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Dissolved silicon in a lake-floodplain system: Dynamics and its role in primary production

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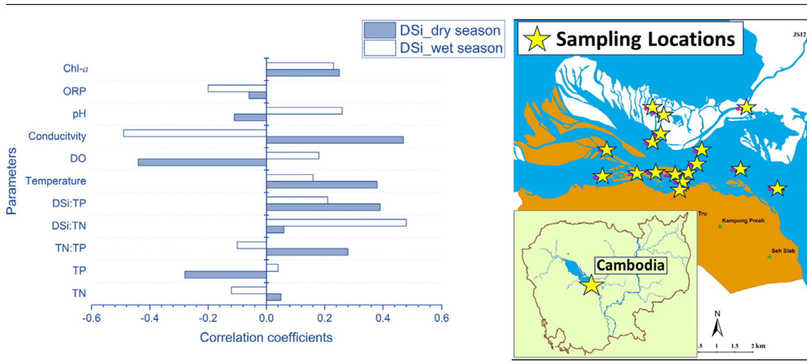
HIGHLIGHTS

- DSi dynamics around floating unique villages at Chhnok Tru, Cambodia.
- Large-scale investigation of water quality parameters in Lake-floodplain System.
- Comparisons with global values for DSi and other related parameters

GRAPHICAL ABSTRACT



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ABSTRACT

Dissolved silicon (DSi) is essential for aquatic primary production and its limitation relative to nitrogen (N) and phosphorus (P) facilitates cyanobacterial dominance. However, the effects of DSi on phytoplankton growth and community structure have yet to be fully determined in tropical lakes, particularly in relation to N and P. Therefore, this study investigated the role of DSi in Tonlé Sap Lake, Cambodia, a tropical floodplain system well known for its flood-pulse characteristics and high productivity. To that end, seasonal water sampling and in situ water quality measurements were performed around the floating villages of Chhnok Tru region. The concentration of DSi was significantly higher in the dry season than in the wet season at 16.3–22.1 versus 7.2–14.0 mg/L, respectively; however, both sets of measurements were comparable with lakes in other parts of the world. Meanwhile, the average molar ratio of TN:TP:DSi was 69:1:33 in the dry season and 39:1:24 in the wet season, which compared with the Redfield ratio of 16:1:16, suggested limitation of TP and DSi in both seasons. In addition, phytoplankton biomass in terms of chlorophyll-*a* was found to be a collective function of DSi, TN:TP, dissolved oxygen, and water temperature in both seasons. Taken together, these results suggest that DSi is affected by the annual hydrological cycle in the Tonlé Sap Lake flood-pulse ecosystem, serving as a secondary limiting nutrient of primary production during both the dry and wet seasons.

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1. Introduction

Diatoms are the most abundant phytoplankton on Earth (Cameron, 2013; Reynolds, 2006). They play an essential role in sequestering carbon dioxide from the atmosphere via the biological pump (Ittekkot, 2006; Schelske, 2010), thereby playing an important role in the global primary production and biogeochemical cycles. Aquatic ecosystems contain an abundance of different phytoplankton, including cyanobacteria, chlorphytes, diatoms, chrysophytes, dinogellates, and crptophytes. However, only diatoms dominantly rely on dissolved silicon (DSi) in its concentrated form, silicon dioxide (SiO_2), to form their skeletal structures (Conley et al., 2000; Harashima et al., 2006; Schelske, 2010). The presence of diatoms therefore depends on the availability of DSi, which in turn has a significant impact on the structure and functioning of the entire food web (Townsend and Cammen, 1988) because diatoms are the main food source of numerous organisms in the upper trophic levels (Ryther, 1969). The availability of DSi therefore has a direct effect on the species composition and biomass of phytoplankton communities (Canfield et al., 2005a, 2005b; Pasztaleniec, 2016; Reid, 2005). Changes in phytoplankton species composition also have an effect on the efficiency of nutrient recycling. For example, when the DSi concentration is low, diatom growth is limited and the subsequent sinking rate increases dramatically (Titman and Kilham, 1976; Bienfang et al., 1982), providing the sediment layer with fresh organic matter. This is because the sinking rate of phytoplankton is dependent on phytoplanton biomass and the setting velocity (Bienfang, 1981; Wang et al., 2022). Moreover, Titman and Kilham (1976) reported that the sinking rate of freshwater phytoplankon is also affected by the nutrient-depleted condition of their cells and the subsequent loss rate from the mixed layer of the lake. Thus, the concentration of DSi in the surface water impacts phytoplankton balance, food chain dynamics, and biogeochemical cycling of aquatic ecosystems (Kristiansen and Hoell, 2002).

DSi is derived from both diffuse and point sources within the river basin. Silica weathering, atmospheric deposition, domestic wastewater and paper pulp production are all sources of DSi in aquatic environments (Canfield et al., 2005a, 2005b; Struyf et al., 2009; Lü et al., 2015; Jennerjahn et al., 2006; Tegen and Kohfeld, 2006; Sferratore et al., 2006). As such, DSi concentrations in aquatic ecosystems depend on the source and subsequent transport, both of which are controlled by watershed geology, hydrology, and water uses in the river basin (Egge and Aksnes, 1992; Canfield et al., 2005a, 2005b). Seasonal fluctuations in DSi concentrations are also affected by flow (high versus low flow rates), which in turn influences the seasonal dominance of phytoplankton in complex reservoirs (An, 2003; Sigleo and Frick, 2003). In addition, seasonal changes in water temperature and pH also affect the solubility of DSi in these aquatic ecosystems (Blanchard, 1988).

As a result, Cloern (2001) revealed that DSi also plays a role in eutrophication of coastal and lake ecosystems. As a result of anthropogenic inputs, nitrogen (N) and phosphorus (P) concentrations have doubled in most major lakes and rivers worldwide (Seitzinger et al., 2005), causing changes in the ratio of Si:N and Si:P, which affects the composition of phytoplankton communities (Conley et al., 1993). Changes in the ratios of Si, N, and P can also result in the dominance of non-diatoms such as flagellates (Officer and Ryther, 1980). Limited DSi and subsequent reductions in phytoplankton can therefore have a potential effect on the entire food web structure because zooplankton dynamics are also affected by the decreased ratios of Si:N and Si:P. The main reason for reductions in DSi and subsequent toxic algal blooms is unbalanced nutrient stoichiometry. Redfield et al. (1963) previously reported the Redfield ratio of nutrient balance (N:P:Si = 16:1:16) required for phytoplankton health, with deviation indicating a growth-limiting deficiency. Meanwhile, Teubner and Dokulil (2002) reported that strong seasonal fluctuations in TN:TP are associated with cyanobacterial dominance, while highly variable DSi concentrations following low seasonal variability in TN:TP favor diatom dominance in hypereutrophic lakes. In addition, a shift in N:P towards P was also found to favor diazotrophic phytoplankton over non-diazotrophs (Havens et al., 2003), while limited DSi was found to cause a shift from siliceous diatoms to non-siliceous algal species (Harashima, 2007). Nutrient balance in terms of N:P:Si therefore has a direct effect on the succession of phytoplankton growth in rivers and lakes (Glooschenko and Alvis, 1973; Pandey and Yadav, 2015; Pandey et al., 2016).

Studies on DSi stoichiometry in relation to N and P as well as the effect of DSi on primary production in lakes and rivers are therefore gaining increasing attention in the fields of biogeochemistry and limnology (e.g., Choudhury and Bhadury, 2015; Dongfang et al., 2005; Pandey et al., 2016; Turner et al., 2003). Accordingly, numerous studies have documented DSi limitations in aquatic ecosystems; for example, in Solina-Myczkowce mountain reservoirs of San River, SE Poland (Koszelnik and Tomaszek, 2008), the Garonne river in France (Pandey et al., 2016; Yadav and Pandey, 2018), and the Upper Mississippi River System (UMRS) (Carey et al., 2019). Moreover, a negative correlation between limitation of DSi and chlorophyll-*a* concentrations was also revealed (Koszelnik and Tomaszek, 2008), suggesting that eutrophication enhances phytoplankton growth, accelerating DSi uptake, which results in depletion (Muylaert et al., 2009). Thus, depletion of DSi can also be caused by eutrophication, resulting in toxic algal blooms and subsequent changes to the ecosystem dynamics (Conley et al., 1993).

Despite this, however, little is known about the stoichiometry of DSi and other nutrients in shallow flood-pulse lakes, which tend to have a close relationship with seasonal hydrological cycles and primary productivity. The relationship between TN/TP and Chl-*a* in flood-pulse lakes suggests that both TN and TP have a limiting effect on phytoplankton biomass (Melack et al., 2021). Moreover, because the concentrations of TN and TP tend to increase during the low water period, the trophic state of shallow flood-pulse lakes also varies seasonally (Melack et al., 2021; Minor et al., 2014; Perŝí and Horvatí, 2011). This is related to the sediment resuspension rate, which is strongly affected by hydrological variations (e.g., fluctuating water levels and flow reversal) (Khanal et al., 2021; Niemistö et al., 2008; Siev et al., 2018). DSi is also significantly positively correlated with flow velocity (Li et al., 2021), while in large floodplain riverscapes, DSi stoichiometry is controlled mainly by the water residence time, inorganic nutrient concentrations, and turbidity (Carey et al., 2019). The dynamics of DSi in shallow lakes is therefore expected to be affected by seasonal variations, which is also likely to affect phytoplankton growth. However, little is known about seasonal variation in nutrient stoichiometry, particularly in terms of the relationship between DSi and Chl-*a*, and the effect of nutrient limitation in flood-pulse lakes.

Therefore, this study investigated the role of DSi in Tonlé Sap Lake (TSL), Cambodia, which is characterized by a seasonal flood pulse. We hypothesized that the effects of DSi on phytoplankton growth would vary according to the seasonal flood pulse. Thus, the specific objectives were 1) to investigate the seasonal variations in DSi, TN, TP, and Chl-*a* in the surface water of TSL, 2) to determine variation in nutrient stoichiometry with seasonal events, and 3) to statistically elucidate the relationships between nutrient stoichiometry and Chl-*a*.

2. Study site and methods

2.1. Study site

The field investigation was conducted in 2020 in the two distinct wet and dry seasons in TSL, the largest freshwater lake in Southeast Asia. This study targeted the area around Chhnok Tru floating villages in Kampong Chhnang province, which is characterized by abundant natural resources (Fig. 1). The water level of TSL is primarily controlled by seasonal reversal flow of Tonlé Sap River (TSR), whereby TSR flows into TSL during the wet season and out from TSL into the Mekong River during the dry season (Yang et al., 2022). In the dry season, the surface area of the lake is approximately 2500 km^2, with an average depth of <2 m. Meanwhile, in the wet season, the lake extends to about 15,000 km^2, with an average depth of between 7and 9 m (Sarkkula et al., 2003). Sedimentation flux in the lake also varies substantially between the dry and wet seasons (Sarkkula et al., 2003). The seasonal hydrological processes within TSL are distinctive and periodical,

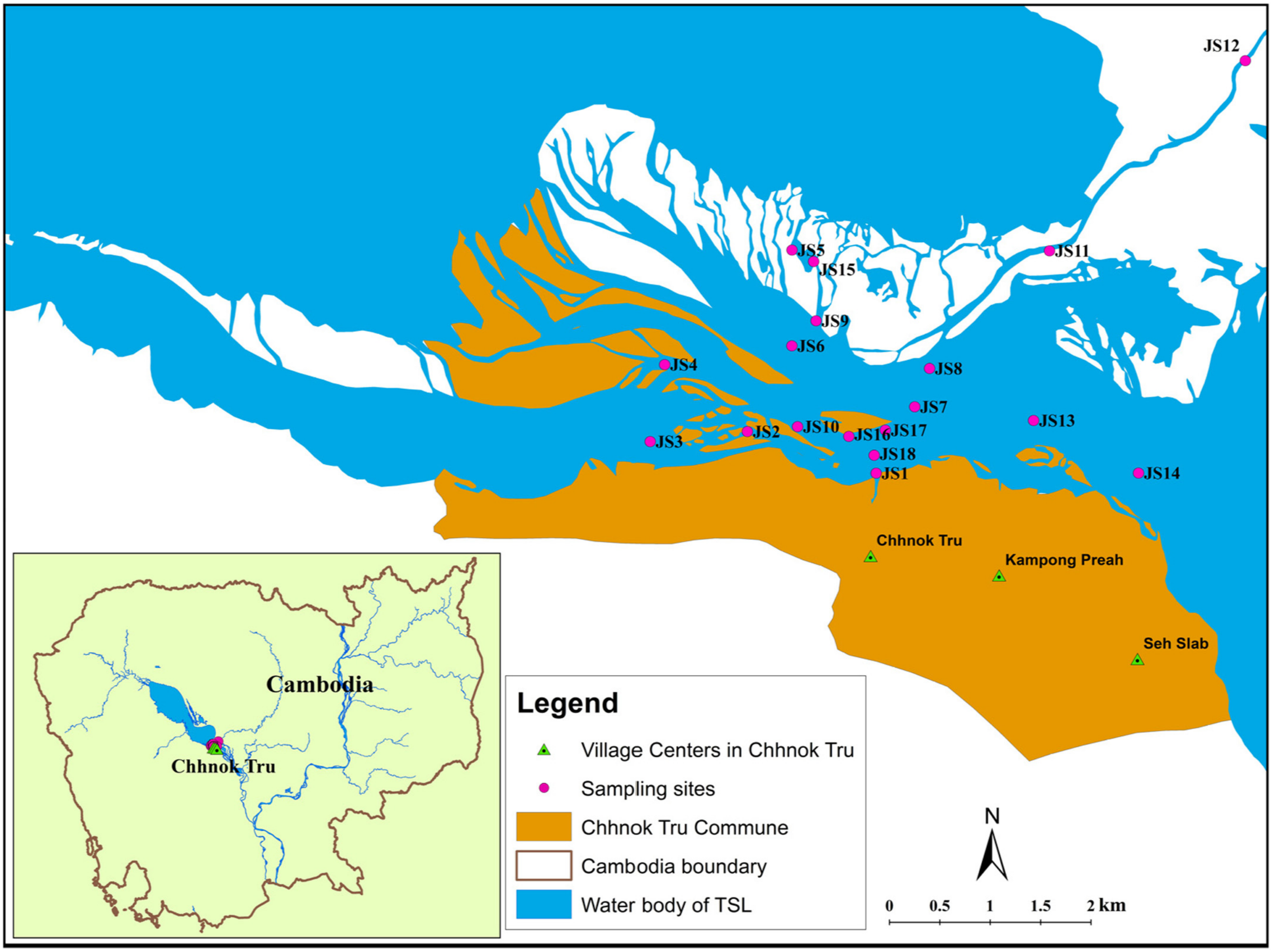

Fig. 1. Sampling sites within the Chhnok Tru region.

although the main hydrological characteristics, such as flow and water depth, remain consistent throughout each respective season as described by Arias et al. (2012), Kummu and Sarkkula (2008), and Lengthong et al. (2022).

The climate in this region is tropical monsoon, with the wind blowing from the northeast during the dry season and the southwest during the wet season (Arias et al., 2014; Sarkkula et al., 2003). The 11 tributaries in TSL drain directly into the lake as a source of water. During the dry season, 88 % of freshwater from the lake drains into the Mekong River through TSR (1 % of which is overland flooding), while the other 12 % evaporates from the lake. Meanwhile, during the wet season, 57 % of inflow floodwater enters TSL from the Mekong River via TSR, while tributaries contribute to 30 % and precipitation to 13 % (Kummu et al., 2014; Kummu and Sarkkula, 2008).

The TSL environment has been degraded by waste load in its watercourses as well as by agriculture, logging of inundated forests, and hunting of waterfowl (Wai et al., 2022). Eutrophication has been reported in some parts of the lake, mainly during the dry or low-water season (Wai et al., 2022). Diatoms dominate TSL from October to December, with the dominant genus Aulacoseria (Planktonic diatom), and more minor Epithemia (Benthic diatom) and Tabularia (Epontic diatom) (Sarkkula et al., 2003; Tudesque et al., 2019). Possible Si limitations have been reported in June and November based on the ratios of DSi: dissolved inorganic phosphorus (DIP) and DSi: dissolved inorganic nitrogen (DIN), while P limitations have been confirmed throughout the year based on DIN:DIP and Dsi:DIP (Burnett et al., 2017). However, based on the monthly mean ratio of N:P, Campbell et al. (2009) revealed that nitrogen is the main limiting factor throughout the year in TSL.

2.2. Field investigation

Sampling and water quality monitoring were conducted on 5th March 2020 during the dry season and on 15th November 2020 during the wet season. Water samples were collected at 18 sites in both the dry and wet seasons. Sampling sites were selected to systematically cover the area of Chhnok Tru, using the MAPS.ME program with an X-Y coordinate system (WGS 1984). As such, sampling was performed across different ecosystems, such as wetlands, floating villages, tributaries, and main rivers (Fig. 1).

On the sampling date in March, no precipitation was confirmed, and the minimum, average, and maximum air temperatures were 26.2 °C, 30.0 °C, and 34.2 °C, respectively. Meanwhile, in November, rainfall was recorded as 6.70 mm/day, and the minimum, average, and maximum air temperatures were 24.8 °C, 25.7 °C, and 27.8 °C, respectively. Water depth was measured at each sampling site in both sampling periods. Water temperature, pH, dissolved oxygen (DO), the oxidation-reduction potential (ORP), conductivity, and Chl-*a* (phytoplankton biomass) were measured in-situ using the EXO2 Multiparameter Sonde (YSI Inc., Yellow Springs, OH) at a depth of 10 cm from the water surface.

2.3. Analysis of nutrient contents

Measurements of DSi were obtained using an MD600 Photometer (Tintometer Ltd., Amesbury, United Kingdom) with a Lovibond® Silica Tablet Reagents set (Tintometer Ltd.) at a wavelength of 600 nm. DSi analysis was based on the silicomolybdate method with a measurable range of SiO_2 ranging from 0.05 to 4 mg/L. The procedure followed the manufacturer's instructions (Lovibond, 2017). A Silica No.1 tablet, Silica PR tablet, and Silica No.2 tablet were added in sequence to a vial containing 10 mL of water sample. After dissolving completely, DSi was then measured based on the "350 silica/silicon dioxide" method in the MD600 Photometer.

TN was also determined using the MD600 Photometer with a Lovibond® VARIO Total Nitrogen LR Reagent Set (Tintometer Ltd.) at a wavelength of 430 nm. This test kit is based on the persulfate digestion method, with a measurable range of 0.5 to 25 mg/L. The procedure followed the manufacturer's instructions (Lovibond, 2017). A TN Hydroxide LR digestion vial, TN Acid LR vial, VARIO TN Persulfate Reagent Powder Pack, VARIO TN Reagent A, VARIO TN Reagent B Powder Pack, and deionized water as a blank sample were used in the analysis. A MG2300 preheated reactor (ELEYA, Japan) was used to digest the vials at a temperature of 100 °C for 30 min. The "280 Nitrogen LR TT" method in the MD600 Photometer was then used to measure the TN concentration of each water sample.

Analysis of TP in the water samples was also performed using the MD600 Photometer at a wavelength of 660 nm with the Lovibond® VARIO Total Phosphorus LR Reagent Set (Tintometer Ltd.). This test kit is based on acid persulfate digestion and the ascorbic acid method, with a measurable range of 0.02 to 1.1 mg/L. The procedure followed the manufacturer's instructions (Lovibond, 2017). PO_4-P Acid reagent vials and 1.54 N sodium hydroxide solution were used for analysis. 5-mL water samples was added to the PO_4-P vial then digested using the MG2300 preheated reactor at a temperature of 100 °C for 30 min. The "326 Phosphorus TT" method in the MD600 Photometer was then used to measure the TP concentration of each sample.

2.4. Data analysis

Prior to analysis, all data were log-transformed ($y = \log(x + 1)$) to ensure normality. Pearson's correlation was used to determine the relationships between DSi and the basic water quality parameters (TN, TP, and Chl-*a*). In addition, multiple linear regression (MLR) models were computed to determine the statistical relationships between the studied variables (DSi, TN, TP, TN: TP, DSi: TN, DSi: TP, pH, Temperature, DO, ORP, and conductivity) and the concentration of Chl-*a*. Pearson's correlation analysis and MLR were performed using R(version 4.0.3) (R Core Team, 2021). The "olsrr" package was used to compute all possible MLR models in order to determine the effect of each variable on Chl-*a*. From these, the most significant model, which contained four explanatory variables (DSi, TN:TP, Temperature, and DO; $p < 0.05$), was then selected to describe the concentration of Chl-*a*.

Ternary plots were used to interpret the nutrient ratios at each site and to compare these ratios with the Redfield ratio. In the ternary plot, the Redfield ratio (16TN:1TP:16DSi) (Redfield et al., 1963) was considered nutrient balance or the optimum nutrient ratio. With the ternary plot, concentrations of TN, TP, and DSi were first converted into molar concentrations then normalized using the following equations.

$$C_{TN} = \frac{C_{TNorig}}{R_{TN}} \tag{1}$$

$$C_{TP} = \frac{C_{TPorig}}{R_{TP}} \tag{2}$$

$$C_{DSi} = \frac{C_{DSiorig}}{R_{DSi}} \tag{3}$$

Here, $R_{TN} = 16$, $R_{TP} = 1$, $R_{DSi} = 16$, and C_{Tnorig}, C_{Tpori} and $C_{Dsiorig}$ represent the nutrient molar concentrations in μmol/L, C represents nutrient concentration and R represents Redfield ratio (Teubner and Dokulil, 2002). The optimum Redfield ratio appears at the center of the ternary plot ($R_{TN} = 0.33$, $R_{TP} = 0.33$, and $R_{DSi} = 0.33$).

Using previously published data, DSi concentrations and DSi stoichiometry were also compared with other lakes and rivers worldwide. The recorded DSi concentrations in TSL were compared with concentrations in Asia, Europe, North America, South America, Africa, and Australasia, as well as with concentrations in lakes, rivers, and freshwater around the world. In terms of DSi stoichiometry, when only nitrate data were available in the literature, the relationship between DIN and nitrate was examined, and DIN was used as a measure of TN (Garnier et al., 2010). Likewise, when only phosphate data were available, the relationship between TP and phosphate was used to represent TP (Garnier et al. (2010).

3. Results

3.1. Seasonal variation in water quality

Water quality in TSL differed significantly between the dry and wet seasons. DSi concentrations during the dry season were significantly higher than during the wet season ($t(34) = 14.66$, $p < 0.05$). Chl-*a* distribution also varied widely during the dry season, and values were significantly higher than during the wet season ($t(34) = 6.78$, $p < 0.05$). The TN results also revealed wide distribution spread during the dry season, with significantly higher values than during the wet season ($t(34) = 3.39$, $p < 0.05$). Similarly, the concentrations of TP were also significantly higher ($t(34) = 1.34$, $p < 0.05$) and the distribution more widely spread during the dry season compared with the wet season (Table 1, Fig. 2). Temperature increased significantly during the dry season ($t(34) = 9.62$, $p < 0.05$), and pH was significantly higher than during the wet season ($t(34) = 35.78$, $p < 0.05$). Meanwhile, the concentration of DO was significantly lower during the dry season ($t(34) = -2.05$, $p < 0.05$), while conductivity was significantly lower during the wet season ($t(34) = 4.23$, $p < 0.05$). ORP values also differed significantly between the wet and dry seasons ($t(33) = -17.79$, $p < 0.05$) (Table 1). Average water depths were recorded as 2.25 m in the dry season and 6.96 m in the wet season (refer to Appendix A for details).

3.2. Relationships between Chl-a concentrations and water quality

Pearson's correlation analysis revealed that Chl-*a* was significantly positively correlated with TN ($r = 0.57$, $p = 0.01$), TN:TP ($r = 0.56$, $p = 0.01$), temperature ($r = 0.59$, $p < 0.01$), and conductivity ($r = 0.54$, $p = 0.02$), and significantly negatively correlated with DSi:TN ($r = -0.55$, $p = 0.02$), DO ($r = -0.57$, $p = 0.01$) and ORP ($r = -0.72$, $p < 0.01$) during the dry season. Meanwhile, during the wet season, Chl-*a* was significantly positively correlated with temperature ($r = 0.65$, $p = 0.004$) and negatively correlated with conductivity ($r = -0.55$, $p = 0.02$) and ORP ($r = -0.67$, $p = 0.004$) (Appendix A). MLR analysis was subsequently performed to determine the best predictors of Chl-*a*. In the dry season, the regression results revealed four variables (DSi, TN:TP, DO, and temperature) as predictors of Chl-*a* with explanatory variance of 59 % ($p < 0.01$). Similarly, during the wet season, the same four variables were identified as predictors of Chl-*a* with explanatory variance of 47 % ($p < 0.05$) (Table 2).

3.3. Limiting nutrients of phytoplankton growth

According to the Redfield ratio (Redfield et al., 1963), the elemental ratios of nutrients required for sustained growth of aquatic organisms are as follows: (1) DSi:TN = 1:1, (2) DSi:TP = 16:1, and (3) TN:TP = 16:1. Turner et al. (2003) found that DSi limitation relative to N was the major component affecting diatom growth, with an optimal ratio of DSi:TN < 1. Accordingly, in the present study, the molar ratio of DSi and TN during the dry season was found to be <1 in 14 of the sites sampled, suggesting

Table 1
Seasonal variation in the water quality parameters.

	Season					
	Dry			Wet		
	Min.	Max.	Mean	Min.	Max.	Mean
DSi (mg/L)	16.3	22.1	19.3 ± 1.5	7.2	14.0	10.8 ± 1.5
Chl-*a* (μg/L)	1.71	14.71	4.32 ± 2.86	0.87	2.51	1.59 ± 0.45
TN (mg/L)	1.60	24.40	9.41 ± 6.23	1.90	9.70	4.02 ± 1.70
TP (mg/L)	0.06	0.65	0.30 ± 0.15	0.05	0.48	0.23 ± 0.12
Temperature (°C)	29.0	33.4	30.5 ± 31.1	27.4	28.8	28.0 ± 0.4
pH	7.67	9.93	8.59 ± 0.59	7.31	7.90	7.60 ± 0.16
DO (mg/L)	0.40	7.23	5.16 ± 0.40	4.75	7.10	6.40 ± 0.68
Conductivity (μS/cm)	76	783	187 ± 160	68	572	102 ± 18
ORP (mV)	−1095	124	21 ± 279	333	239	290 ± 31
Water depth (m)	0.10	4.50	2.25 ± 1.49	3.92	11.34	6.96 ± 1.75

Note: DSi, dissolved silicon; Chl-*a*, chlorophyll-*a*; TN, total nitrogen; TP, total phosphorus; DO, dissolved oxygen; ORP, oxidation reduction potential.

that DSi limitation relative to TN occurred in 77 % of the study area. During the wet season, DSi limitation occurred in 88 % of the study area. The molar ratio of DSi and TN during the dry season ranged from 0.21 to 2.77, with a mean value of 0.82 ± 0.76, while during the wet season, the molar ratio ranged from 0.29 to 1.36, with a mean value of 0.71 ± 0.28. Moreover, a previous study revealed DSi limitation relative to TP at a ratio of DSi:TP < 16 (Carey et al., 2019). Based on this, only 5 % of the study area showed DSi limitation relative to TP during the dry season, with a molar ratio of DSi

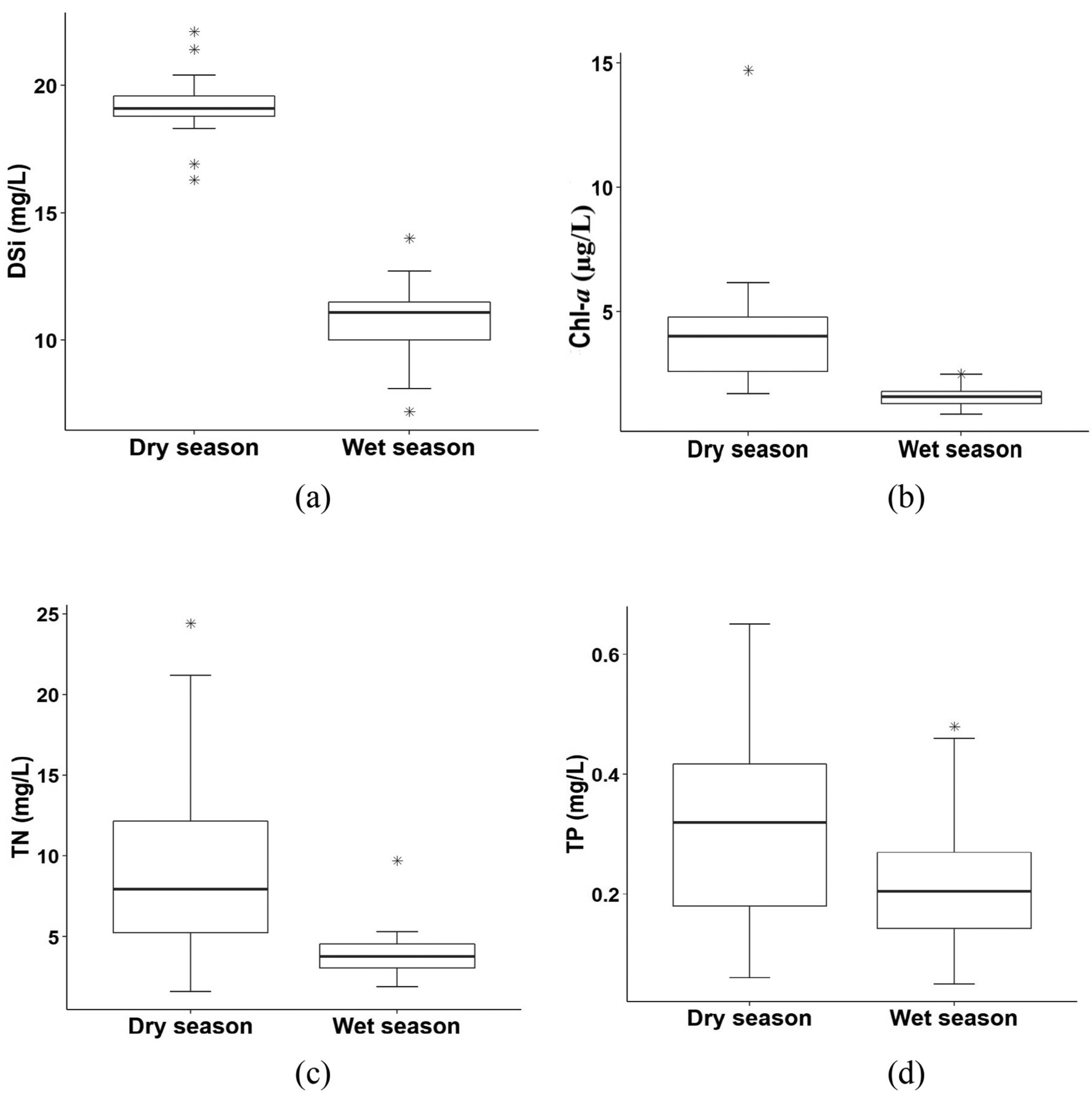

Fig. 2. Seasonal variation in (a) dissolved silicon (DSi), (b) chlorophyll-a (Chl-*a*), (c) total nitrogen (TN), and (d) total phosphorus (TP). Upper * and lower * represent data from <10th and > 90th percentile.

Table 2
Multi-linear regression models of Chl-*a* and the explanatory variables.

	Model		Unstandardized coefficients		Standardized coefficients	t	*p*
			B	Std. Error	Beta		
Dry season	1	(Constant)	−12.55	6.05		−2.08	0.058
		DSi	−1.27	1.14	−0.20	−1.11	0.287
		TN:TP	0.28	0.10	0.46	2.80	0.015
		DO	−0.31	0.14	−0.41	−2.21	0.046
		Temperature	5.659	2.53	0.40	2.24	0.044
Wet season	2	(Constant)	−18.98	6.51		−2.92	0.012
		DSi	0.11	0.35	0.056	0.31	0.762
		TN:TP	−0.04	0.085	−0.082	−0.41	0.688
		DO	1.05	0.47	0.417	2.25	0.043
		Temperature	12.97	4.29	0.59	3.02	0.010

and TP of <16 at only one sampling site. Meanwhile, during the wet season, two sampling sites showed a molar ratio of DSi and TP of <16, and DSi limitation relative to TP occurred in 11 % of the study area. During the dry season, the molar ratio of DSi and TP varied from 14.51 to 183.85, with a mean value of 49.69 ± 42.31, while during the wet season, the ratio ranged from 8.07 to 11.92, with a mean value of 34.07 ± 22.57. In contrast, there were no significant differences in the seasonal variations in DSi:TN ($t(34) = -0.43$, $p > 0.05$) and DSi:TP ($t(34) = 1.46$, $p > 0.0.5$).

Overall, the ternary plot indicated six sectors based on the combination of TN:TP, DSi:TN, and DSi:TP. After normalizing the molar concentrations using Eqs. (1) to (3), the results showed that in the dry season, most points fell within sectors 1, 2, and 3, while in the wet season, they fell within sectors 1, 2, 3, and 5. In addition, the average ratio of TN:TP:DSi was 69.3:1:33.1 (58 % TN, 14 % TP, and 28 % DSi) in the dry season and 39.4:1:24.7 (49 % TN, 20 % TP, and 31 % DSi) in the wet season, respectively (Fig. 4).

3.4. Comparison of DSi stoichiometry with other lakes and rivers

The results of this study were also compared with those of other lakes and rivers around the world. Accordingly, Riverine Lake of the Upper Mississippi River System (UMRS) (Carey et al., 2019); Hanfeng Lake in China (Li et al., 2021); Lake Biwa in Japan (Goto et al., 2013); the San River in Southeast Poland (Koszelnik and Tomaszek, 2008); the Licunhe, Daguhe, Yanghe, Moshiuihe, and Bashahe rivers in China (Su et al., 2005); the Daliaohe, Changijiang, Minjiang, and Zhujiang rivers in China (Zhang, 1996); and the Upmasjakka, Sarkajakka, Tarfalajakka, Ladtjojakka1, Pitealven, Skelleftealven, and Umealven rivers in Sweden (Humborg et al., 2004) were retrospectively examined using the literature (Fig. 5). The results revealed DSi limitation relative to TN in most of the rivers in China, with DSi limitation relative to TP also observed in some, but not all of these rivers. These findings suggest that limitation of DSi relative to TN is widespread and not limited to TSL. Overall, the values observed here were lower in terms of DSi:TN compared with the global lake and river values.

4. Discussion

Observations of seasonal variation in DSi and DSi stoichiometry relative to TN and TP as well as the effects of seasonal hydrological variation on nutrient limitation can enhance our understanding of limnology. The findings presented here provide an important reference for further studies on Si cycling in relation to hydrological alternations and Si balance models. The results suggest that DSi varies significantly in TSL between the dry and wet seasons, suggesting a significant seasonal effect in this shallow flood-pulse lake. Blanchard (1988) previously reported that the solubility of siliceous solids is affected by temperature and pH, while Koszelnik and Tomaszek (2008) revealed that DSi dissolves more rapidly in the summer and autumn. Furthermore, Iler (1979) reported that solubility increases sharply in more basic waters. Seasonal variation in water depth and flow are also thought to affect the concentration of DSi, with a larger volume of water flowing from the Mekong River and tributaries into TSL in the wet season (Kummu et al., 2014; Kummu and Sarkkula, 2008). Based on a review of the literature, the global average concentration of DSi was found to range from 8.90 to 9.70 mg/L depending on the approach (Beusen et al., 2009; Clarke, 1924; Meybeck, 1993, 2003; Probst et al., 1994; Treguer et al., 1995). According to Meybeck et al. (2011), the concentration of DSi was found to be 10, 5.6, 8, 9, 12.6, and 11.8 mg/L in Asia, Europe, North America, South America, Africa, and Australasia, respectively. In addition, the general concentrations of DSi in lakes, rivers, and freshwater ecosystems around the world were previously reported to be 13.1, 4.1, and 0.4–26 mg/L, respectively (Falcone, 1982; Vymazal, 1995). Thus, the concentration of DSi in our study was within the range of the freshwater concentration (0.4–26 mg/L) in both the dry and wet seasons. However, if we compare the concentration of DSi between our study and the average concentration in Asia, the value observed here in the dry season was approximately two times greater, while that during the wet season was within the reported range (Fig. 3). Seasonal mean variation in Chl-*a* in TSL was less than the eutrophication level reported in Li et al. (2021), who suggested that eutrophication occurs at a concentration of 10 μg/L Chl-*a*. In contrast, the average values of TN in both the dry and wet seasons exceeded the eutrophication level (TN = 0.2 mg/L). Similarly, the mean concentration of TP in both the dry and wet seasons also exceeded the eutrophication level (TP = 0.02 mg/L) of freshwater ecosystems reported by Li et al. (2015) .

This study also examined the relationship between DSi and Chl-*a*, revealing the effect of DSi on the structure of phytoplankton species in TSL. The significant negative correlation between DSi:TN and Chl-*a* during the dry season suggests an increase in TN with decreasing DSi, resulting in a potential increase in the dominance of harmful algae. Moreover, the positive relationship between TN:TP and Chl-*a* also suggests the potential for eutrophication during the dry season. Meanwhile, the negative correlation between DSi and Chl-*a* suggests that depletion of DSi increases the concentration of Chl-*a* by favoring the growth of non-siliceous, potentially toxic algae during the dry season. In addition, the accelerated growth of phytoplankton (i.e., algal blooms) further depletes concentrations of DO due to eutrophication, as supported by the negative relationship between Chl-*a* and DO during the dry season. Bartoszek and Koszelnik (2016) further reported that increases in the concentrations of TN and TP stimulate both primary and secondary production, while a previous report in TSL suggested that eutrophication occurs mainly during the dry season (Shivakoti et al., 2020; Nakatani et al., 2022; Samal et al., 2022). Studies also suggest that cyanobacteria in TSL are dominated by species such as *Synechococcus*, *Anabaena*, and *Microcystis* during the dry season (Ann et al., 2022; Samal et al., 2022; Ung et al., 2019). Thus, the relationship between DSi and Chl-*a* in the dry season clearly suggests that depletion of DSi resulted from the high input of TN. Diatom growth is subsequently limited by DSi depletion, while growth of harmful algae is enhanced, leading to algal blooms and eutrophication. The results of DSi limitation relative to TN and TP further support these findings in terms of diatom growth. During the dry season, the average molar ratio of DSi and TN was <1, while the average ratio of DSi and TP was >16. A previous study by Campbell et al. (2006) reported 37 species of Bacillariophyta (diatoms), 34 of Chlorophyta (green algae), 34 of Cyanobacteria (blue-green algae), 15 of Euglenophyta, and a small number of several other groups in TSL. However, Ohtaka et al. (2010) suggested that green-blue algae and diatoms dominate. During the dry season, blue-green algae such as *Anabaena*, *Oscillaatoria*, *Lyngbia*, and *Microscystis* as well as diatoms such as *Aulacoseria granula* were previously recorded, and of these, *Microscystis* was abundant throughout, with algal scum observed on the lake surface (Ann et al., 2022; Mizuno and Mori, 1970; Nakatani et al., 2022; Ohtaka et al., 2010; Samal et al., 2022). Thus, during the dry season, harmful algae such as *Microscystis* are thought to dominate phytoplankton communities, with diatom growth limited by the depletion of DSi relative to TN.

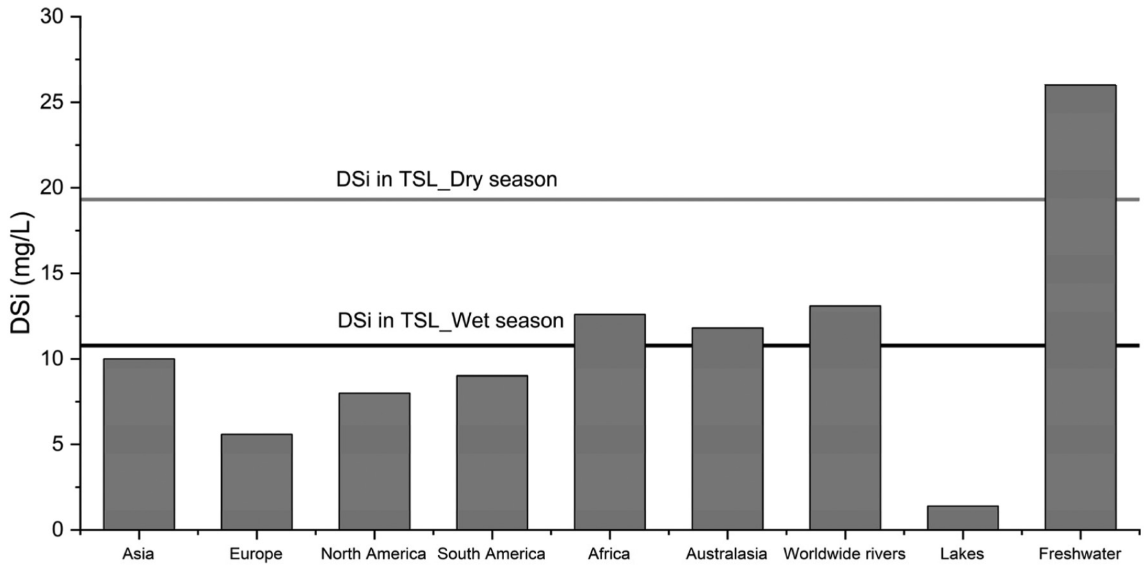

Fig. 3. Average dissolved silicon (DSi) concentrations in Tonlé Sap Lake (TSL) during the wet and dry seasons compared with other areas around the world.

In contrast, a positive correlation was found between DSi and Chl-*a* concentrations during the wet season, as supported by Blanchard (1988). The negative relationship between TN and TP suggests that a reduction in the ratio of TN:TP causes an increase in the concentration of Chl-*a*, as previously reported in Li et al. (2021). Moreover, DO was found to be positively correlated with Chl-a during the wet season, probably due to the increase in water depth, which is conducive to phytoplankton growth causing an increase in DO (Li et al., 2021). Thus, changes in the phytoplankton species dominating phytoplankton assemblages also occur during the wet season. Meanwhile, the average molar ratios of DSi and TN remained <1 during the wet season, while those of DSi and TP remained >16. According to Ohtaka et al. (2010), green algae, dinoflagellates, Dinobryon sp. (Chrysophyceae), blue-green algae such as *Anabaena* and *Microscystis*, and diatoms such as *Aulacoseria graulata* dominate TSL during the wet season, with *A. granulata* thought to dominate overall (Blache, 1951; Ohtaka et al., 2010). Meanwhile, the occurrence of cyanobacteria has also been reported during the wet season (Samal et al., 2022; Ung et al., 2019), suggesting that even though *A. granulate* dominates at this time, cyanobacteria still occur and DSi continues to be limited by TN. These findings therefore suggest the existence of growth-limiting deficiencies for diatom growth in both the dry and wet seasons. Despite this, Samal et al. (2022) reported that the abundance of cyanobacteria was higher in the dry season than the wet season. Furthermore, according to Officer and Ryther (1980), when the molar ratio of DSi and TN is <1, phytoplankton communities are dominated by flagellated algae, notably dinoflagellates and noxious bloom-forming communities, thereby impacting the entire food web structure of the river or lake. Moreover, studies also suggest that phytoplankton community composition and production can be controlled by reducing the abundance of diatoms relative to other algae (Dugdale and Wilkerson, 1998; Egge and Aksnes, 1992; Egge and Jacobsen, 1997; Rabalais et al., 1996). The results of this study therefore highlight the impact of anthropogenic activities on N concentrations in TSL in both the dry and wet seasons. Furthermore, in both seasons, DSi limitations exist relative to both N and P, even though the mean Chl-*a* concentration was below the eutrophication level in all sampling sites except one.

In both the dry and wet seasons, there was a positive correlation between temperature and Chl-*a*, as in a previous study by Fuentes and Petrucio (2015). This suggests that the amount of variable solar radiation is also a partial driving factor of phytoplankton growth. Therefore, in the regression models, four variables were included (DSi, TN:TP, DO, and temperature) as predictors of Chl-*a* in both the dry and wet seasons. However, it should be noted that the concentration of Chl-*a* is also dependent on other variables, including local factors such as the ionic water composition, light, and water velocity, and large-scale factors such as the drainage area and land use within the watershed (Urrea-Clos et al., 2014).

The ternary plots shown in Fig. 4 show that most points fell within sector 1 in both the dry and wet seasons, suggesting that phytoplankton growth is primarily controlled by P and secondarily by DSi. Meanwhile, when the ratios were compared with the Redfield ratio (TN16:TP1:DSi16; 33.33 % TN, 33.33 % TP, and 33.33 % DSi), the ratio in the wet season was found to be closer to the point of nutrient balance than that in the dry season, suggesting better conditions for phytoplankton growth in the wet season. Furthermore, average nutrient ratio points for both the dry and wet seasons fell within sector 2, representing TN:TP > 16:1, DSi:TP > 16:1, and DSi:TN < 1. These results further suggest that both TP and DSi limitations occur in both the dry and wet seasons in the Chhnok Tru region of TSL. The results of our study also suggest high concentrations of TN compared with other rivers and lakes around the world, thus resulting in depletion of TP and DSi (Fig. 5).

5. Conclusions

This study investigated the role of DSi in TSL in Cambodia, which is characterized by seasonal flood pulse conditions. The results of this study confirm that seasonal changes in the chemical and physical properties of the lake affect water quality. The low molar ratio of DSi and TN is thought to increase concentrations of Chl-*a* as shown by the negative correlation between DSi:TN and Chl-*a* in the dry season. Coincidently, the highest concentration of Chl-*a* (approximately 14.4 μg/L) was recorded in the dry season, which was greater than the eutrophication level in the study area. Consequently, the model of Chl-*a* included DSi plus three other variables (TN:TP, DO, temperature) in both the dry and wet seasons, suggesting that DSi is an important factor in terms of phytoplankton dynamics in the area. In addition, the average molar ratios of DSi:TN < 1 and DSi:TP > 16:1 suggest that diatom growth was limited because of DSi depletion resulting from an excess amount of TN in both seasons. Accordingly, TP is thought to be the primary limiting nutrient of phytoplankton growth, while DSi is an important secondary factor. Moreover, although the molar ratios of DSi:TN and DSi:TP were not significant, the findings were affected by hydrological variation, with DSi limited throughout much of the year. Overall, these findings confirm seasonal nutrient limitations in this flood-pulse ecosystem. Further studies are now needed to determine the effect of temperature and land slope on hydrology, and that of climate on

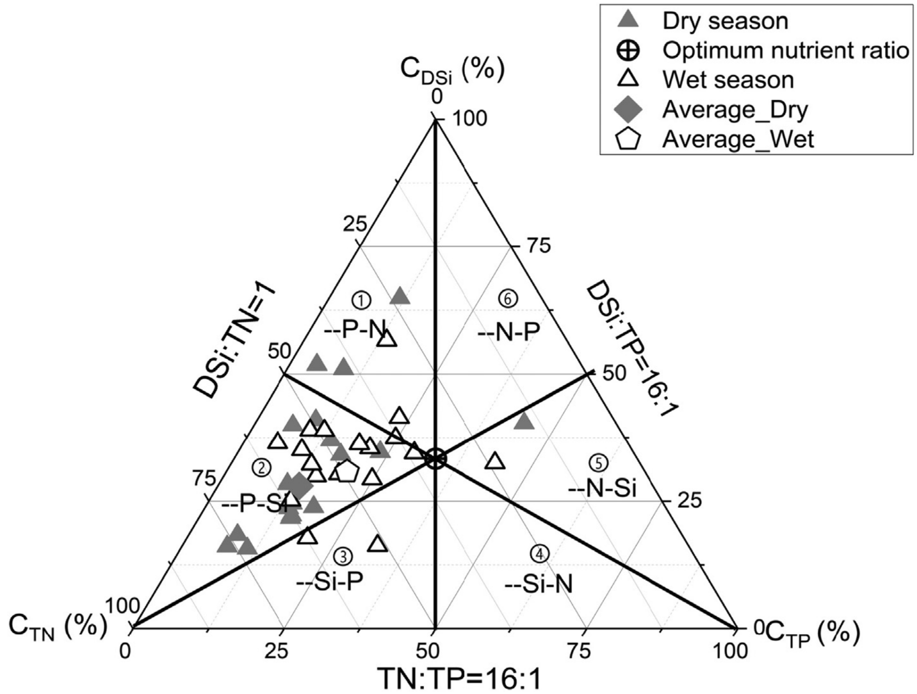

Fig. 4. Ternary plot showing the seasonal variations in TN:TP:DSi. Sector 1: TN:TP > 16:1, DSi:TP > 16:1 and DSi:TN > 1 (algal growth primarily controlled by P and secondly by N). Sector 2: TN:TP > 16:1, DSi:TP > 16:1 and DSi:TN < 1 (algal growth primarily controlled by P and secondly by Si. Sector 3: TN:TP > 16:1, DSi:TP < 16:1 and DSi:TN < 1 (algal growth primarily controlled by Si and secondly by P). Sector 4: TN:TP < 16:1, DSi:TP < 16:1 and DSi:TN < 1 (algal growth primary controlled by Si and secondly by N), Sector 5: TN:TP < 16:1, DSi:TP < 16:1 and DSi:TN > 1 (algal growth primarily controlled by N and secondly by Si). Sector 6: TN:TP < 16:1, DSi:TP > 16:1 and DSi:TN > 1 (algal growth primarily controlled by N and secondly by P).

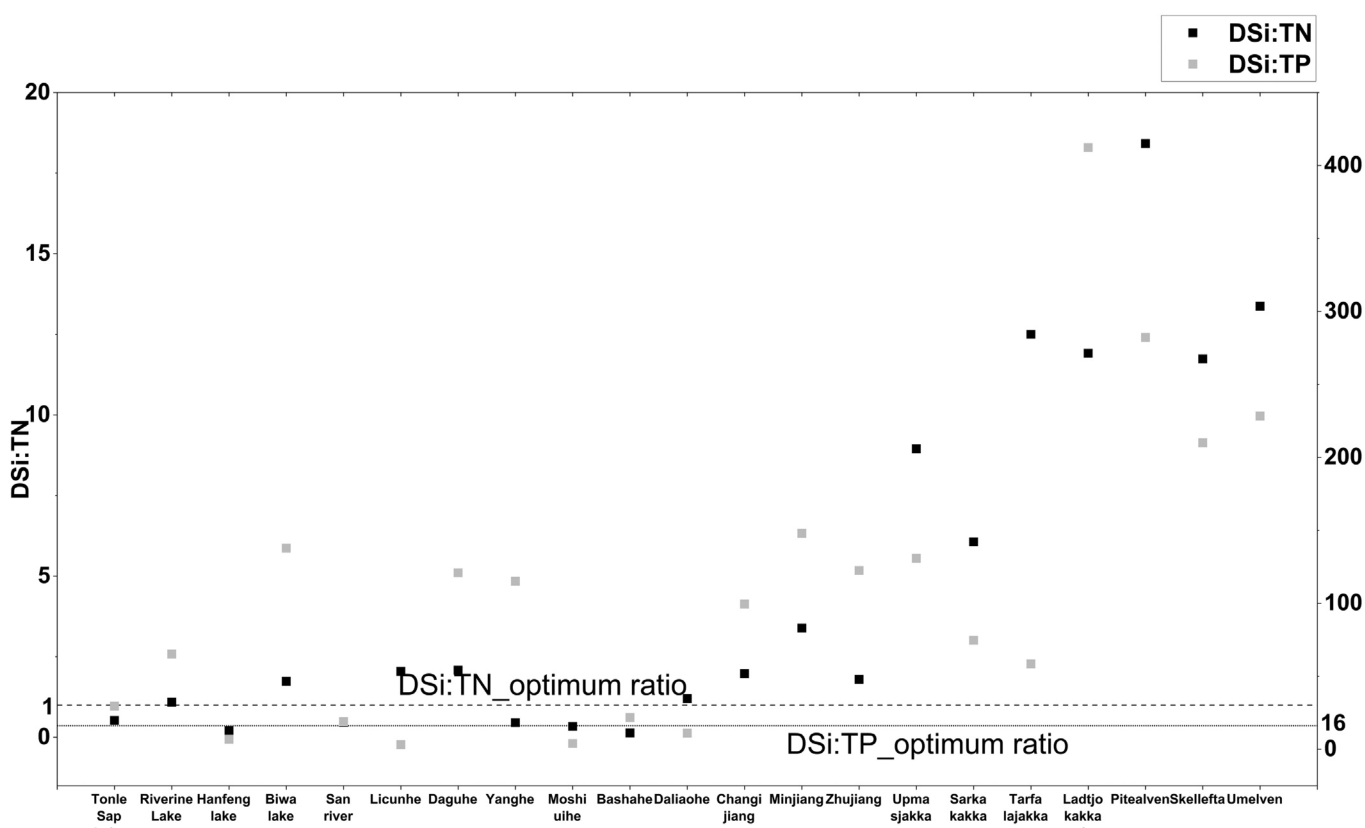

Fig. 5. Comparison of DSi stoichiometry in Tonlé Sap Lake with lakes and rivers around the world.

concentrations of DSi in order to elucidate the process of DSi cycling in ecosystems exposed to hydrological variation.

CRediT authorship contribution statement

Conceptualization: R.H, C.Y.; Formal analysis: M.P·W, S·S, V·C, K.E.E, V.A, Writing original manuscript: R.H., M.P·W; Writing, reviewing and editing: All authors.

Data availability

Data will be made available on request.

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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Appendix A

Table A1
Seasonal water depth variations in each sampling site.

Sampling sites	Water depths (m)	
	Dry season	Wet season
JS1	0.1	11.34
JS2	1.10	4.64
JS3	0.1	5.40
JS4	2.40	6.70
JS5	4.30	8.65
JS6	2.00	6.93
JS7	2.90	7.80
JS8	0.50	4.87
JS9	4.50	7.90
JS10	2.83	5.95
JS11	4.30	8.09
JS12	4.00	8.27
JS13	3.30	6.84
JS14	1.70	6.88
JS15	3.20	8.50
JS16	1.40	6.30
JS17	1.40	6.32
JS18	0.50	3.92

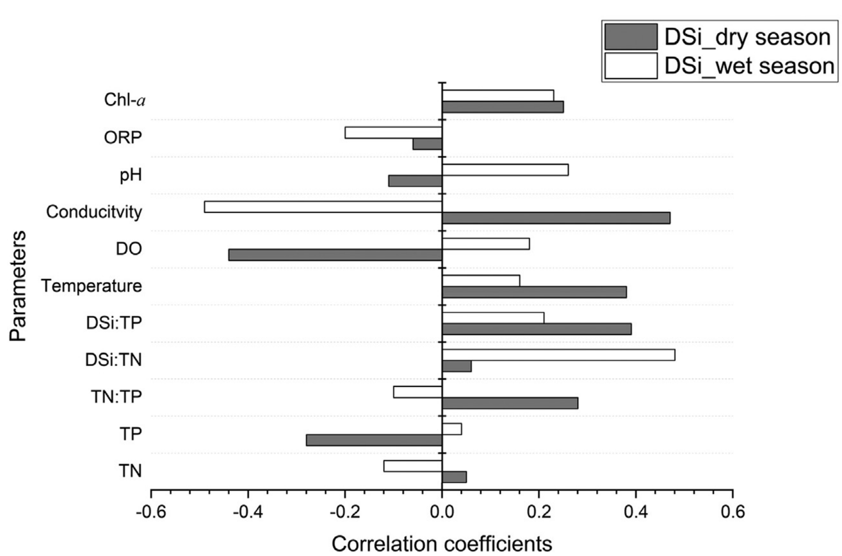

Fig. A1. Correlation coefficients of DSi with basic water quality, Chl-*a* concentration, TN and TP.

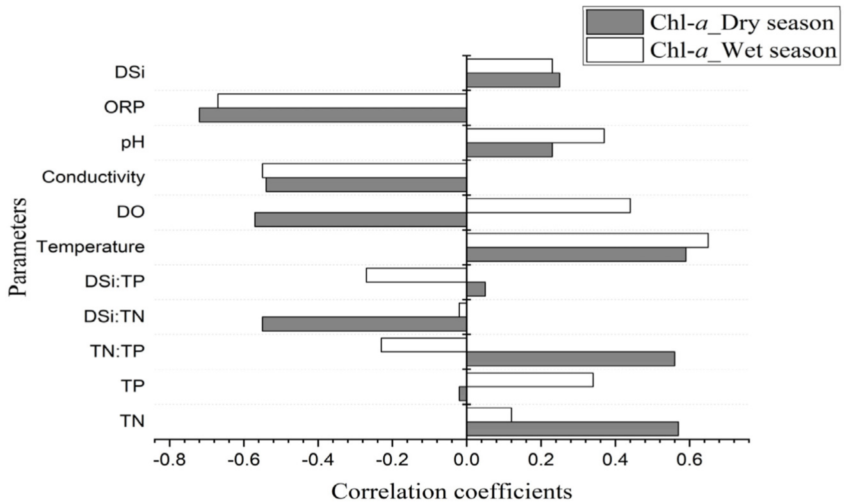

Fig. A2. Correlation coefficients of Chl-a with water quality.

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