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Short-term rainfall limits cyanobacterial bloom formation in a shallow eutrophic subtropical urban reservoir in warm season

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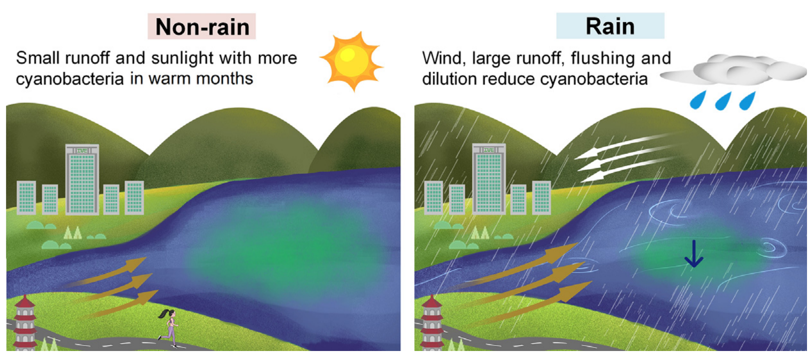
HIGHLIGHTS

- High-frequency monitoring revealed reservoir cyanobacterial responses to rainfall.
- Cyanobacteria had a negative response to short-term rainfall in warm months.
- Cyanobacterial biomass increased after short-term rainfall in cool months.
- Winter rainfall might increase the sensitivity of cyanobacteria to sunlight.

GRAPHICAL ABSTRACT



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ABSTRACT

The global increase in dominance of toxic blooms of cyanobacteria has severely impacted aquatic ecosystems and threatened human health for decades. Although it has been shown that high levels of rainfall may inhibit the growth of bloom-forming cyanobacteria, it is still unclear how cyanobacteria respond to short-term rainfall events. Based on five-year (2016–2020) high-frequency (half-week) sampling data from a shallow eutrophic urban reservoir in subtropical China, we explored the short-term effects of rainfall events on cyanobacterial biomass (CBB) by constructing generalized additive models of CBB in rainy periods during warm (April to September) and cool (December and January) months, respectively. We find evidence in support of the hypotheses that short-term rainfall events significantly reduce CBB in warm months, but the opposite response was observed in the cool months. We also highlight a difference in the factors explaining CBB decreases in warm months (precipitation, air temperature, relative humidity, dissolved oxygen and total phosphorus) compared with factors explaining the response of CBB in cool months (sunshine hours, pH and total carbon). In particular, meteorological factors (precipitation, wind speed and sunlight) might drive changes in water temperature and hydro-dynamics of the reservoir, thereby causing a rapid reduction of CBB after rainfall events in warm months. This varying response of cyanobacteria to short-term rainfall events in the shallow eutrophic subtropical reservoir may also be expected in temperate or cool lakes as climate change effects become stronger.

1. Introduction

Water is a natural resource, which is essential to all ecosystems and societies. In recent decades, climate warming and human activities have

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caused a further deterioration of global freshwater quality, through increasing the magnitude and frequency of cyanobacterial blooms in inland freshwater ecosystems (Sinha et al., 2017; Huisman et al., 2018; Ho et al., 2019). Harmful cyanobacterial blooms are serious issues that threaten human health and the water supply of millions of people with associated huge economic losses (Carmichael and Boyer, 2016; Michalak, 2016; Qin et al., 2015; Yang et al., 2022).

Climate variables are one of the main driving factors of cyanobacterial biomass change at different latitudes (Richardson et al., 2019; Giani et al., 2020). Higher temperatures generally favour cyanobacterial growth and lengthen the optimal growth periods through reducing vertical mixing (Paerl and Huisman, 2008). Rainfall events can affect specific regional and watershed environments through impacts on surface runoff, temperature and wind direction (Piao et al., 2010; Ho et al., 2019; Weber et al., 2020) and thus change the physico-chemical conditions in water bodies, further boosting or abating the cyanobacterial blooms (Reichwaldt and Ghadouani, 2012; Yang et al., 2017; Wang et al., 2022). Hydrological alterations can also affect water quality, ecosystem structure and function (Webster et al., 2005; Piao et al., 2010; Yang et al., 2017). Shallow lakes in particular are highly sensitive to wind-induced turbulence due to resuspended particulates from the bottom sediments (Qin et al., 2015). Previous studies have found that the phytoplankton (algae) biomass mostly decreases after rainfall events (Havens et al., 2017). It has also been observed that high flushing rates can affect the dominance of cyanobacteria (Carvalho et al., 2011; Tang et al., 2021). The timing, frequency and volume of heavy rainfall are key factors influencing cyanobacterial biomass (Ahn et al., 2002; Yang et al., 2017; Richardson et al., 2019).

Lake ecosystems have unique characteristics with differences in morphometry, hydrology, and human activities in individual watersheds. These differences result in varying responses, such as frequency and magnitude of harmful algal blooms, to environmental drivers (Paerl et al., 2016). Rainfall-induced hydrological changes of watersheds may benefit cyanobacterial growth by increasing nutrient inputs (Michalak et al., 2013), but large storm events can have a negative effect on cyanobacterial blooms by flushing cells from the waterbody (Reichwaldt and Ghadouani, 2012). The urbanization caused by human activities can decrease precipitation infiltration and increase surface runoff (Paul and Meyer, 2001; Grimm et al., 2008). Moreover, urbanization-driven increase of point source pollution and non-point source pollution can facilitate the occurrence and development of harmful algal blooms (Havens et al., 2003; Hall and Leavitt, 1999).

A key challenge is to understand how climate change affects shorter-term meteorological factors such as precipitation, temperature and wind in specific regions, and how these factors interact to produce changes in environmental conditions in a lake, and ultimately, changes in water quality and cyanobacteria biomass (Michalak, 2016). Moreover, it is necessary to strengthen our understanding of how phytoplankton communities respond to short-term storm events at fine scale (Stockwell et al., 2020). However, the bulk of previous studies have primarily explored the relationship between seasonal averages of cyanobacterial biomass and weather (Bouvy et al., 2003; Robson and Hamilton, 2004; Hampel et al., 2020) or single extreme precipitation events (Zhang et al., 2012; Paerl et al., 2020; Gao et al., 2021; Qin et al., 2021). Although we know rainfall can have a strong influence on the occurrence of cyanobacterial blooms (Mu et al., 2019), we still don't fully understand how these rainfall events change lake conditions and consequently affect cyanobacterial biomass across space and time. Furthermore, there are no publications that use long-term, high-frequency monitoring data to analyze the cyanobacteria-rainfall relationship in subtropical climates. In view of these gaps, this study aimed to: 1) explore the cyanobacterial response in a subtropical reservoir to short-term rainfall events using high-frequency (half a week) monitoring data; 2) construct models explaining the dynamics of cyanobacterial biomass (CBB) during rain or non-rain periods in both warm and cool months; 3) explore the specific driving factors behind the response of CBB to rainfall episodes.

We hypothesize that: 1) the short-term decline of cyanobacterial biomass is relevant to the magnitude and frequency of rainfall events; 2) short-term rainfall events affect the cyanobacterial biomass-environment relationship differently in warm versus cool months.

2. Materials and methods

2.1. Study area, sampling and dataset

High-frequency field sampling was conducted in the Xinglinwan Reservoir which is located in the lower reaches of the Houxi River (about 25 km long), Xiamen City, southeast China (Fig. 1a). The study site belongs to the subtropical maritime monsoon climate and the average temperature of the year is 20.9 °C, the average wind speed is 5–6 m/s, the average annual rainfall is 1357 mm. Xinglinwan Reservoir is a shallow and eutrophic reservoir with low transparency and long hydraulic retention time (Peng et al., 2020; Yang et al., 2022). The total storage capacity of Xinglinwan Reservoir is about 2568 m^3, the average water depth is about 2.5 m and the water level (with mean of about −0.5 m) always below the sea level (Fig. S1). The Xinglinwan Reservoir was heavily influenced by agricultural activities and urbanization-induced land-use change and sewage effluent in the past decades (Zhu et al., 2019). It's also worth noting that Xinglinwan Reservoir is an enclosed water body as a dam blocks the outflow with limited flushing (Fig. 1a), therefore precipitation across the natural catchment is the major source of water for this reservoir and seawater intrusion in the bottom water layer is stronger in winter (dry and cool) than in summer (wet and warm) seasons (Mo et al., 2021).

Xinglinwan Reservoir has a lower phytoplankton species richness than the headwaters (Shidou Reservoir and Bantou Reservoir) of the Houxi river-reservoir system largely due to the urbanization-induced pollution (Yang et al., 2022). Phytoplankton and cyanobacteria communities fluctuated overtime at genus level (Nyirabuhoro et al., 2021; Yang et al., 2022). The general characteristics of the study reservoir are presented in Fig. S1 and Table S1. The phytoplankton taxonomic composition and biomass including cyanobacteria (Cyanophyta) of Xinglinwan Reservoir from 2016 to 2018 were directly obtained from our previous publication (Yang et al., 2022). The cyanobacterial community exhibited a temporal variation and a cyanobacterial bloom or dominance occurred in the summer of 2017 (Fig. S2). Typically, the highest cyanobacterial biomass occurred in summer and autumn (warm months) and the lowest in winter and spring (cool months) from 2016 to 2020 (Fig. S3).

Water samples were normally taken from the surface water (about 0.5 m depth) at two stations (station L: 24° 36′ 32″ N, 118° 03′ 31″; station G: 24° 36′ 19″ N, 118° 03′ 41″ E) twice a week (Tuesday and Friday) from January 2016 to December 2020. In addition, 12 more samples were taken at station C (near station L) from August 12 to August 30 in 2016 (Mo et al., 2021). Our dataset ($N = 1064$) consists of a range of cyanobacterial and physicochemical data of Xinglinwan Reservoir, the meteorological data of Xiamen City. In this study, the cyanobacterial chlorophyll-*a* was used to represents the cyanobacterial biomass (CBB). The cyanobacterial chlorophyll-*a* was specifically measured using a PHYTO-PAM Phytoplankton Analyzer (Heinz Walz GmbH, Effeltrich, Germany). For each sampling, we took three replicate measurements and calculated the average value for each sample. Seven physical and chemical parameters (water temperature, pH, dissolved oxygen, turbidity, electrical conductivity, salinity and oxidation-reduction potential) were measured at the same time in situ using a Hydrolab DS5 multiparameter water quality analyzer (Hach Company, Loveland, CO, USA). The chemical or nutrient data including total carbon (TC), total organic carbon (TOC), total nitrogen (TN), ammonium-nitrogen (NH_4-N), nitrate-nitrogen (NO_3-N), nitrite-nitrogen (NO_2-N), total phosphorus (TP), and phosphate-phosphorus (PO_4-P) were measured following standard methods (Clesceri et al., 1998).

The meteorological data (precipitation, evaporation, the average relative humidity, min relative humidity, sunshine hours, average air temperature, max air temperature, min air temperature, average surface temperature, max surface temperature, min surface temperature, the average wind speed and max wind speed) were extracted from the China Meteorological Data Service Centre (http://data.cma.cn). In addition, daily

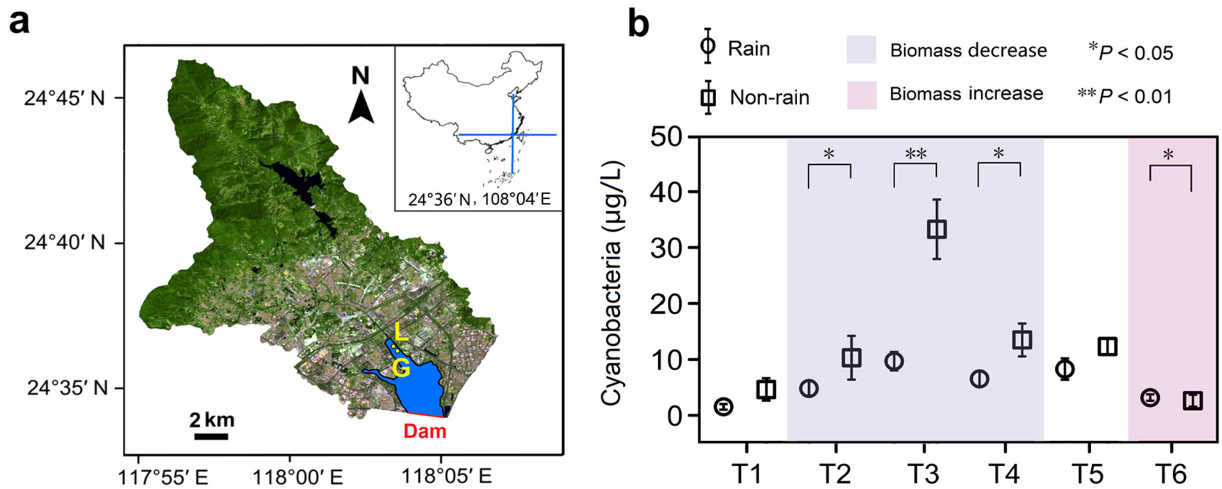

Fig. 1. Map of Houxi River watershed showing the sampling sites in Xinglinwan Reservoir, Southeast China (a) and seasonal differences in cyanobacterial chlorophyll-*a* between rain and non-rain periods from T1 to T6 (b). Stations G and L are two sampling sites. The statistic is nonparametric Mann-Whitney *U* test. T1, February and March; T2, April and May; T3, June and July; T4, August and September; T5, October and November; T6, December and January.

temperature range was calculated by the difference between the max and min air temperatures (Table S1).

2.2. Defining rainfall events and grouping

In this study, we examined the cyanobacterial response within 7 days following rainfall events. The total precipitation (mm) was calculated for X days prior to sampling day ($Pcpt_X$), where X indicates 1, 2, 3, 4, 5, 6 and 7 days, and used to define whether rainfall events had occurred in the X days before the sampling time (day). If $Pcpt_X > 0$, it was classified as a "rain" period. Otherwise, it was classified as a "non-rain" period. The year was artificially divided into 6 bi-monthly periods ("Tgroup") for considering the seasonal changes in CBB based on meteorological factors (air temperature, wind speed and wind direction): T1 (sampled in February and March, $N = 166$), T2 (sampled in April and May, $N = 174$), T3 (sampled in June and July, $N = 174$), T4 (sampled in August and September, $N = 208$), T5 (sampled in October and November, $N = 166$) and T6 (sampled in December and January, $N = 176$). The T2–T4 are considered the warm months, whereas the T6 covers the cool months (Table S1, Fig. S4). For each "Tgroup", we used the nonparametric Mann-Whitney *U* test to assess the significant differences in the CBB between rain and non-rain periods. Only Tgroups with significant differences ($P < 0.05$) in CBB were analyzed further.

2.3. Factor analysis

Factor analysis (FA) was used to remove the collinearity of variables in the dataset and identify common factors in the environment variables that represent the correlated variables. Initially, parallel analysis was used to identify the optimal number of factors explaining CBB during rainy periods in warm and cool months, respectively. Through the factor loading matrix, the variables with the highest factor scores were selected as the common factors (Tables S2, S3). The FA was performed using the package of R studio 3.6.3 (R Core Team, 2020).

2.4. Generalized additive model

The identified factors that significantly explained the effects of rainfall in warm or cool months were used to model CBB based on a generalized additive model (GAM). Generally, the factors with the highest score selected in FA were separately fitted to CBB in warm or cool months, and the factors with *P* value less than 0.05 were selected as explanatory factors. pH was artificially selected as it had a great influence on the explanatory power of the model in cool months. The selected covariates from FA were used as explanatory factors for CBB. The covariate factors that had high influence on the R^2-adjust of the two response variables were identified, in order to explore the role of these explanatory factors in the rainfall-CBB relationship.

Two regression functions were constructed based on CBB and their explanatory factors in rain periods of the warm months (y1) or the cool months (y2). The y1 ($N = 350$) is the regression function of CBB and corresponding explanatory variables (precipitation, temperature, relative humidity, dissolved oxygen and total phosphorus) in rain period of warm months (T2, T3 and T4). The y2 ($N = 72$) is the regression function of CBB and corresponding explanatory variables (sunshine hours, pH and total carbon) in rain period of cool months (T6). In addition, difference tests were performed again for these significant explanatory variables between rain and non-rain datasets using the nonparametric Mann-Whitney *U* test. GAM was performed using the mgcv package of R studio 3.6.3 (R Core Team, 2020).

2.5. The PLS path model

Partial least squares path modeling (PLS-PM) is a general framework that can analyze structural relationships between variables (Tenenhaus et al., 2005). We constructed a statistic for detecting the relationship between meteorological factors and CBB in warm months. In this study, PLS-PM described the causal links between the meteorological factors in rain (precipitation, wind speed and sunlight) or non-rain (wind speed and sunlight) periods, environmental factors (water temperature, pH and dissolved oxygen), and CBB. PLS-PM was performed with the plspm package in the R studio 3.6.3 (R Core Team, 2020).

3. Result

3.1. Seasonal changes of cyanobacterial biomass in rain or non-rain periods

The plot of seasonality in cyanobacterial biomass (CBB) showed a clear pattern with an increase from T1 to T3 and general decrease from T3 to T6 (Figs. 1b; S3). Meanwhile, from T2 to T4 (the warm months – April to September), CBB showed a significant ($P < 0.05$) negative response to rainfall over the previous 1–4 days (particularly 1–3 days) prior to the sampling day, compared with non-rainy periods during the same months (Fig. 2a). The negative response to rainfall appeared to increase from T2 to T4 consistent with the changes in the intensity of sunshine hours, and the frequency of precipitation (Fig. 2b; c). After October (T5 and T6), the CBB showed a tendency to increase after rainfall events, particularly in T6 in response to rainfall over the previous 1–3 days (Fig. 2a).

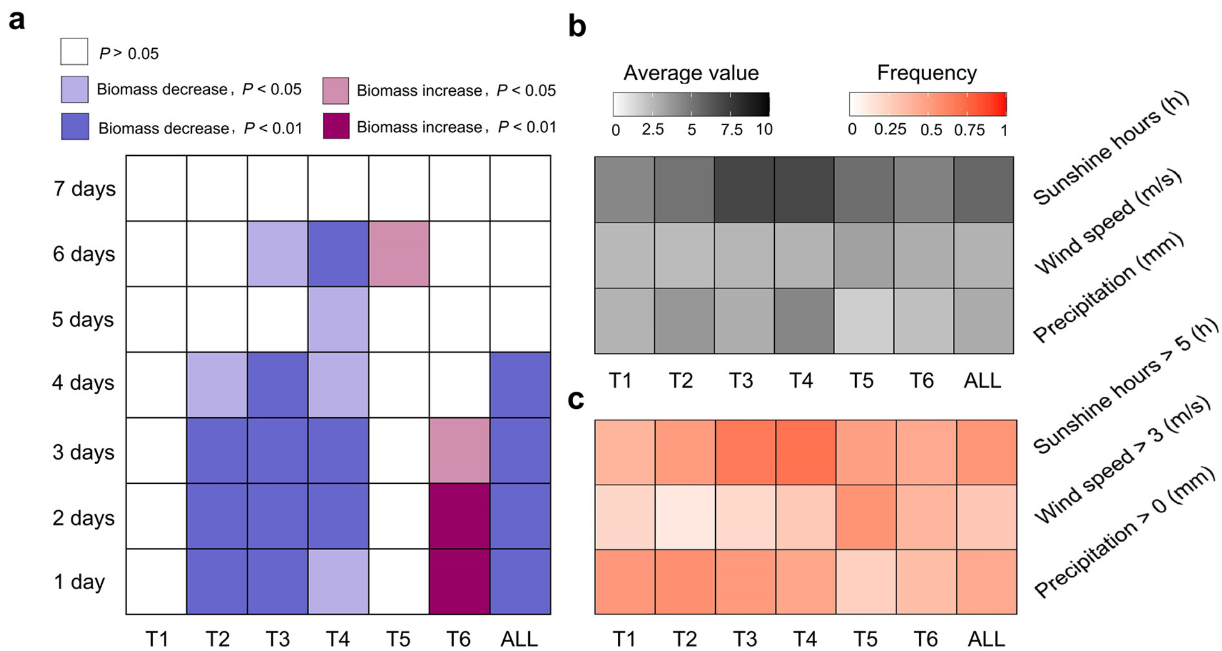

Fig. 2. The response of cyanobacteria biomass to rain events in 1–7 day/days (a), and the meteorological conditions from T1 to T6 (b, c). (a) The colored squares represent significant differences in cyanobacterial biomass before and after rainfall events. Darkness or lightness of color represents the level of significant difference in cyanobacteria. The purple color represents a significant decrease in cyanobacterial biomass after rainfall, while the red/pink color represents a significant increase in cyanobacterial biomass after rainfall. X day/days (X = 1, 2, 3, 4, 5, 6 and 7) represents the total rainfall for X days prior to sampling day. (b) The colored squares represent the average of meteorological factors from T1 to T6. (c) The occurrence frequency of conditionally meteorological factors in the periods of T1–T6. T1, February and March; T2, April and May; T3, June and July; T4, August and September; T5, October and November; T6, December and January.

Considering samplings with prior rain events, the meteorological factors of precipitation, air temperature, relative humidity and sunshine hours in warm months (T2, T3 and T4) were generally higher than that in the cool months (T6), in particular air temperature and sunshine hours in T3 and T4, and precipitation in T4 (Figs. S5; S6). T1 to T4 had more than 100 days of rain, while T5 had only 58 days with rain. The number of rainfall days in T6 (72 days) was slightly higher than that in T5 (58 days), but it was much less than that from T1 to T4 (Table 1). The CBB significantly decreased in rain periods in T2, T3 and T4 (the warm months) with the higher average values of sunshine hours and precipitation and higher frequency of sunshine hours >5 h and more days when precipitation >0 (Fig. 2). Conversely, the average value of CBB significantly increased in rain periods in T6 (the cool months) corresponding with lower average values and frequency of sunshine hours and precipitation (Fig. 2). Unexpectedly, during the 3-day rain period when cyanobacterial biomass decreased from T2 to T4 in Xinglinwan Reservoir, our data showed a lower wind speed (low average wind speed and low frequency of wind speed >3 m/s) in warm than cool months (Fig. 2b; c).

3.2. Explanatory factors of CBB in warm or cool months

In the warm months (T2–T4), this long-term and high-frequency study of Xinglinwan Reservoir demonstrates that an increase of rainfall within 1–3 days can significantly reduce the CBB, meanwhile the dissolved oxygen (DO) decreased in general (Fig. S5), simultaneously. Considering the decreasing response of CBB after rainfall events (Fig. 2a), the significant explanatory variables ($P < 0.05$) included precipitation (Pcpt), air temperature (AT), relative humidity (RH), dissolved oxygen (DO) and total phosphorus (TP). These environmental factors explained 33.1% of variance in the CBB in warm months, and both AT and DO exhibited a better fit with CBB than precipitation and relative humidity (Table 2). AT (R^2-adjusted = 0.12) and DO (R^2-adjusted = 0.16) explained more than precipitation (R^2-adjusted = 0.06). The fitting of 3-day precipitation and CBB showed a significant negative response in rain period of warm months (Fig. 3). However, DO and total phosphorus showed different patterns in GAM fitting performance in warm months between rain period and non-rain period (Fig. 3).

Table 1
Seasonal dynamics of cyanobacterial biomass (CBB) and all explanatory factors in rain period from 2016 to 2020.

Variables	T1	T2	T3	T4	T5	T6
	(*N* = 101)	(*N* = 121)	(*N* = 100)	(*N* = 129)	(*N* = 58)	(*N* = 72)
CBB (μg L^{-1})	1.54 ± 4.94	4.81 ± 14.29	9.69 ± 18.31	6.53 ± 15.47	8.29 ± 14.57	2.32 ± 4.93
Pcpt (mm)	16.07 ± 22.14	18.02 ± 22.66	19.49 ± 24.96	28.60 ± 42.63	13.90 ± 23.63	14.60 ± 24.91
AT (°C)	14.69 ± 3.07	21.75 ± 3.29	27.35 ± 1.85	27.62 ± 1.31	21.05 ± 2.96	14.46 ± 3.17
RH (%)	80.08 ± 12.73	80.33 ± 11.98	86.91 ± 7.11	82.23 ± 8.57	74.95 ± 12.64	76.75 ± 12.86
SH (h)	3.27 ± 3.45	4.21 ± 3.15	6.11 ± 3.96	5.72 ± 3.10	3.57 ± 2.75	2.99 ± 2.89
pH	7.76 ± 0.47	7.99 ± 0.56	7.92 ± 0.62	7.81 ± 0.50	7.81 ± 0.62	7.89 ± 0.56
DO (mg L^{-1})	7.98 ± 4.11	7.40 ± 3.60	7.93 ± 3.39	5.77 ± 2.62	6.66 ± 2.82	6.97 ± 3.74
TC (mg L^{-1})	25.17 ± 9.59	27.09 ± 9.91	23.64 ± 6.42	21.17 ± 9.53	27.01 ± 11.59	31.73 ± 15.28
TP (mg L^{-1})	0.75 ± 0.22	0.65 ± 0.24	0.50 ± 0.17	0.45 ± 0.17	0.63 ± 0.29	0.87 ± 0.31

T1, February and March; T2, April and May; T3, June and July; T4, August and September; T5, October and November; T6, December and January. CBB, cyanobacterial biomass based on cyanobacterial chlorophyll-*a*; Pcpt, the three-day precipitation prior to sampling day; AT, air temperature; RH, relative humidity; SH, daily sunshine hours; DO, dissolved oxygen; TC, total carbon; TP, total phosphorus.

Table 2
The R^2-adjusted and P values of generalized additive model incorporating all significant explanatory variables and the value of each explanatory variable.

y1	Log(Pcpt)	Log(AT)	Log(RH)	Log(DO)	Log(TP)	All
R^2-adjusted	0.06	0.12	0.05	0.16	0.02	0.31
P	0.014	<0.001	0.007	<0.001	<0.001	<0.001

The y1 is the regression function based on CBB and their explanatory factors in CBB decreased periods (warm months) with precipitation greater than 0 in the 3 days before sampling day. Pcpt, the three-day precipitation prior to sampling day; AT, daily air temperature; RH, daily relative humidity; DO, dissolved oxygen; TP, total phosphorus; All; whole y1 equation. Note that all factors explained 33.1% variation of cyanobacterial biomass in warm months.

Similarly, the explanatory factors in the cool months (T6) differed between rain and non-rain periods. A non-linear relationship was observed between sunshine hours and total carbon with CBB in rainfall periods of the cool months (Fig. 4). During the cool months, the increasing response of CBB to rainfall events was significantly explained ($P < 0.05$) by daily sunshine hours (SH), pH and total carbon (TC), which explained 49.3% of variance in T6 ($P < 0.001$) (Table 3). In addition, the GAM fitting results of sunshine hours and CBB, pH and CBB, total carbon and CBB between rain and non-rain periods also showed differences in cool months. Specifically, the fitting curves of these significant factors were almost nonlinear in the rain period, while tends to be linear or stable in the non-rain period (Fig. 4). The GAM fitting of total carbon performed better (R^2-adjusted = 0.18) than sunshine hours or pH (Table 3). Total carbon showed a slight trend of decreasing after rainfall in general during the cool months, but this didn't make a significant contribution (Fig. S6).

3.3. The meteorological-environment relationship and the environment-CBB relationship in rain or non-rain periods

The relationship between CBB and meteorological variables (precipitation, wind speed and sunlight) was significantly different between rain and non-rain periods in the warm months from April to September. A combination of precipitation, wind speed and sunlight significant resulted in the rapid short-term decrease of CBB in rain periods ($P < 0.05$), while no significant causal relationship was found on the PLS-PM results between CBB and the inputted combination of wind speed and sunlight in non-rain periods (Fig. 5). In detail, when Xinglinwan Reservoir experienced short-term rainfall, the overall combined effect of these meteorological factors (precipitation, wind speed and sunlight) had a significant negative correlation (path coefficient = −0.40) with the environmental factors (water temperature, pH, dissolved oxygen) which had a positive correlation (path coefficient = 0.43) with cyanobacterial biomass (Fig. 5a). However, The PLS-PM inputted combination of wind speed and sunlight have a significant positive relationship (path coefficient = 0.55) with the combined effect of water temperature, pH, and DO, which did not have a significant relationship (path coefficient = 0.07) with cyanobacterial biomass in non-rain periods (Fig. 5b). In addition, the combination of wind speed and sunlight contributed less (path coefficient = −0.17) to the reduction of cyanobacterial biomass in non-rain conditions (Fig. 5b).

4. Discussion

Descriptions of rainfall events directly or indirectly controlling cyanobacterial biomass in subtropical reservoirs or lakes have, until now, been mostly based on extreme rainfall events, such as tropical storms, or a relatively long-term "seasonal average" temporal scale (Michalak, 2016; Yang et al., 2017; Gao et al., 2021). Few studies have analyzed the short-term effects of rainfall events on cyanobacterial biomass at a high temporal resolution (Michalak, 2016). This paper focused on the effects of rainfall events on the environmental conditions that led to changes in cyanobacterial biomass in the short-term.

4.1. Changes of explanatory factors of CBB after short-term rainfall

In warm months of the Xinglinwan Reservoir, dissolved oxygen (DO) decreased after the short-term rainfall in general perhaps due to its inhibition on phytoplankton (algae) photosynthesis efficiency or intensity. Short-term rainfall seems to strongly affect the relationship between cyanobacterial biomass (CBB) and DO only under low DO concentrations in Xinglinwan Reservoir in warm months (Fig. 3). Recent meta-analysis showed that water depth underpins the relative roles and fates of nitrogen and phosphorus in lakes, and eutrophication is favoured in shallow lakes, frequently with N limitation while P limitation predominated in most lakes especially in deep ones (Qin et al., 2020). However, the more eutrophic conditions would promote aerobic heterotrophic respiratory processes and DO depletion (Aguirrezabala et al., 2021). Stormwater runoff can increase the inputs of organic matter to aquatic ecosystems, which could explain declining DO concentrations and increasing turbidity in lake waters in urbanized catchments (McCabe et al., 2021). However, the duration and extent of this impact is related to the frequency and intensity of rainfall events in a specific reservoir (Li et al., 2015). Mostly, the small or moderate rainfall in Houxi River watershed may have limited effects of disturbance on the relationship between DO and CBB. At the same time, DO may

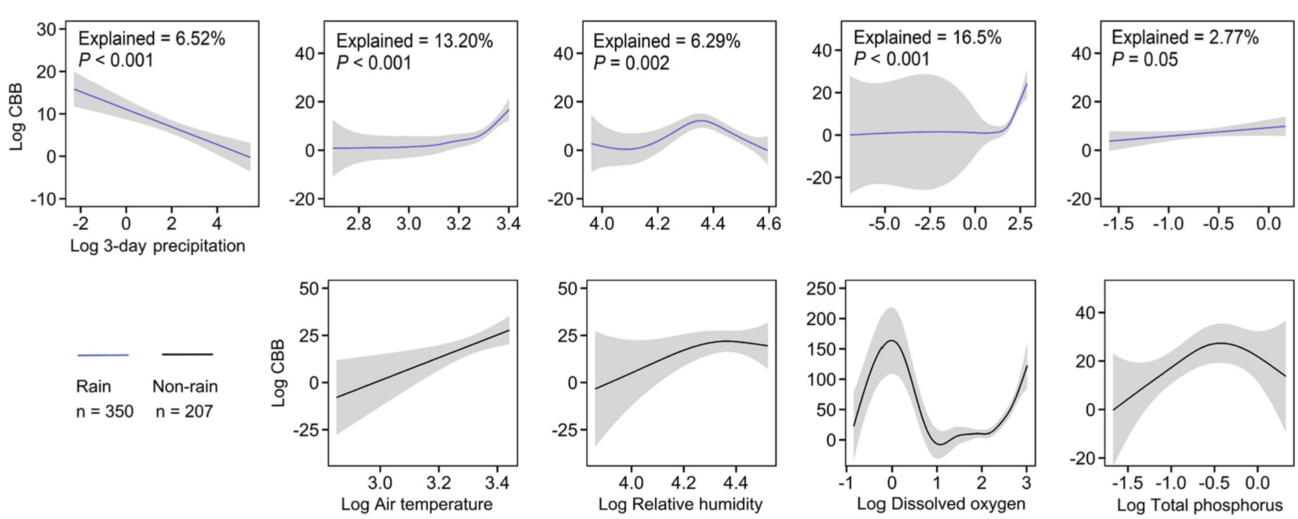

Fig. 3. Fitted plot of generalized additive models between response variable (y1) and each significant explanatory factor in rain (top plots) and non-rain (bottom plots) periods, respectively. y1 is the regression function of cyanobacterial biomass (CBB) and corresponding explanatory variables (precipitation, air temperature, relative humidity, dissolved oxygen and total phosphorus) in the warm months from April to September (T2, T3 and T4).

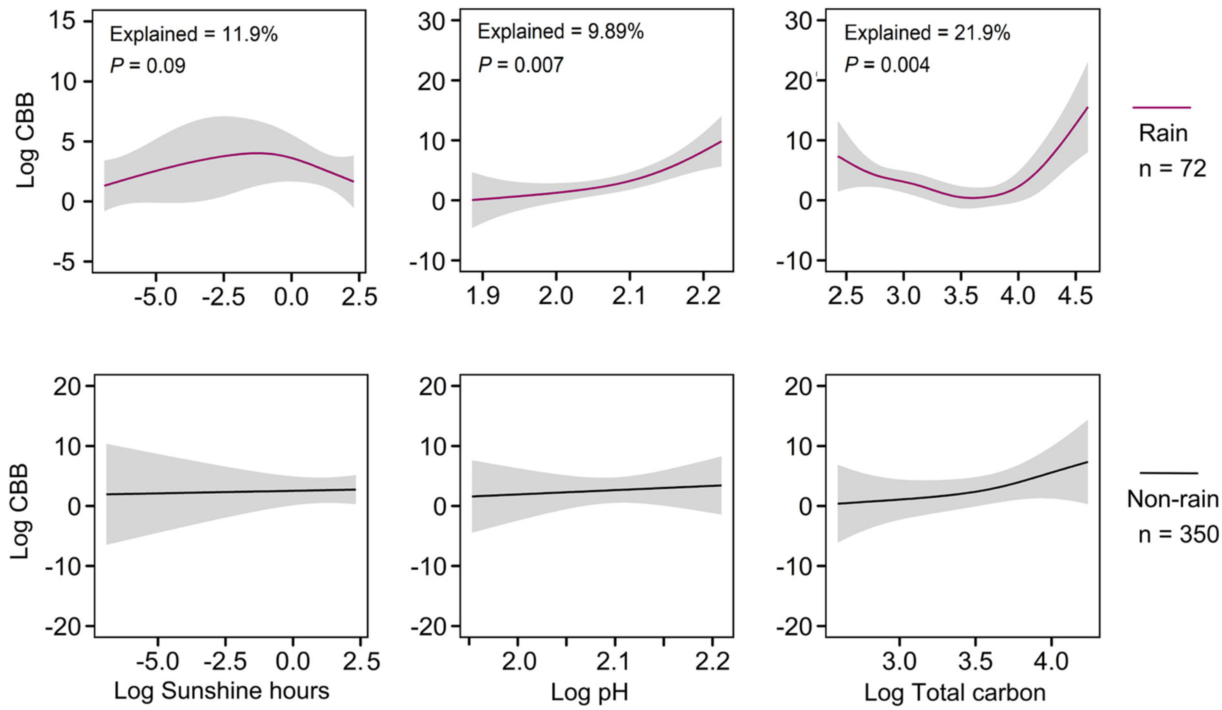

Fig. 4. Fitted plot of generalized additive models between response variables (y2) and each significant explanatory factor in rain (top plots) and non-rain (bottom plots) periods, respectively. y2 is the regression function of cyanobacterial biomass (CBB) and corresponding explanatory variables (sunshine hours, pH and total carbon) in the cool months (T6, December and January).

fluctuate greatly during a short-term rainfall period. In poor-quality rivers of temperate maritime climates of the UK, increased rainfall events can flush away phytoplankton blooms and result in a large diurnal variation in DO (Whitehead et al., 2009). The increasing vertical stratification and precipitation in summer also may cause variations in hypoxia volumes in deep waters (Zhou et al., 2014). The decline in DO took place in the presence of strong precipitation and weak winds in Xinglinwan Reservoir during the warm months.

In cool months, rainfall events changed the fitted relationship between CBB and environmental factors to sunshine hours, pH, and total carbon and with CBB increasing in Xinglinwan Reservoir. Sunshine hours, which have been observed as the primary factor affecting cyanobacterial growth (Becker et al., 2010), also showed a positive correlation with cyanobacterial abundance (Zhang et al., 2012; Hu et al., 2018). Sunshine hours, as an explanatory factor in y2, were significantly decreased by 3-day rainfall, meanwhile an increase of CBB sensitivity to sunlight hours. Weak sunlight and low temperature may result in decreased cyanobacterial biomass from warm to cool months, conversely increased available light, may facilitate underwater photosynthetic active radiation, which encourages phytoplankton growth (Álvarez et al., 2009). The relationship between pH and CBB in Xinglinwan Reservoir changed slightly with rainfall in cool months and exhibited a linear fitting in general, except for a slightly positive relationship in rain periods. At the same time, a nonlinear relationship was observed during the rainfall events between the total carbon and CBB.

Table 3
The R^2-adjusted and P values of generalized additive model incorporating all significant explanatory variables and the value of each explanatory variable.

y2	Log(SH)	Log(pH)	Log(TC)	All
R^2-adjusted	0.008	0.009	0.18	0.43
P	<0.001	0.003	0.003	<0.001

The y2 is the regression function based on CBB and their explanatory factors in CBB increased periods (cool months) with precipitation greater than 0 in the 3 days before sampling day. SH, daily sunshine hours; TC, total carbon; All, whole y2 equation. Note that all factors explained 49.3% variation of cyanobacterial biomass in cool months.

4.2. Short-term precipitation reduced the cyanobacterial biomass in warm months

The spatial and temporal extent of cyanobacterial blooms is normally affected by changing patterns in meteorological and hydrological conditions of specific watershed (Vaiciute et al., 2021). In Xinglinwan Reservoir, the increase in the intensity and frequency of short-term rainfall, ultimately led to the decline of CBB in warm months. Precipitation is considered to be the driving factor for the reduction of cyanobacterial biomass in Xinglinwan Reservoir as the results of the path analysis in rainy period and non-rain period were opposite due to the loading of the precipitation factors (Fig. 5). An 18-year dataset analysis from seven shallow lakes in Florida showed evidence that hydrologic factors (rainfall and flow) can suppress the cyanobacterial blooms (Havens et al., 2017). The increasing frequency of rainfall events often results in higher precipitation, lower temperatures and increases in wind speed, which can further increase the disturbance in lakes. Alongside this, there are increased loss rates through flushing that reduced the biomass of cyanobacteria in a short-time in Xinglinwan Reservoir.

Lower sunlight appears as another significant factor in the decline of CBB in the rainy period while no significant contribution to the increases of CBB in 3-day non-rain period in Xinglinwan Reservoir. It is well known that warmer temperatures favour the growth of bloom-forming cyanobacteria because they create the warm and static conditions that reduce vertical mixing in the lake (Michalak et al., 2013; Woolway et al., 2019). The sensitivity of cyanobacterial dynamics to climatic conditions can, however, vary by specific region or lake (Shi et al., 2017). Our results highlight that high sunlight is strongly correlated with increased CBB in non-rain periods, but the effects were not significant in the short-term (within 3 days). In the warm months of Xinglinwan Reservoir, the average value of wind speed and the frequency of strong wind are less than those in the cool months, but the cyanobacterial biomass decreases significantly during rainfall in the

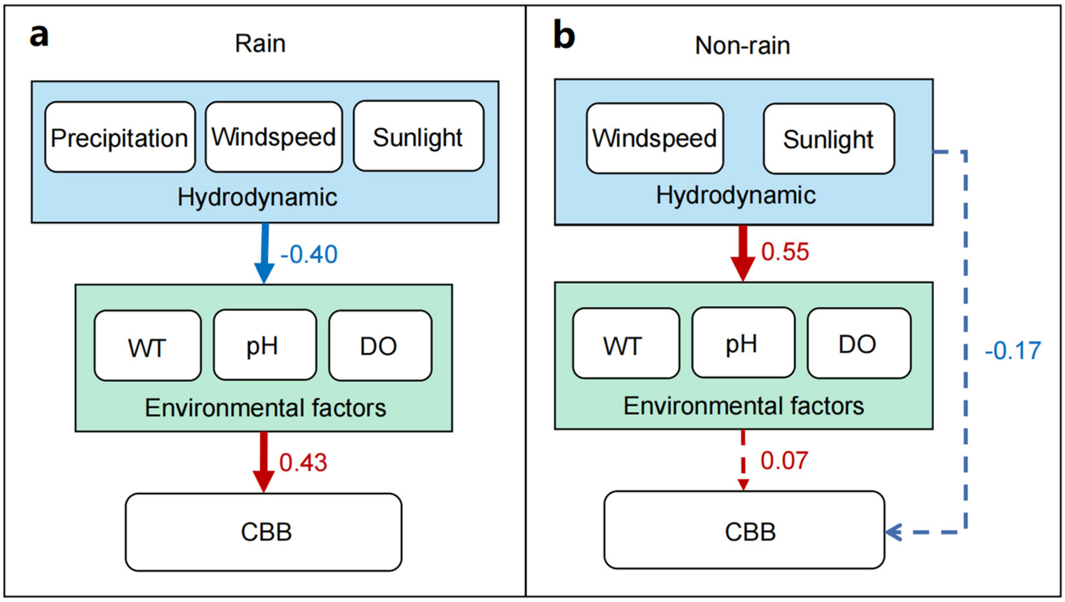

Fig. 5. Path analysis of the relationship between hydrodynamic factors and cyanobacterial biomass in the warm months from April to September in rain (a) or non-rain (b) periods, respectively. The red and blue lines represent positive and negative correlations, respectively. The number represents the significant path coefficient. The solid lines represent the significant paths, while the dashed lines represent non-significant paths. The blue rectangle represents the hydrodynamic driving factors, while the green rectangle represents water environment factors. Wind speed, the average wind speed of the three days prior to sampling date; Precipitation, the total precipitation of the three days prior to sampling date; Sunlight, the average sunshine hours of the three days prior to sampling date. WT, water temperature; DO, dissolved oxygen; CBB, cyanobacterial biomass based on cyanobacterial chlorophyll-*a*.

warm months (Fig. 2). It is noteworthy that the relationship between CBB and relative humidity may be correlative, rather than causal, with rainfall affecting both parameters. In the end, the negative effects of rainfall events (especially precipitation increase and low sunshine) appear to be the main reasons for the decrease of CBB in Xinglinwan Reservoir in the short-term in warm months.

In addition, Xinglinwan reservoir has been in a state of high eutrophication with a low resource utilization efficiency of cyanobacteria compared to the upstream low-nutrient reservoirs (Yang et al., 2022). In this study, we only considered the response of cyanobacterial biomass to a rainfall event within three days. Although precipitation can cause nutrient inputs through increased surface runoff, much of these nutrients are in complex forms and so are not readily available for cyanobacteria to use efficiently within the first three days in Xinglinwan Reservoir. As Alvarez-Cobelas et al. (2006) indicated, rainfall events can have a delayed effect on groundwater fluxes in seepage lakes, and catchment run-off may not have an immediate effect on lake nutrient concentrations, resulting in limited direct effects of nutrients on cyanobacterial blooms from rainfall in the short term. Following this process, it seems impractical to consider nutrient factors in the path analysis at Xinglinwan Reservoir. Another reason which cannot be ignored is that a given cyanobacterial bloom may move to the central water body (Umehara et al., 2015). Stations L and G are located at the inflow (upstream) of Xinglinwan Reservoir where cyanobacteria can be transferred to open water by physical processes such as water flushing and dilution caused by rainfall-driven water flow.

4.3. The reasons that cyanobacterial biomass increased in T6 (cool months)

Unexpectedly, CBB significantly increased following the rainfall in the cool months within 3 days in Xinglinwan Reservoir, unlike the warm months (Fig. 2a). Besides, large differences in cyanobacterial communities were found in Xinglinwan Reservoir between summer (July) and winter (January). Further, individual species responses to rainfall in warm or cool months may differ from these more general responses observed for cyanobacteria as a whole. The effect of precipitation and wind on CBB was great as in periods of T1 vs T6 and T2 vs T5 there were similar values for air temperature, relative humidity and daily sunshine hours but the significance of CBB change from rain to non-rain periods was different (Figs. 1b; 2a) and appeared to be strongly influenced by precipitation and wind. During the cool months (T6), the CBB was relatively low in Xinglinwan Reservoir, while meteorological conditions were characterized by a relatively weaker intensity of sunshine (less than 5 h), relatively high frequencies of higher wind speeds (more than 3 m/s), a relatively lower frequency of precipitation (Fig. 2). This is not, however, the first study that shows cyanobacteria can increase in subtropical regions in cool months. Many studies have already indicated negative relationships between wind speed and sunshine hours to cyanobacteria, such as *Microcystis* (Jöhnk et al., 2008; Zhang et al., 2012; Qu et al., 2019). One example was observed in Lake Chaohu, where the cyanobacterial biomass in winter was highest sometimes while the phytoplankton abundance in general was lowest in summer (Jiang et al., 2014; Guan et al., 2020). Specifically, this may be because these studies are in, or include, subtropical climates where cool months are still relatively warm and favourable to cyanobacteria. The growth and the dominance of cyanobacteria will be promoted when the average air temperature is mostly over 20 °C (Anneville et al., 2015; Yang et al., 2017; Weber et al., 2020). This may happen in Xinglinwan Reservoir which has relatively warm days in winter (Yang et al., 2017). On the other hand, the low temperature of the cool months (compared to the warm months) can reduce the loss rate of some cyanobacteria by low zooplankton predation pressure (Ma et al., 2016). In this way, the weakening effect in the cool months could be due to less intense and frequency of rainfall events on cyanobacterial biomass, compared to the high intensity storms of the warm months (i.e. high-frequency storm-driven perturbations in warm months).

Our study highlights the need for more published studies from subtropical regions, where patterns observed between "cool" and "warm" months may be very different from the dominant published studies from cool temperate and boreal regions. In addition, this complex or multiple responses of cyanobacteria to short-term rainfall events in the eutrophic subtropical reservoir may also be expected in temperate or cool lakes as climate change effects become stronger in the future.

5. Conclusion

To elucidate the short-term effects of rainfall events on cyanobacterial biomass, we analyzed high-frequency (half a week) sampling data of Xinglinwan Reservoir combined with local meteorological and environmental information from 2016 to 2020. We considered the rainfall-related events, and examined the 3-day response of cyanobacteria to specific environmental factors in both warm and cool months. We found that in both warm and cool months, short-term rainfall events (within 3 days) significantly explained reduced or boosted cyanobacterial biomass, respectively. Furthermore, this correlative relationship between proximal meteorological (especially precipitation) forcing factors and the reduction of cyanobacterial biomass was shown to be significant in warm months and we have provided potential causative mechanisms to explain these observations. The approaches and findings of this study offer an important insight into short-term response of cyanobacterial biomass to rainfall in shallow eutrophic lakes from subtropical monsoon regions. It can provide an analytical framework for the study of the relationship between cyanobacteria and rainfall events in the future. Finally, it is also an important study to understand the impacts of hydrological variability that informs water quality managers when they are developing strategies to reduce harmful cyanobacterial blooms in subtropical water bodies.

CRediT authorship contribution statement

J.Y. conceived the ideas and designed the experiments; H.C., L.J. and X.G. collected and determined the samples; A.L. and J.Y. analyzed the data and led the writing of the manuscript; L.C. and Y.X. discussed the analytical approach and contributed to the writing. All authors contributed to revisions and approved the final version of the manuscript.

Declaration of competing interest

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

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Appendix A. Supplementary data

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