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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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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 cyanobacterial blooms, 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 an eutrophic, urban, subtropical reservoir, we explored the short-term effects of rainfall events on cyanobacterial biomass (CBB) by constructing general additive models of CBB in rainy periods during warm (April to September) and cool (December and January) months. 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) drive changes in water temperature and hydro-dynamics of the reservoir causing a rapid reduction of CBB after rainfall events. This varying response 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.

Keywords: Climate change; phytoplankton; Precipitation; Inland water; Meteorological factors

1. Introduction

Water is a natural resource, which is essential to all ecosystems and societies. In recent decades, climate warming and human activities have caused a further deterioration of global freshwater quality, through increasing the magnitude and frequency of cyanobacterial blooms in inland freshwater systems (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 et al., 2001; Michalak et al., 2013; Qin et al., 2015; Carmichael and Boyer, 2016).

Climate variables are one of the main driving factors of cyanobacterial biomass at different latitudes (Richardson et al., 2019; Giani et al., 2020). Rainfall events can affect specific regional and watershed environments through impacts on surface runoff, temperature and wind direction (Piao et al., 2010; Ho and Michalak, 2019; Weber et al., 2020) and thus change the physico-chemical conditions in water bodies, further boosting or abating cyanobacterial blooms (Reichwaldt et al., 2012; Yang et al., 2017). 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 (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 events 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 H 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 increase surface runoff and decrease precipitation infiltration (Paul and Meyer, 2001; Grimm et al., 2008). Moreover, urbanization-driven increases 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 (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 analyse the cyanobacteria-rainfall relationship in sub-tropical climates. In view of these gaps, this study aimed to:

1) explore the cyanobacterial response in a sub-tropical 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 rainy 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 m3, 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).

Water samples were normally taken from the surface water (0.5 m depth) at two stations (station L: 24° 36' 21" N, 118° 03' 37"; station G: 24° 36' 09" N, 118° 03' 59" E) twice a week (Tuesday and Friday) from 6th January 2016 to 29th December 2020. 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), taking three replicate measurements and calculate the average value for each sample. The physical data (water temperature, pH, dissolved oxygen, turbidity and salinity) were measured at the stations using a Hydrolab DS5 multiparameter water quality analyzer (Hach Company, Loveland, CO, USA). The chemical data including total carbon (TC), total nitrogen (TN), total organic carbon (TOC), ammonium-nitrogen (NH_4-N), nitrate-nitrogen (NO_3-N), nitrite-nitrogen (NO_2-N), total phosphorus (TP), orthophosphate-phosphorus (PO_4-P) were measured following standard methods (Greenberg et al., 1992). 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 Center (CMDC) of the National Meteorological Information Center in China (http://data.cma.cn). In addition, daily temperature range was calculated by the difference between the max and min air temperatures. Table S1 presents a descriptive analysis of all variables.

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 ($Pcpt_X$), 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 divided into 6 bi-monthly periods ("Tgroup") for considering the seasonal changes in CBB: T1 (sampled in February and March, N = 165), T2 (sampled in April and May, N = 175), 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. 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 (Table S2; Table 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 influenced the effects of rainfall in warm or cool months were used to model CBB based on a generalized additive model (GAM). 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. 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 analyse structural relationships between variables (Tenenhaus et al., 2005). We constructed a statistic for detecting the relationship between meteorological factors and CBB. 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 and dissolved oxygen et al), and CBB. PLSPM was performed with the plspm package in a R studio 3.6.3 (R Core Team, 2020).

3. Result

3.1. Seasonal changes of cyanobacterial biomass in rain and 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 (Fig. 1b; Fig. S1). 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. 1b; 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). 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).

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 all higher than that in the cool months (T6), in particular air temperature and sunshine hours in T3 and T4, and precipitation in T4 (Table 1). T1 to T4 had more than 100 days of rain, while T5 had only 58 days with rain. Days of rainfall in T6 (72 days) is slightly higher than that in T5 (58 days), but it is still less than that from T1 to T4 (Table 1). The CBB significantly decreased 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 days when precipitation > 0 (Fig. 2). Conversely, the average value of CBB significantly increased 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 in Xinglinwan Reservior, our data showed a lower wind speed (low average wind speed and low frequency of wind speed > 3m/s) in warm months (Fig. 2b; Fig. 2c).

3.2. Explanatory factors of CBB in warm or cool months

In the warm months, 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. S2), 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 factors explained 33.1% of variance in the warm months ($P < 0.001$) of the meteorological factors (Table 2). AT (R^2-adjusted = 0.16) and DO (R^2-adjusted = 0.12) explained more than Pcpt, AT and RH and DO also showed a fit with CBB. The fitting of 3-days 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).

Similarly, the explanatory factors in the cool months differed before and after short-term rainfall events. 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 before and after rain period also showed differences in cool months. Specifically, the fitting curve of these significant factors are almost nonlinear in the period of rain, while tends to be linear or stable in the period of non-rain (Fig. 4). The GAM fitting of TC performed better (R^2-adjusted = 0.18) than SH or pH (Table 3). Total carbon showed a slight trend of decreasing after rainfall in general the cool months (Fig. 4), but this didn't make a significant contribution to the CBB decreased (Fig. S2).

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. A combination of precipitation, wind speed and sunlight significant resulted in the 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 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 analysed 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. Short term rainfall seems to affect the relationship between cyanobacterial biomass (CBB) and DO only at low concentrations in Xinglinwan Reservoir. The relationship between CBB and DO may be correlative, rather than causal, with rainfall affecting both these parametrs. Stormwater runoff can increase the inputs of organic matter to aquatic ecosystems, which could explain declining DO concentrations and increasing turbidity in lake waters (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 may have limited the effects of disturbance in the relationship between DO and CBB. At the same time, DO may 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 algal blooms and result in a large diurnal variation in DO (Whitehead et al., 2009). The increasing vertical stratification and precipitation in summer may cause variations in hypoxia volumes (Zhou et al., 2014). The decline in DO took place in the presence of strong precipitation and southwesterly 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 have been observed as the primary factor affecting cyanobacterial growth (Becker et al., 2010), and have been shown to be positively correlated with cyanobacterial abundance (Zhang et al., 2012; Hu et al., 2018). Sunshine hours, as an explanatory factor in y2, was significantly decreased by 3-days of rainfall, meanwhile an increase of CBB sensitivity to sunlight hours. Weak sunlight and temperature may result in decreased cyanobacterial biomass, conversely increased available light , may facilitate underwater photosynthetic active radiation, which encourages phytoplankton growth (Álvarez et al., 2005). 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.

4.2 Precipitation reduced the cyanobacterial biomass in Xinglinwan Reservoir in short term

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 both warm and cool 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 are 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 cyanobacterial blooms (Havens et al., 2017). The increasing frequency of rainfall events results in higher precipitation, lower temperatures and increases in wind speed, which increase the disturbance in lakes. Alongside this, there are increased loss rates through flushing that reduced the biomass of phytoplankton 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, 2013; Woolway et al., 2019). The sensitivity of cyanobacterial dynamics to climatic conditions can, however, vary by specific region (Shi et al., 2017). Our results highlight high sunlight is 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 warm months. 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 addition, Xinglinwan reservoir has been in a state of eutrophication with a low resource utilization efficiency (RUE) 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 Xinglingwan Reservoir. Another reason 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 of Xinglinwan Reservoir, where cyanobacteria can be transferred to open water by physical processes such as water flushing and dilution caused by rainfall.

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 in Xinglinwan Reservoir during the cool months showed a relatively weak intensity of sunshine (less than 5 hours), relatively high frequencies of high wind speeds (more than 3 m/s), a relatively low frequency of precipitation and a decline of CBB. 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. On the other hand, the lower temperature of the cool months (compared to the warm months) can reduce the loss rate of some cyanobacteria by lower 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 more typical 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. 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 information from 2016 to 2020. We considered the condition of rainfall events, and examined the 3-day response of cyanobacteria to specific environmental factors in both warm and cool months. We observed that in both warm and cool months, short-term rainfall (with 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 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 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.

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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Author contributions

J.Y. conceived the ideas and designed the experiments; H.C. 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.

Supplementary materials

Supplementary material associated with this article can be found online.

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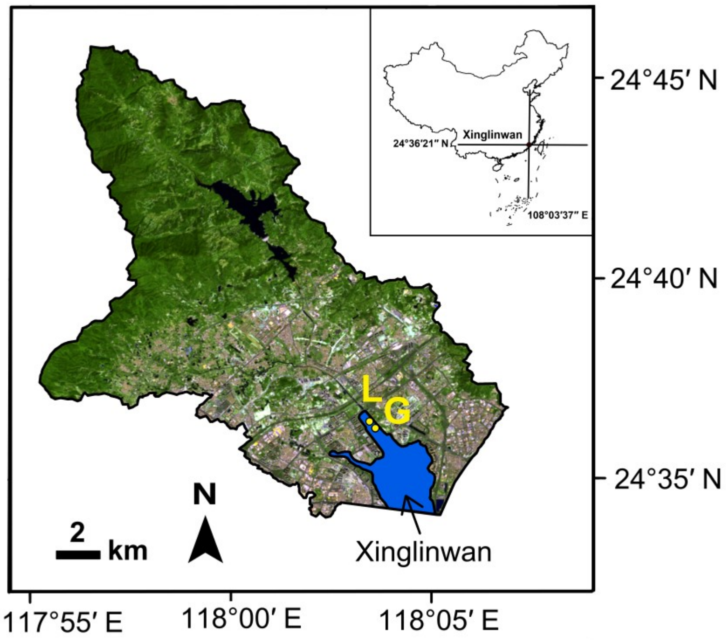

Fig. 1. Map of Houxi River watershed showing the sampling sites in Xinglinwan Reservoir, Southeast China. Stations G and L are two sampling sites.

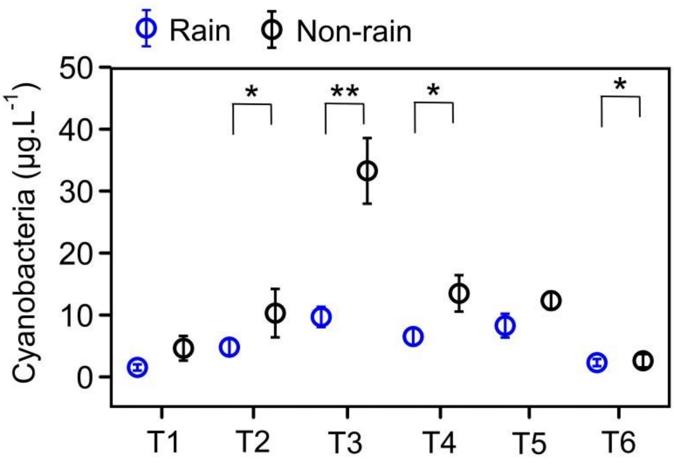

Fig. 2. Seasonal d~~D~~ifferences in cyanobacterial biomass between rain and non-rain periods from T1 to T6. T1, February and March; T2, April and May; T3, June and July; T4, August and September; T5, October and November; T6, December and January. (*, $P < 0.05$; **, $P < 0.001$)

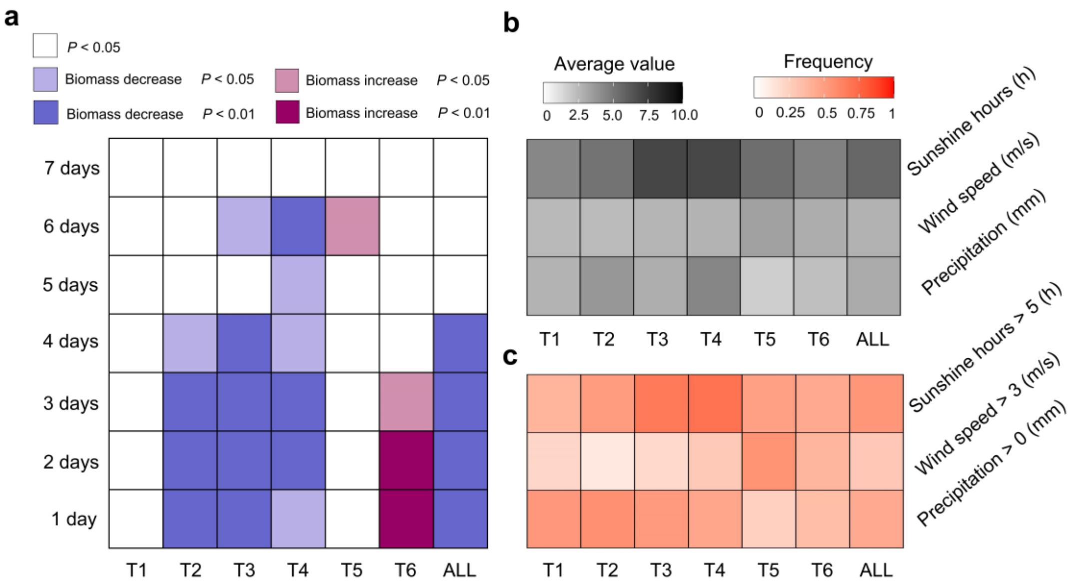

Fig. 3. The response of cyanobacteria biomass to rain events in 1-7 day/days (a), and the meteorological conditions from T1 to T6 (b, c). For (a), the colored squares represented significant differences in cyanobacterial biomass before and after rainfall events. Darkness or lightness of color represented the level of significant difference in cyanobacteria. The purple color represents a significant decrease in cyanobacterial biomass after rainfall, while the pink color represents a significant increase in cyanobacterial biomass after rainfall. X day/days (X = 1, 2, 3, 4, 5, 6) represented the total rainfall for X days prior to sampling. For (b), the colored squares represented the average of meteorological factors during T1-T6. (c) the occurrence frequency of conditionally meteorological factors in the period of T1-T6.

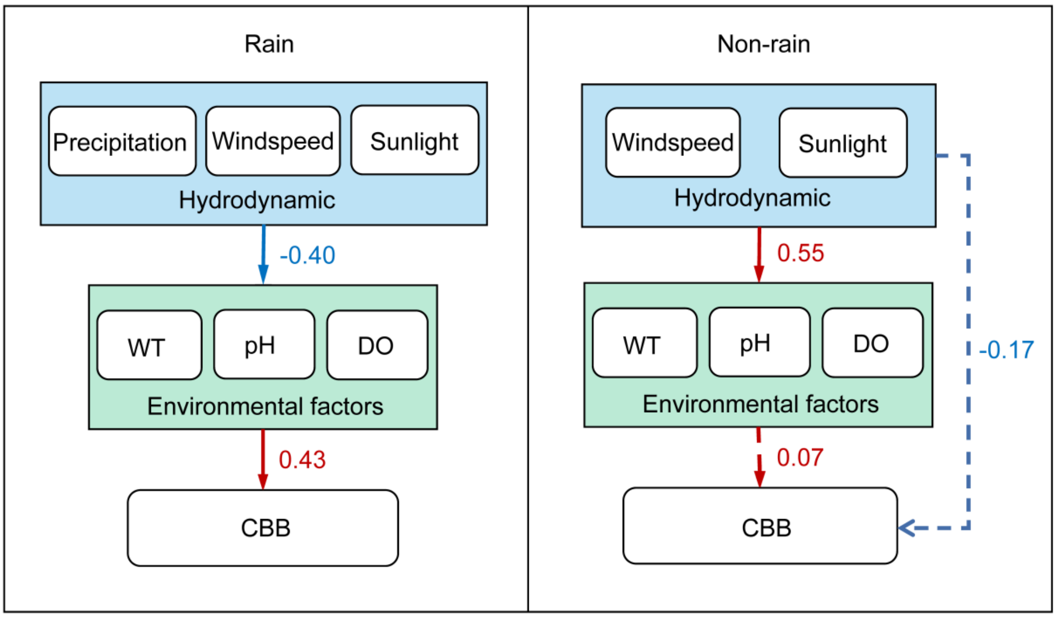

Fig. 4. Path analysis of the relationship between hydrodynamic and cyanobacterial biomass. The red and blue lines represent positive and negative correlations, respectively. The number represents the significant path coefficient. The solid lines represented the significant paths and dotted lines represented the non-significant paths. The blue rectangle represents the hydrodynamic driving factors. The green rectangle represents the environmental factors. Windspeed, the average wind speed of the three days prior to sampling; Precipitation, the total precipitation of the three days prior to sampling; Sunlight, the average sunshine hours of the three days prior to sampling; Environmental factors composed of water temperature (WT), pH, dissolved oxygen (DO).

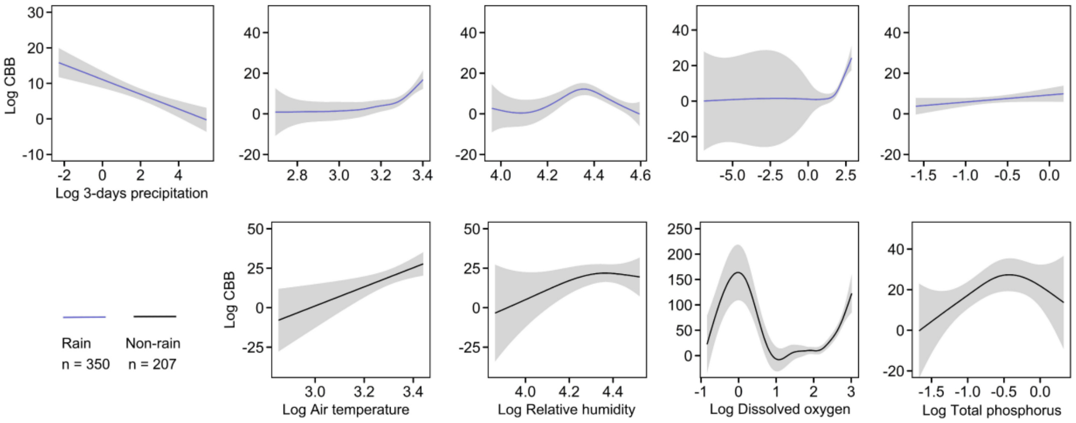

Fig. 5. Fitted plot of generalized additive models between response variables (y1) and each of significant explanatory factors. y1 is the difference between expected cyanobacterial biomass (CBB) derived from 95% quantile regression for warmer season (T2, T3 and T4, April to September).

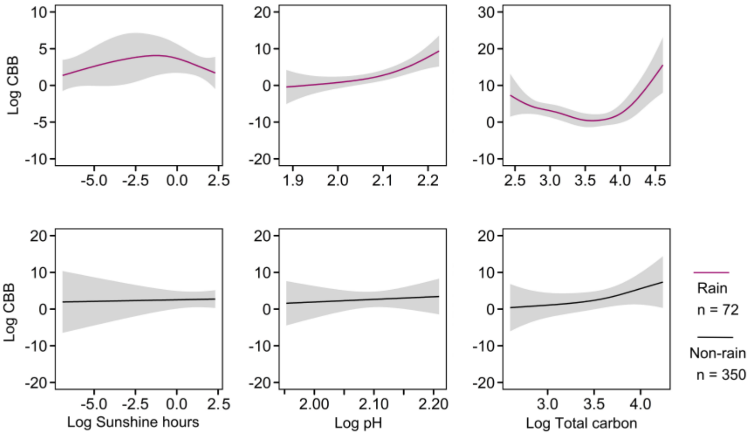

Fig. 6. Fitted plot of generalized additive models between response variables (y2) and each of significant explanatory factors. y2 is the difference between expected cyanobacterial biomass (CBB) derived from 95% quantile regression for colder season (T6, December and January).

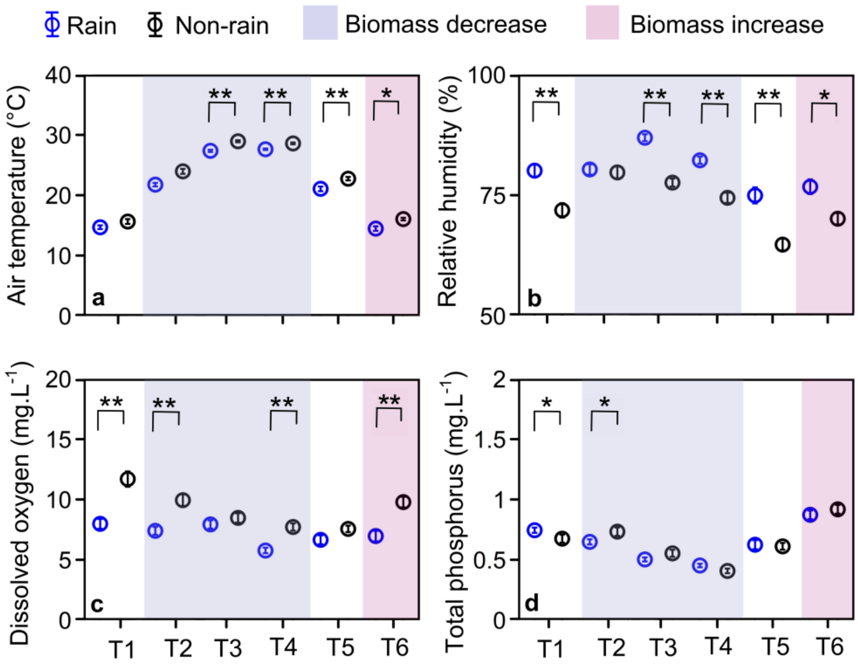

Fig. 7. The seasonal difference (*, $P < 0.05$; **, $P < 0.001$) of the explanatory factors for y1 between rain and non-rain periods. y1 is the difference between expected cyanobacterial biomass (CBB) derived from 95% quantile regression for warmer season.

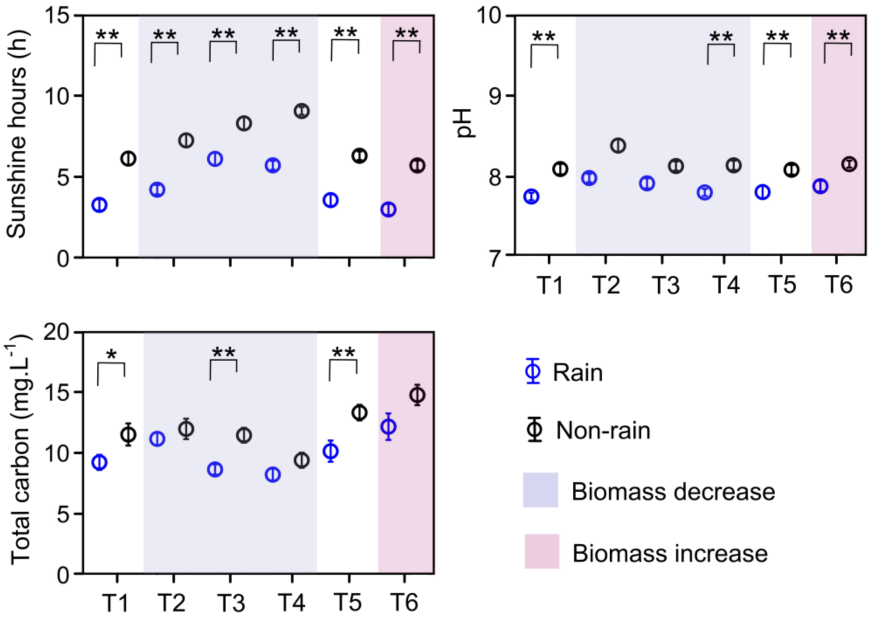

Fig. 8. The seasonal difference (*, $P < 0.05$; **, $P < 0.001$) of the explanatory factors for y2 between rain and non-rain periods. y2 is the difference between expected cyanobacterial biomass (CBB) derived from 95% quantile regression for colder season.

Table 1

Seasonal analysis of cyanobacterial biomass (CBB) and all explanatory factors for samplings with prior rain events (2016-2020).

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) and T6 (December and January); CBB, cyanobacterial biomass; Pcpt, the total precipitation 3-days prior to sampling; AT, air temperature; RH, relative humidity; DO, dissolved oxygen; TC, total carbon; TP, total phosphorus.

Table 2

The R^2-adjusted and *P* value of significant explanatory variables in the generalized additive model for CBB for the T2 to T4 warm period (April to September).

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

y1 is the difference between expected cyanobacterial biomass (CBB) derived from 95% quantile regression in CBB decreased periods (warm seasons) with precipitation greater than 0 in the 3 days before sampling. Pcpt, the total precipitation during the first three days of sampling; AT, daily air temperature; RH, daily relative humidity; DO, dissolved oxygen; TP, total phosphorus; All; whole y1 equation.

Table 3

The R^2-adjusted and P values of significant explanatory variables in the generalized additive model of CBB for the T6 cold period (December & January).

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

y2 is the difference between expected cyanobacterial biomass (CBB) derived from 95% quantile regression in CBB increased periods (cold seasons) with precipitation greater than 0 in the 3 days before sampling. SH, daily sunshine hours; TC, total carbon; All, whole y2 equation.

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Supplementary information of the article

Short-term responses of cyanobacteria to the environment after rainfall events in a subtropical urban reservoir

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This supplementary information contains:

- 5 Pages
- 1 Figure
- 3 Tables

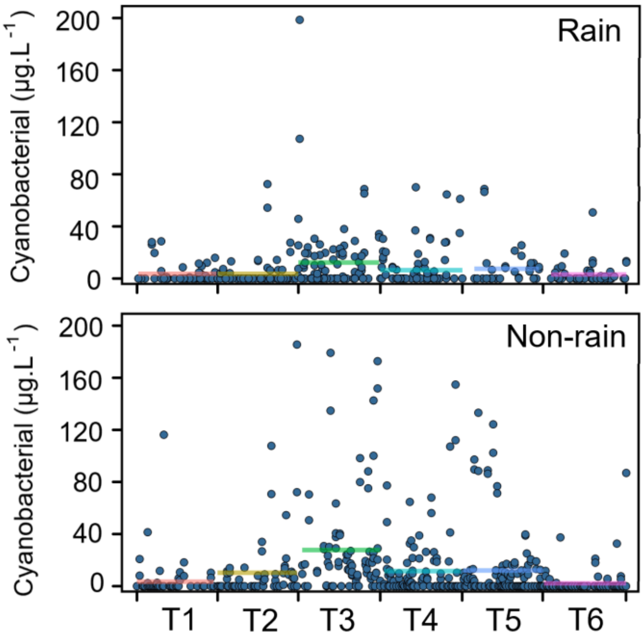


Fig. S1. Scatter plot of cyanobacteria biomass in periods of rain or non-rain from T1 to T6 (2016-2020). The colored horizontal lines represent the average value of cyanobacterial biomass in each Tgroup (T1 to T6).

Table S1

Factor load matrix of warmer season (T2, T3 and T4). The bold black number represent the factors with the highest absolute value score of each Factor (Factor1-Factor6).

Variables	Factor1	Factor2	Factor3	Factor4	Factor5	Factor6
Water temperature (°C)	-0.08	0.929	0.147	-0.093	-0.001	-0.024
pH	-0.05	0.103	0.827	-0.124	0.074	-0.177
DO (mg.L^{-1})	0.004	0.085	**0.858**	0.005	0.029	-0.049
Turbidity	0.038	0.048	-0.069	-0.123	-0.267	0.602
EC (μS/cm)	0.858	-0.131	0.167	0.243	-0.031	0.023
Salinity	0.85	-0.129	0.169	0.247	-0.036	0.027
ORP (mV)	-0.115	-0.165	-0.159	-0.002	**-0.739**	0.041
TC (mg.L^{-1})	0.689	0.071	-0.003	0.204	0.512	-0.210
TOC (mg.L^{-1})	0.601	0.050	0.044	0.209	0.607	-0.194
TN (mg.L^{-1})	0.688	-0.212	-0.061	-0.035	0.459	-0.247
NH$_4$-N (mg.L^{-1})	0.672	-0.076	-0.242	-0.039	-0.014	-0.438
NO$_3$-N (mg.L^{-1})	-0.644	-0.306	-0.137	0.027	0.226	0.395
NO$_2$-N (mg.L^{-1})	-0.164	-0.104	0.099	-0.147	0.555	-0.402
TP (mg.L^{-1})	**0.871**	-0.148	0.015	-0.059	0.144	0.071
PO$_4$-P (mg.L^{-1})	0.745	-0.167	-0.220	-0.096	0.019	0.155
Large evaporation (mm)	0.329	0.425	0.168	0.709	-0.032	-0.122
Relative humidity (%)	-0.231	0.058	-0.219	**-0.795**	-0.102	0.220
Sunshine hours (h)	-0.022	0.569	0.518	0.399	0.123	-0.023
Air temperature (°C)	0.246	**0.939**	-0.009	-0.004	0.020	0.046
Surface temperature (°C)	-0.154	0.925	0.204	0.068	0.078	-0.066
Wind speed (m/s)	-0.147	-0.111	-0.293	0.660	-0.072	0.007
AT$_{max}$-AT$_{min}$ (°C)	0.091	0.270	0.557	0.326	0.230	-0.061
Precipitation (mm)	-0.163	-0.119	-0.176	-0.138	-0.066	**0.674**

DO, dissolved oxygen; EC, electrical conductivity; ORP , oxidation-reduction potentia; TC, total carbon; TOC, total oxygen carbon; TN, total nitrogen; NH_4-N, ammonium nitrogen; NO_3-N, nitrate nitrogen ; NO_2-N, nitrite nitrogen; TP, total phosphorus; PO_4-P, phosphate phosphorus; AT_{max}-AT_{min}, value of the maximum temperature minus minimum temperature; Precipitation, The total rainfall for the first three days of the sampling date.

Table S2

Factor load matrix of colder season (T6). The bold black number represent the factors with the highest absolute value score of each Factor (Factor1-Factor8).

DO, dissolved oxygen; EC, electrical conductivity; ORP , oxidation-reduction potentia; TC, total carbon; TOC, total oxygen carbon; TN, total nitrogen; NH_4-N, ammonium nitrogen; NO_3-N, nitrate nitrogen ; NO_2-N, nitrite nitrogen; TP, total phosphorus; PO_4-P, phosphate phosphorus; AT_{max}-AT_{min}, value of the maximum temperature minus minimum temperature; Precipitation, The total rainfall for the first three days of the sampling date.

Variables	Factor1	Factor2	Factor3	Factor4	Factor5	Factor6	Factor7	Factor8
Water temperature (°C)	0.067	0.084	0.903	0.050	0.121	-0.050	0.112	0.115
pH	-0.078	0.231	0.091	-0.249	-0.094	-0.504	-0.199	0.614
DO ($mg.L^{-1}$)	0.430	0.420	-0.092	-0.164	0.138	-0.167	-0.162	0.497
Turbidity	0.299	-0.127	0.116	-0.702	-0.219	0.438	-0.089	-0.050
EC (μS/cm)	0.376	0.053	0.025	0.041	0.880	-0.163	0.135	-0.084
Salinity	0.367	0.054	0.022	0.036	**0.886**	-0.161	0.129	-0.083
ORP (mV)	-0.094	-0.151	-0.139	-0.116	-0.051	-0.132	0.052	**-0.813**
TC ($mg.L^{-1}$)	**0.883**	-0.077	0.061	-0.058	0.166	-0.115	0.251	0.126
TOC ($mg.L^{-1}$)	0.882	0.001	0.051	0.038	0.255	-0.035	0.177	0.238
TN ($mg.L^{-1}$)	0.459	0.026	-0.013	**0.738**	-0.120	0.202	-0.015	0.145
NH_4-N ($mg.L^{-1}$)	0.338	-0.003	0.045	0.405	0.254	-0.253	-0.027	-0.526
NO_3-N ($mg.L^{-1}$)	-0.137	0.096	-0.171	-0.011	-0.350	0.846	-0.099	0.147
NO_2-N ($mg.L^{-1}$)	0.240	0.100	0.189	0.214	-0.178	0.075	0.113	0.727
TP ($mg.L^{-1}$)	0.882	0.115	-0.021	0.043	0.275	-0.092	-0.155	-0.071
PO_4-P ($mg.L^{-1}$)	0.690	0.044	-0.136	0.363	0.239	0.034	-0.295	-0.374
Large evaporation (mm)	0.133	0.687	-0.074	-0.200	0.203	-0.075	0.532	0.093
Relative humidity (%)	-0.105	-0.813	0.196	0.046	-0.215	0.055	-0.360	-0.063
Sunshine hours (h)	-0.053	**0.912**	0.096	0.012	-0.062	-0.026	-0.027	0.176
Air temperature (°C)	-0.054	-0.137	0.931	-0.026	-0.071	-0.105	-0.164	0.075
Surface temperature (°C)	0.016	0.005	**0.935**	-0.096	-0.014	-0.129	-0.153	0.088
Wind speed (m/s)	0.057	0.044	-0.159	0.065	0.148	-0.173	**0.881**	-0.074
AT_{max}-AT_{min} (°C)	-0.019	0.803	0.037	0.254	-0.084	-0.019	-0.202	0.087
Precipitation (mm)	-0.088	-0.141	-0.143	-0.073	-0.036	**0.895**	-0.153	0.045

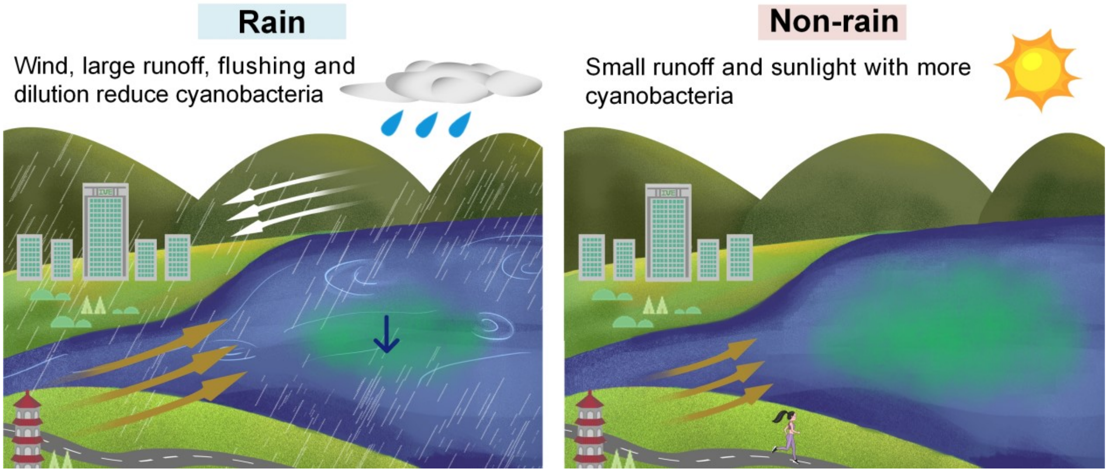
Table S3

The GAM fitting between each selected factor with cyanobacteria, from y1 (warmer season) or y2 (colder season) respectively. The bold black number represent the factors with the $P < 0.05$ of each Factor (Factor1-Factor8).

TP, total phosphorus; DO, dissolved oxygen; ORP , oxidation-reduction potentia; Precipitation, The total rainfall for the first three days of the sampling date; TC, total carbon; TN, total nitrogen.

Variables	y1		y2	
	Explained	*P*	Explained	*P*
Air temperature (°C)	13.20 %	**< 0.001**		
Relative humidity (%)	6.29 %	**0.002**		
TP ($mg.L^{-1}$)	2.77 %	0.050		
DO ($mg.L^{-1}$)	16.5 %	**< 0.001**		
ORP (mV)	2.73 %	**0.020**		
Precipitation (mm)	6.52 %	**< 0.001**	4.05 %	0.342
Sunshine hours (h)			11.2 %	**0.090**
Surface temperature (°C)			4.15 %	0.392
Wind speed (m/s)			20.1%	0.050
Salinity			15.4 %	0.102
pH			9.89 %	**0.007**
TC ($mg.L^{-1}$)			21.9 %	**0.004**
TN ($mg.L^{-1}$)			6.57 %	0.297

GRAPHICAL ABSTRACT



Short-term responses of cyanobacteria to the environment after rainfall events in a subtropical urban reservoir

Keywords: climate change; harmful algal bloom; hydrodynamics regimes; flushing; dilution; subtropical reservoir

Highlight：

1. The short-term (3 days) effects of rainfall events on cyanobacterial biomass and hydrodynamic conditions were analyzed using the long-term (5 years), high-frequency (half a week) sampling data from Xinglinwan Reservoir.

2. Rainfall events reduced cyanobacterial biomass within 3 days by changing the magnitude and frequency of rainfall (and sunshine) in both warm season and cold seasons.

3. Cyanobacterial biomass decreased in warmer season in response to precipitation, air temperature, relative humidity, dissolved oxygen and total phosphorus compared with decreased in the colder season in response to sunshine hours, pH, total carbon.

4. Hydrodynamic factors that rainfall, wind speed and sunshine hours are the driving factors for the short-term reduction of cyanobacterial biomass.

5. The explanatory factors for cyanobacterial biomass in warmer season and colder season were examined using factors analysis combined with generalized additive models. And used the least-square path analysis to explore the relationship between cyanobacterial biomass and hydrodynamic regimes.

Hypothesis:

1. The short-term response of cyanobacterial biomass varies seasonally in relation to the magnitude and frequency of rainfall (and sunshine) events.

2. Short-term rainfall events indirectly affected cyanobacteria biomass by changing different environmental factors in warmer season and colder season.

3. Hydrodynamic regimes are the main factors that affects the relationship between cyanobacterial biomass and rainfall in the short term.