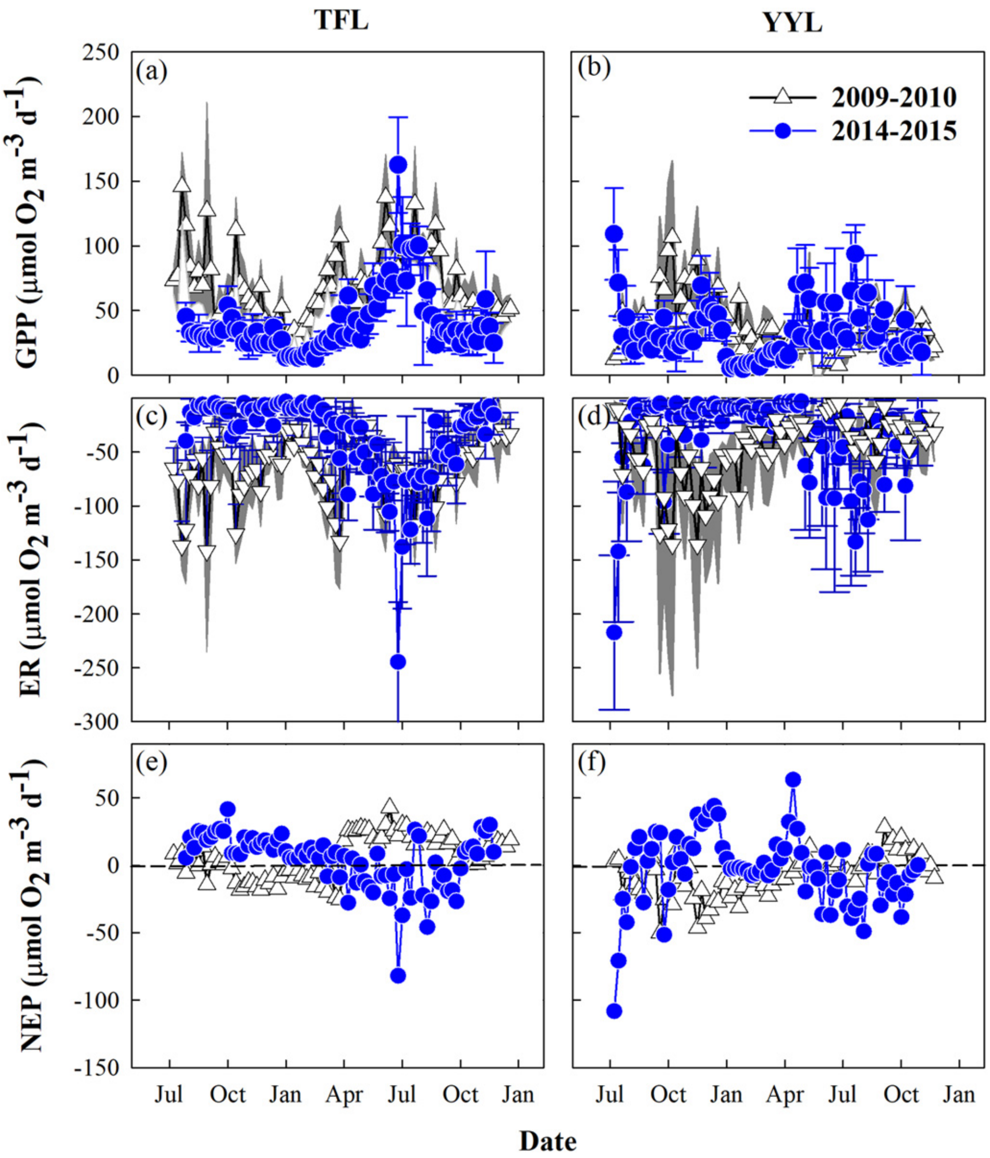

Fig. 6. Comparison of the temporal variance in (a, b) gross primary production (GPP), (c, d) ecosystem respiration (ER), and (e, f) net ecosystem production (NEP) between July 2009–December 2010 (a normal year, empty triangles) and July 2014–December 2015 (the dry year, filled circles) in the two study lakes. Data are shown as weekly averages ± standard error (SD). The gray shaded area shows the SD in the normal year. Positive and negative values of NEP indicate the autotrophy and heterotrophy of the ecosystem, respectively.

months or years (Naden and McDonald, 1989; Worrall et al., 2002). For example, typical post-drought periods of elevated surface DOM levels have been reported in UK (Fenner et al., 2001; Tipping et al., 1999; Worrall et al., 2004), and Swedish and Irish (Jennings et al., 2009) catchments and persist for 3–5 years.

In general, increased precipitation will increase runoff and terrestrial DOM loads to recipient ecosystems (Worrall et al., 2004), however, decreased discharge could also increase DOM concentration due to less dilution (Tranvik and Jansson, 2002), as could simple evapoconcentration during dry periods (Waiser, 2006). Regardless of the cause of increased CDOM during and following summer droughts, these results show that inter-annual CDOM levels in lakes are strongly associated with variation in annual precipitation patterns.

CDOM levels were negatively correlated with nutrients (TP) and pH, especially in TFL (Fig. 5a–b). The two study lakes stratified seasonally from spring to autumn, and their annual mean mixing depths were shallower in the dry year (2014) and the following wet years (2015) (Figs. 2c, 3c). This stratification pattern could reduce the supply of hypolimnetic nutrients to the epilimnion in these two years (Salonen et al., 1984; Tsai et al., 2008). Additionally, for humic-rich lakes with oxygenated waters, phosphorus (PO_4^{3-}-P) tends to interact abiotically with DOM-Fe complexes to form inert colloidal aggregates, which may further reduce the concentration of epilimnetic dissolved nutrients (de Haan, 1990; Hessen, 1998; Wetzel, 2001) because these aggregates will precipitate out of the water column (Findlay and Sinsabaugh, 2003; Henneberry et al., 2012; Stumm and Morgan, 1996). Higher CDOM recorded in the dry year (2014) was generally associated with a lower annual R values (Figs. 2e, 3e and 6c–d). This pattern implies that higher terrestrial organic matter did not directly fuel heterotrophic process, and thus facilitated the extraction of nutrients from terrestrial DOM, because allochthonous material generally contains the recalcitrant compounds in humic substances, such as lignin, which can be degraded only by more specialized microbial groups within lakes (Brett et al., 2017; Frey and Smith, 2005; Mcknight et al., 2001; Pagano et al., 2014).

4.2. Alternations in C flux

Ecosystem metabolism is as a key biological factor driving temporal patterns of DIC (CO_2) in lakes (Bade et al., 2004). The two study lakes shifted from net autotrophy during comparatively dry conditions

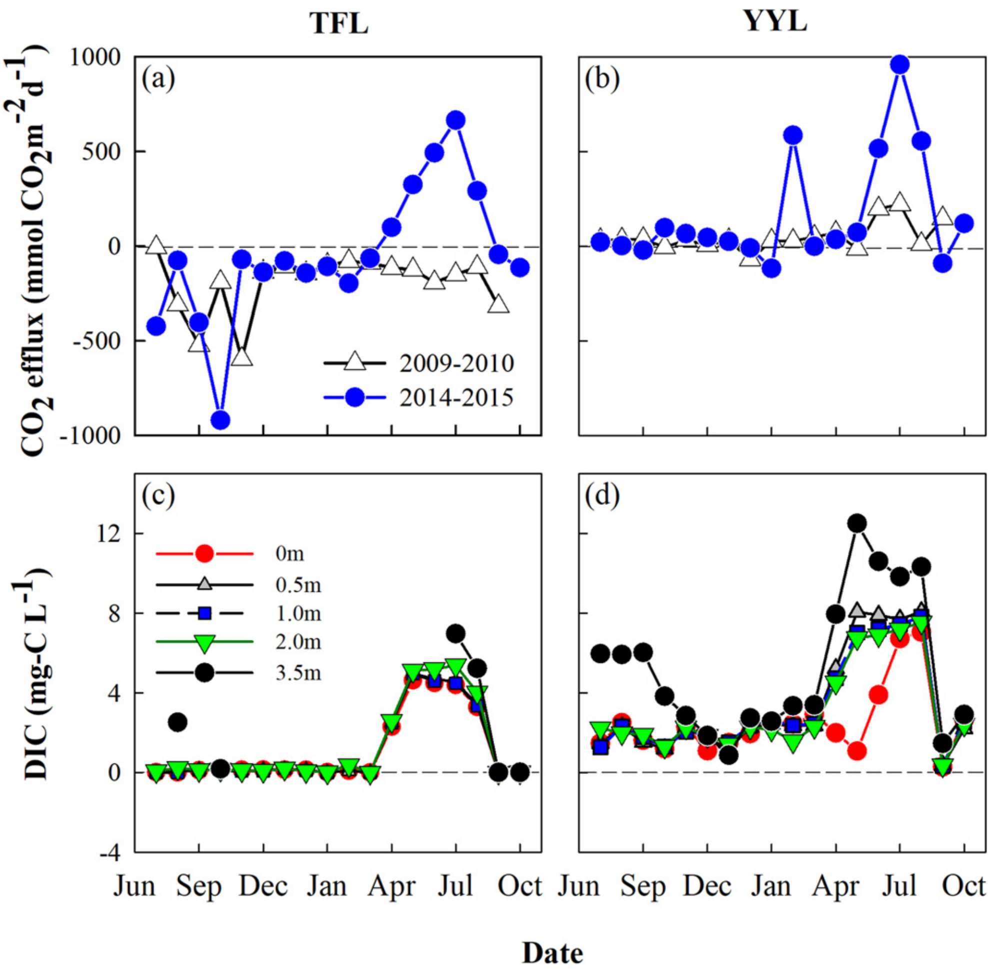

Fig. 7. Comparison of the inter-annual variation in CO_2 efflux and dissolved inorganic carbon (DIC) gradient in water column between a typical normal year (January 2009–December 2010) and the dry year (January 2014–December 2015) in (a, c) Tsui-Fen Lake (TFL) and (b, d) Yuan Yang Lake (YYL). Negative values represent the transfer of CO_2 from the atmosphere to the lake (sink), whereas positive values indicate the transfer of CO_2 from the lake (source) to the atmosphere.

during 2014 to net heterotrophy when summer precipitation returned in 2015 (NEP < 0, Fig. 6e–f). According to our multiple regression results, a GPP recovery from a low in 2014 provided an increased labile organic carbon source, such as proteins and amino acids from algal exudates which can be readily utilized by bacteria (Rosenstock and Simon, 2001) in 2015, and then fueled ER in the study lakes (Table 2). This finding may also account for higher DIC level in lakes (Fig. 7c–d), and thus may be the primary cause for higher CO_2 evasion in both lakes in the period subsequent to the dry year (Fig. 6a, d, Table 1). Compared to the wet years (2009–2010), a higher regression slope between ER and GPP was measured during 2014–2015 in both study lakes, implying that ecosystem ER is greater than GPP. This greater ER appears to be subsidized from additional DOM originating from autochthonous DOM produced by GPP and additional allochthonous DOM from terrestrial loading (GPP; Fig. 9a–b). Water dominated by recalcitrant allochthonous material may fuel microbial heterotrophic respiration under favorable conditions. The evidence of a priming effect, which is the addition of labile organic matter, such as algal exudates, may facilitate microbial degradation of the recalcitrant DOM pool. Such biochemical processes should be considered when examining causalities between DOM composition and ecosystem respiration (Guenet et al., 2010; Roiha et al., 2016). In addition to the biological processes, geochemical processes may have also contributed to variations in CO_2 flux. Surface or underground flow can bring in CO_2 produced from respiration in the surrounding terrestrial ecosystem, and contribute to an external input of DIC. We suggest that further investigation into the effects and relative contribution of internal and external geochemical DIC sources to the total DIC pool in lakes is warranted.

CO_2 concentrations in this study were determined by the bicarbonate equilibrium model (Butler, 1991; Tonetta et al., 2017; Wetzel and Likens, 2000), which describes the effects of pH on DIC speciation and concentration in lakes. The cumulative effect of trophic status changing at longer time scales (>seasonal) can alter lake pH, and thus CO_2 concentration and the direction of C flux (Bortolotti et al., 2016). In lakes with a large DIC pool, CO_2 supersaturation can occur when bicarbonate (HCO^{3-}) partially converts to CO_2 under sufficiently low pH conditions (Bortolotti et al., 2016). The higher ecosystem R that resulted from higher CDOM (terrestrial DOM) levels (Figs. 2e, 3e) and a recovering GPP (Fig. 6a–d) in the summer of 2015 increased DIC (Fig. 7c–d) and lowered pH in both lakes (Figs. 2e, 3e, 9a–f) resulting in a negative correlation between the two variables (Fig. 9c–d; Table 1). Allochthonous dissolved humic substances with higher organic acid concentrations contribute to the naturally low pH observed in meso-eutrophic lakes and seem to corroborate this observation (Kortelainen and Mannio, 1990; Lydersen, 1998; Nydahl et al., 2019). Because the excitation and emission wavelengths of the deployed submersible fluorometers represent the level of terrestrial humic-like substances in lakes (about 325 nm and 470 nm, respectively) (Lee et al., 2015), our results suggest that lowered annual pH levels resulted from higher tDOM in lakes during and after the dry year (Figs. 2e, 3e; Table 1). The decrease in pH

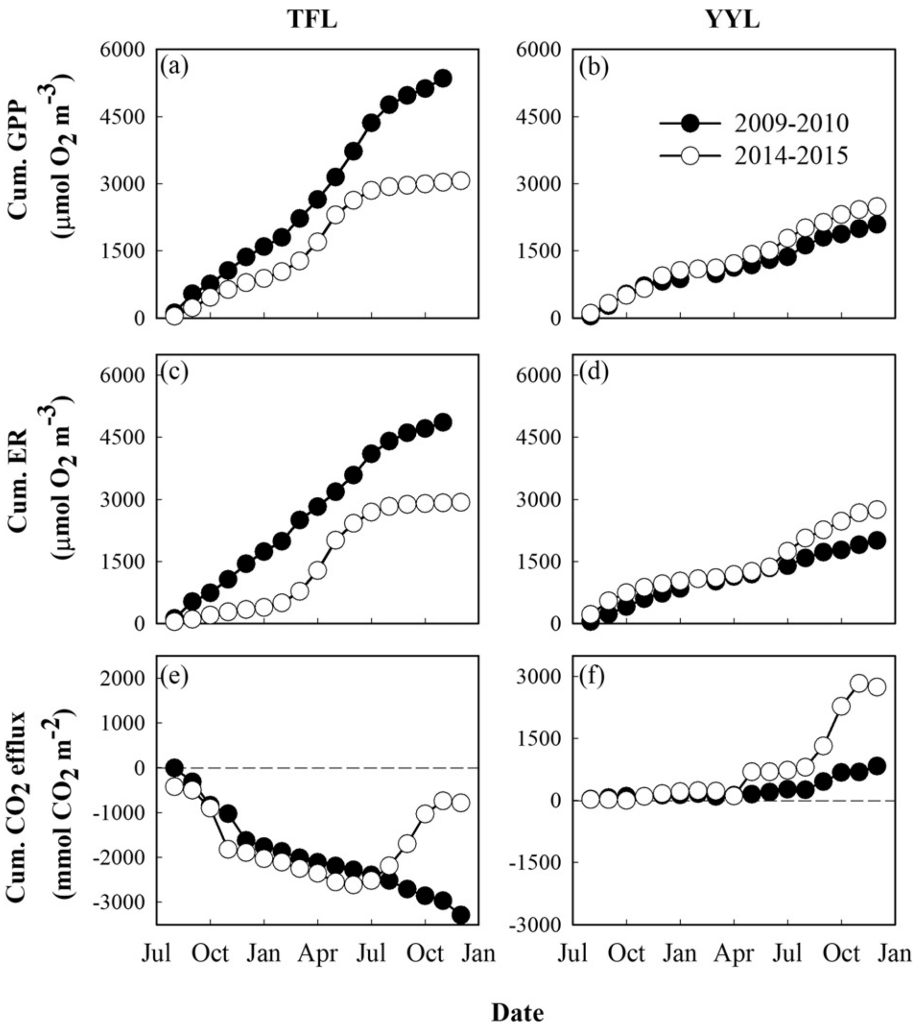

Fig. 8. Comparison of monthly cumulative values of (a, b) gross primary production (GPP), (c, d) ecosystem respiration (ER), and (e, f) CO_2 efflux during the normal year (2009–2010) and the dry year (2014–2015) in Tsui-Fen Lake (TFL) and Yuan Yang Lake (YYL), respectively. Monthly values of carbon fluxes are the sum of daily values.

values from 8.1 to 5.2 in TFL and 7.2 to 5.5 in YYL coincided with the shift from net autotrophy in 2014 to net heterotrophy in summer 2015 (Figs. 2e, 3e and 6e–f). We observed supersaturation and efflux of CO_2 at pH 6.2 and 7.4 in TFL and YYL respectively (Fig. 9e–f); thus, it seems the lowered pH that coincided with the shift towards net heterotrophy and likely has determined the direction of CO_2 flux. As metabolic processes noticeably affect CO_2 concentration, CO_2 flux is a reliable indicator of metabolic status under changing precipitation patterns (Nydahl et al., 2019).

We adopted epilimnetic DIC measurements as a proxy for whole-lake CO_2 concentration, because the majority of whole-lake GPP (86%–72%) and R (80%–67%) occurs in the upper mixed layer of the lake (Coloso et al., 2008; Staehr et al., 2012). Despite the diel pattern of DIC in terms of CO_2 concentration could be higher in the late afternoon and early night, because of the higher R fueled by autochthonous DOM produced by photosynthesis (Sadro et al., 2011a, 2011b); however, the persistently positive daily values of NEP were observed in the two study lakes during spring and summer in the dry year (2014) as opposed to the negative values in the wet year (2015) (Fig. 6e–f). This contrast supports the observed inter-annual variation of DIC (Fig. 7c–d) and helps reinforce that dry conditions can cause both immediate and prolonged effects on lake C flux. The pattern shows lakes are CO_2 sinks or neutral during dry periods, but may rapidly shift towards net CO_2 emitters in subsequent wet years. In addition, significant vertical DIC gradients and hypolimnetic DIC accumulation were observed from early spring to late autumn in the wet year (2015; Fig. 7c–d). The trapped CO_2 in the metalimnion and hypolimnion can be released to the atmosphere directly during episodic mixing in typhoon and monsoon seasons (S.E. Jones et al., 2009; Tsai et al., 2008). Consequently, determining the net direction of the CO_2 flux based solely on epilimnetic DIC measurements does not undermine our conclusions, but may conservatively underestimate the magnitude of subtropical lakes as CO_2 sources to the atmosphere in years following dry periods.

4.3. Sensitivity of C flux to precipitation

Although patterns of C flux in of both study lakes were similar, our clear and deeper meso-eutrophic lake (TFL) was more strongly influenced by changes in annual precipitation. Variation in CDOM, and thus nutrients, light attenuation (k_d) and Chl-*a* concentration (Figs. 2e, 3e and 5a–b; Table 1) as well as the pH-CO_2 relationship (Fig. 9e–f), were more affected by altered precipitation patterns than in the shallower, colored, oligotrophic lake. Because these differences were associated with precipitation changes between the dry and wet years (e.g. between 2014 and 2009; Figs. 2e and 3e) in TFL, changes in C flux may be dampened in colored oligotrophic lakes.

Our findings are also consistent with those from studies in arctic or temporal pristine lakes, where the responses of lake metabolism to the changes in tDOM loads are more evident in clear-water lakes (Huisman and Weissing, 1999; Sommer et al., 1986). In shallow clear-

Table 2
Best stepwise model describing the temporal variation in CO_2 efflux throughout the study (January 2009–December 2015), and GPP, ER, and CO_2 efflux in the dry year (January 2014–December 2015) in TFL and YYL.

	Multi-regression model	Coefficient	Partial correlation	*p*-Level
TFL	CO_2 efflux (all year) ($r^2 = 0.86$)			
	Intercept	469.11		<0.01
	Wind speed	−199.96	−0.83	<0.01
	DIC	109.12	0.77	<0.01
	pH	−68.00	−0.58	<0.01
	Mixing depth	50.32	0.58	<0.01
	CO_2 efflux (dry year) ($r^2 = 0.96$)			
	Intercept	293.93		<0.01
	CDOM	−272.27	−0.95	<0.01
	DIC	137.05	0.94	<0.01
	GPP	−4.42	−0.62	0.02
	GPP ($r^2 = 0.59$)			<0.01
	Intercept	89.47		<0.01
	Mixing depth	−8.82	−0.75	<0.01
	pH	−8.09	−0.56	<0.05
	CDOM	0.62	0.47	<0.01
	ER ($r^2 = 0.76$)			0.106
	Intercept	9.77	−0.77	0.19
	GPP	−0.96	−0.87	<0.01
	DIC	−3.78	−0.43	0.09
YYL	CO_2 efflux (all year) ($r^2 = 0.95$)			
	Intercept	207.78		0.17
	DIC	139.37	0.96	<0.01
	pH	−96.19	−0.77	<0.01
	CDOM	4.93	0.80	<0.01
	DOC	15.63	0.58	<0.01
	Mixing depth	19.51	−0.57	<0.01
	CO_2 efflux (dry year) ($r^2 = 0.87$)			
	Intercept	1111.56		<0.01
	DIC	128.70	0.91	<0.01
	pH	−208.31	−0.80	<0.01
	GPP ($r^2 = 0.92$)			
	Intercept	−36.97		0.15
	Water temp.	4.26	0.93	<0.01
	CDOM	−0.87	−0.84	<0.05
	Wind speed	−29.74	−0.82	<0.05
	k_d	17.58	−0.70	0.12
	TP	3666.55	0.64	0.17
	Mixing depth	8.35	0.72	0.11
	R ($r^2 = 0.95$)			
	Intercept	−21.24		0.18
	Precipitation	−0.40	−0.96	<0.01
	Water temp.	−3.61	−0.92	<0.01
	TP	7541.14	0.85	<0.01
	k_d	18.86	0.75	<0.05

water lakes, benthic primary production can account for a substantial portion of the whole lake primary production (Karlsson et al., 2009; Vadeboncoeur et al., 2003). This benthic production is primarily limited by light availability, instead of nutrients, because epipelic algae can use sediment pore water nutrients which typically occur in higher concentrations than in lake water (Bonilla et al., 2005; Enell and Lofgren, 1988). In support, in the shallower colored lake (YYL), light penetration and availability are generally high (ratio of euphotic zone/mixing depth > 1, Figs. 2d, 3d and 5e–f) and less strongly correlated with CDOM in both dry and wet years (Fig. 5d). Hence, stronger changes in benthic light availability due to variation in CDOM may account for the higher response sensitivity of C fluxes in the deeper clear lake (Gu and Wyatt, 2016). Our results demonstrate the need to consider changes in light availability, associated with CDOM levels, when evaluating the effects of variation in nutrient availability on whole-lake primary production in mesotrophic clear lakes under changing precipitation patterns at an inter-annual scale.

4.4. Epilimnetic vs. whole-lake C fluxes

As mentioned above, only the epilimnion was monitored to estimate whole-lake metabolism, thus assuming complete vertical and horizontal mixing of the lake in these two small, relatively shallow and frequently well-mixed lakes (Hanson et al., 2003; Sadro et al., 2011b; Staehr et al., 2012; Tsai et al., 2008). Most GPP (86%–72%) and ER (80%–67%) occurs in the upper mixed layer of lakes (Coloso et al., 2008; Staehr et al., 2012), however when heterotrophy (NEP < 0) is substantial in the hypolimnion, ecosystem metabolism could be underestimated by up to 60% for GPP and 80% for ER when whole-lake metabolism estimation is based only on epilimnetic data. This is especially prominent during periods of stratification or when the euphotic zone extends below the epilimnion (Coloso et al., 2008; Obrador et al., 2014; Staehr et al., 2012). In TFL and YYL, the euphotic zone (Z_{eu}) often extends below the mixing depth (Z_{mix}) (i.e., the ratio of euphotic zone to mixing depth > 1; Fig. 5e–f), implying that downwelling photosynthetically active radiation is sufficient to support benthic primary production within or below the metalimnion (Obrador et al., 2014; Van de Bogert et al., 2007). Vertical concentration gradients of TP and DIC, and algal maxima layers were common in the hypolimnion of both lakes during summer and autumn stratification (Tsai et al., 2008, 2016). Thus, despite frequent mixing events, a substantial fraction of GPP, ER and CO_2 efflux of these lakes may be unaccounted for by focusing solely on the pelagic epilimnion. Our methodology may contribute to a conservative estimate of the magnitude and sensitivity of the metabolic response to precipitation in the two study lakes and lake-specific responses to altered precipitation could be even greater than what we currently estimate.

An evaluation of internal spatial differences in C flux was beyond the scope of this study, but horizontal and vertical spatial variability in C flux within small shallow lakes with larger littoral zones like TFL and YYL (accounting for 20% and 30% of the lake area in TFL and YYL, respectively) should be investigated in future studies. This information would strengthen whole-lake interpretations of carbon cycling and improve the application of this research for sub-tropical lakes around the globe.

5. Conclusion

Our findings reveal that predicted and ongoing climate change, especially decreases in annual precipitation, will have both immediate and prolonged effects on the GPP and ER within lakes. GPP and ER declined equally and both lakes were either CO_2 sinks or neutral during the drought year. In the subsequent wet year, ER increased by 110% and both lakes shifted to strong net CO_2 emitters. Recovery from drought can be delayed and leads to greater carbon loss to the atmosphere, driven by the differential sensitivity of GPP and ER to drought events. Furthermore, C flux was more responsive to reduced precipitation in the mesotrophic clear lake as opposed to the oligotrophic colored lake. This study suggests, at annual and inter-annual scales, the temporal variation pattern and magnitude of variation in lake C flux were governed by tDOM-mediated changes in epilimnetic nutrient levels and hypolimnetic light availability. This study adds to the current understanding of how lake DOM pool and eventually carbon cycling in subtropical lakes might respond to future changes in precipitation patterns under changing climate conditions.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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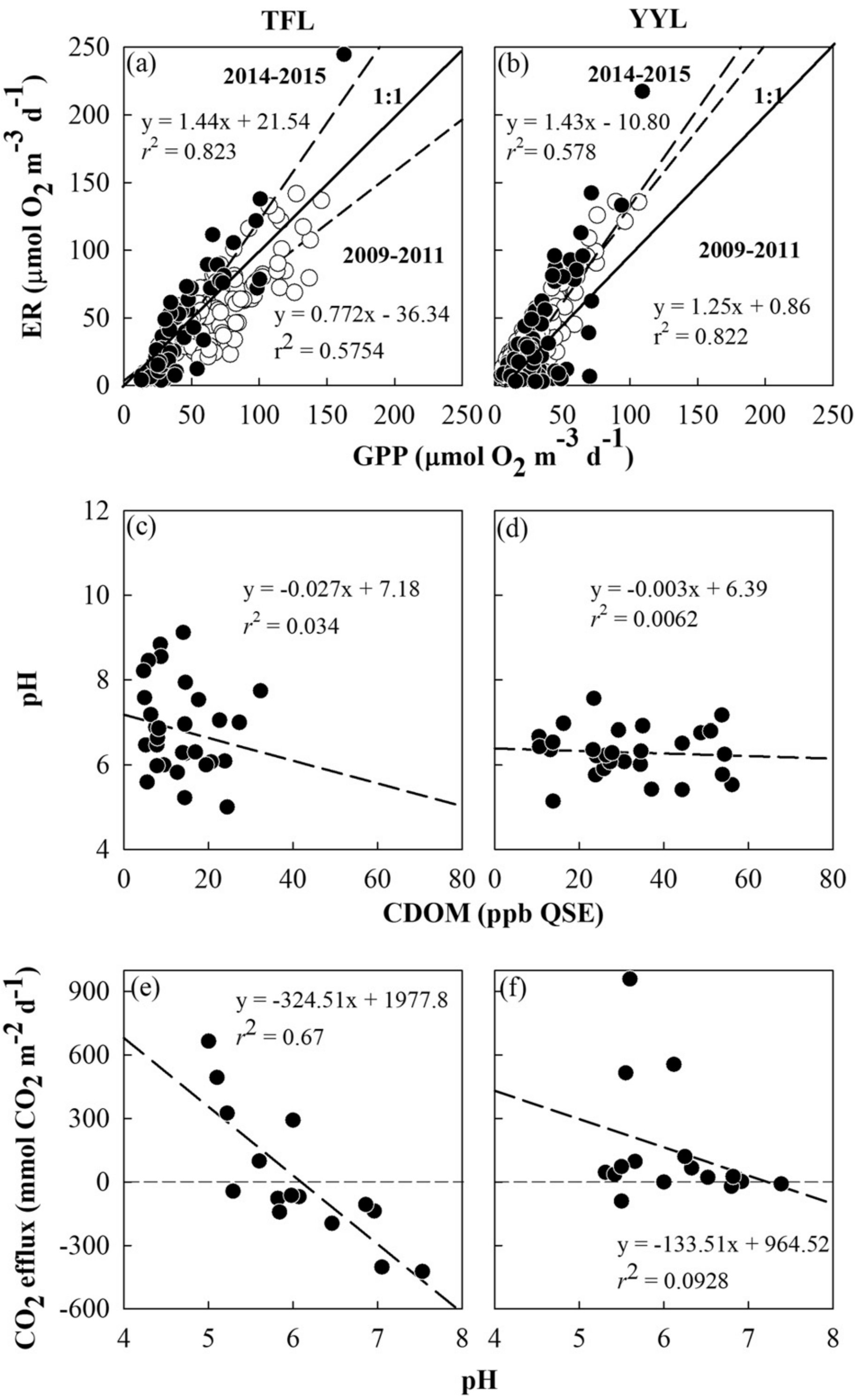

Fig. 9. Scatter plots of weekly averaged gross primary production (GPP) corresponding to (a, b) ecosystem respiration (ER), (c, d) the relationship between colored dissolved organic matter (CDOM) and pH through the entire study course (July 2009 to December 2015), and (e, f) the relationship between pH and CO_2 efflux in Tsui-Fen Lake (TFL) and Yuan Yang Lake (YYL) during the dry year (2014–2015), respectively. Analysis was performed on all available measured data. Dashed lines represent the regression models for the normal and dry years and the solid lines represent 1:1 lines in (a, b).

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