Nutrient–chlorophyll relationships in tropical–subtropical lakes: do temperate models fit?

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Abstract. In tropical lakes relatively little is known about the general relationship between nutrient concentration and phytoplankton biomass. Using data from 192 lakes from tropical and subtropical regions we examine the relationship between total P (TP) and chlorophyll (Chl). The lakes are all located between 30° S to 31° N include systems in Asia, Africa, and North and South America but are dominated by Brazilian ($n = 79$) and subtropical N. American ($n = 67$) systems. The systems vary in morphometry (mean depth and lake area), trophic state as well total N (TN) to total P (TP) ratios and light extinction. Despite a nearly 500-fold range in TP concentrations (2–970 μg P l^{-1}), there was a poorer relationship between log TP and log Chl ($r^2 = 0.42$) than is generally observed for temperate systems from either narrow or broad geographic regions. N limitation is not a likely explanation for the relatively weak TP–Chl relationship in the tropical–subtropical systems. Systems had high average TN:TP ratios and neither a multiple regression with log TP and log TN nor separating systems with high TN:TP (> 17 by weight) improved the predictive power of the log TP–log Chl relationship.

Introduction

The relationship between nutrients and phytoplankton biomass in aquatic systems has yielded insights on nutrient limitation and is a valuable management tool (Peters 1986). For freshwater lakes the great majority of studies on the relationship between nutrients and phytoplankton biomass are for temperate systems (Peters 1986; Kalff 2002). These studies have advanced from early studies (Sakamoto 1966; Vollenweider 1968), which focused on simple, linear relationships between log total P (log TP) and log chlorophyll (log Chl), to include the secondary impacts of N, lake depth, color, inorganic turbidity and food web relationships (Smith 1982; Quirós 1990; Mazumder 1994; Nürnberg 1996). However, compared to even what was known nearly half a century ago for temperate systems, little is known about the general relation-

ship between nutrients and chlorophyll in tropical systems or the primary limiting nutrient in these systems (Canfield and Hodgson 1983; Lewis 1990; Salas and Martino 1991; Fisher et al. 1995; Sarnelle et al. 1998; Kalff 2002).

One prevailing view is that nitrogen limitation may be more common in tropical than in temperate systems (Talling and Lemoalle 1998; Lewis 2000) possibly due to greater P supply by chemical weathering of rocks and greater internal N loss at higher temperatures (Lewis 2000, 2002). This possible N limitation suggests that tropical systems may have a poorer relationship between TP and Chl than temperate systems but Chl may be more closely related to total N (TN) concentrations. To date, however, there are relatively few studies examining the relationship between Chl and nutrients in either tropical (Walker and Tyler 1983 *apud* Ferris and Tyler 1985; Salas and Martino 1991; Lewis 1990; Sarnelle et al. 1998; Jones et al. 2000) or subtropical regions (e.g., Canfield 1983; Brown et al. 2000). Further, many of the existing studies are based on relatively narrow geographic regions (e.g., Florida, Thailand), or relatively small data sets. Thus, it is not yet clear if there is a general difference in nutrient limitation or nutrient–chlorophyll relationships between temperate and tropical areas (Fisher et al. 1995; Kalff 2002). The question of nutrient limitation and the relationship between nutrient concentration and Chl is increasingly important as human activity in tropical systems is accelerating rapidly and tropical systems are increasingly confronted with water quality problems associated with eutrophication (Meybeck et al. 1990; Downing et al. 1999).

In this study we examine nutrient status of lakes from tropical to subtropical regions. We develop empirical models of the relationship between Chl and nutrients and compare these relationships to those developed based largely on temperate data sets.

Methods

Database. Our data set of tropical and subtropical inland waters are from both N and S. Hemisphere between latitude 31° N and 30° S. This working definition is based on a minimum water temperature of 10 °C under normal conditions with a minimum annual average of 15 °C as used by Salas and Martino (1991). High altitude tropical lakes (>3000 m above the sea level) and saline lakes were not included in the analysis.

The data set includes 192 aquatic systems (136 lakes, 56 reservoirs) sampled on seasonal bases at least during 1 year and we use average annual values in our analysis. Samples are from surface mixed waters. The data base is primarily drawn from Florida, United States ($n = 67$, Beaver and Crisman 1991) and from 3° N to 30° S in Brasil ($n = 79$). Brazilian data were taken from the following publications: (FEEMA 1982; Pontes 1980; Andrade et al. 1988; Branco 1991; Salas and Martino 1991; Thomaz 1991; Huszar 1994; Rodrigues 1994; Silva 1995; Konrath 1995; Debertd 1997; Mitamura and Hino 1997;

Salomoni 1997; Oliveira 1998; Rodrigues 1998; Sant'Anna et al. 1998; Laudares-Silva 1999; Loverde-Oliveira 1999; Barroso 2000; Bressan 2001; Melo 2001; Szawka 2001; Ferreira 2002; Marinho and Huszar 2002; Cardoso and Motta Marques 2004) but also included unpublished data (D.C. Bicudo, personal communication and L.H.S. Silva, personal communication). The remaining 46 lakes are from Africa ($n = 18$, Sarnelle et al. 1998; Lewis 1990; Kalff and Watson 1986), China ($n = 18$, Jin 1994), Phillippines ($n = 1$, Lewis 1990), and from Mexico ($n = 5$), Puerto Rico ($n = 1$), Texas, United States ($n = 1$) and Venezuela ($n = 2$) (Salas and Martino 1991). All data are from tables from the above references except for Sarnelle et al. (1998), which were taken by measurement from Figure 3b. The complete data set is available on request. For all 192 systems we obtained data for chlorophyll (Chl) and total phosphorus (TP). For many of them we were able to also obtain total N (TN), Secchi depth (SD), lake area and mean depth (Table 1).

Analysis. Statistical analysis of data was done in StatView® (version 5.01). Least square regressions were done on logarithmic (base 10) transformed data. Differences between data sets were calculated by non-paired *t*-tests. To test if the slopes were significantly different ($p < 0.05$), a covariance analysis was used (Zar 1996). With the exception of light extinction all analysis were performed on raw data.

Total light extinction (K) was calculated from SD as: $K = -1 \times \ln (SDlight)/SD$. SDlight is the fraction of surface light penetration at the SD and is generally reported as 0.1 (e.g., 10%, Wetzel and Likens 1991). Light extinction (K) is the sum of extinction from phytoplankton themselves (K_p) as well as extinction from colored organic matter and inorganic turbidity (residual K, K_r). $K_r = K - K_p$. K_p was calculated as: $K_p = EP \times Chl\text{-}a$, where EP, is the biomass specific extinction (in m^2 mg Chl^{-1}) of phytoplankton, which generally varies between 0.01 and 0.02 for different phytoplankton (McBride et al. 1993) here we use a value of 0.016.

For some analyses we grouped the systems by N status. We followed the procedure of Smith (1998) in considering high N:P systems to have TN:TP ratios (by weight) greater than 17.

Table 1. Summary statistics of available average limnological data from 192 tropical–subtropical lakes.

Entire data set	Median	Mean	SD	Minimum	Maximum	*n*
Lake area (km^2)	6.6	770.6	6079.7	0.1	66250.0	148
Mean depth (m)	4.1	12.7	60.9	0.7	700.0	132
Secchi depth (m)	0.9	1.4	1.4	0.1	6.6	132
Extinction coefficient (m^{-1})	2.5	3.2	2.6	0.4	16.5	132
Chlorophyll-*a* ($\mu g\ l^{-1}$)	11.0	34.2	67.0	0.9	556.0	192
Total phosphorus ($\mu g\ l^{-1}$)	59.0	131.9	181.4	2.0	970.0	192
Total nitrogen ($\mu g\ l^{-1}$)	925.1	1506.4	2064.6	42.4	21000.0	156
TN:TP (by weight)	19.8	26.0	30.9	0.7	221.5	156

Results

Lakes used in this study represent a wide range of limnological conditions. For example mean annual TP and TN ranged nearly 3-orders of magnitude across systems (Table 1). Phytoplankton biomass and light extinction (K) also varied greatly between systems but was generally high (Table 1). On average, 19% and 10%, respectively, of the light extinction is due to phytoplankton (K_p,) the remainder being due to inorganic turbidity or dissolved color.

Combining all systems, there was a highly significant relationship between log TP and log Chl ($p<0.0001$) but log TP explained only 42% of the variance in log Chl (Figure 1). Further the slope of the log TP–Chl relationship was significantly lower ($p<0.0001$) than that from temperate relationships (Figure 2). Thus predicted chlorophyll at a given TP level was, on average, slightly but significantly ($p<0.001$) lower than that expected from published relationships for temperate systems. In addition the prediction of Chl did not improve separately considering systems with high TN:TP (<17; $r^2=0.37$; Figure 1). The relationship between log TN and log Chl was also significant and had significantly similar ($p<0.0001$) explanatory power ($r^2=0.39$) to TP. The residuals of the TP–Chl relationship were significantly related to TN concentration ($p=0.03$) but TN explained only 3% of the variance in these residuals (Figure 3). Similarly, a multiple regression which included both TN and TP, improved only modestly ($r^2=0.47$) the prediction of Chl with TP alone (Table 2). Lastly, a regression of predictions from a non-linear regression that considers both TP and TN (McCauley et al. 1989) did not perform substantially better than linear regressions with or without TN ($r^2=0.49$).
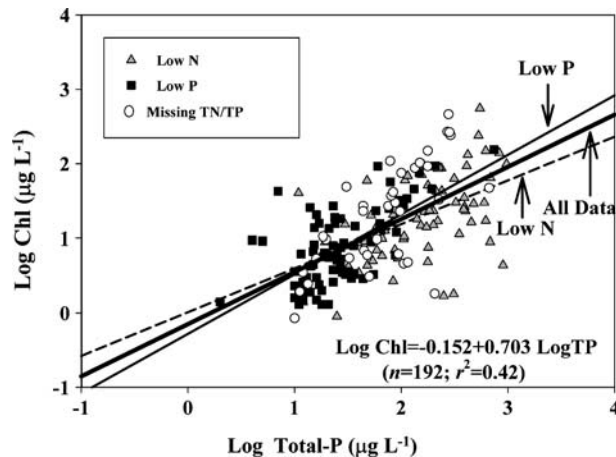

Figure 1. Relationship between annual mean of log-total phosphorus ($\mu g\ l^{-1}$) vs. log chlorophyll ($\mu g\ l^{-1}$) for surface waters of 192 tropical and subtropical lakes from Africa, Asia, and South and North America. The data are coded as P-limited lakes (TN:TP>17, by weight) and N- or N and P-limited lakes (TN:TP<17, by weight).

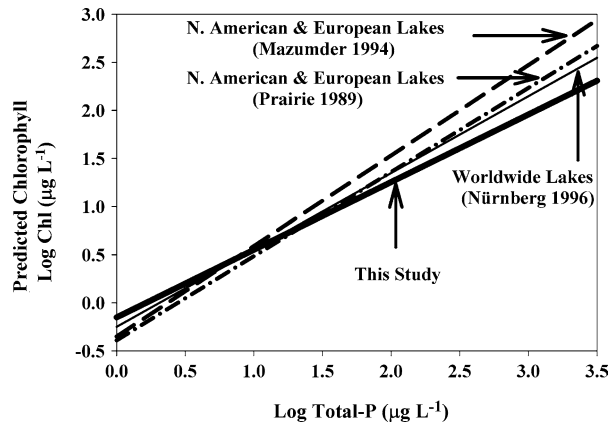*Figure 2.* Comparison of the log-total phosphorus (µg l⁻¹) vs. log chlorophyll (µg l⁻¹) relationship among our tropical and subtropical lakes with selected temperate regressions (see Table 3).

The generally high light extinction (low SD, Table 1) and the high proportion of light extinction by non-phytoplankton particulates or dissolved organic matter suggest that light limitation could account for the high variability between TP and Chl and the generally low Chl yield at a given P concentration. However, indicators of light limitation were either significantly positively related to the residual of the log TP–log Chl relationship or were not significantly related to these residuals. There was no significant relationship between residuals and K_r ($p = 0.69$) and residuals were positively related to total K ($p < 0.05$) and negatively related to both log SD and log SD/average depth ($p < 0.01$).
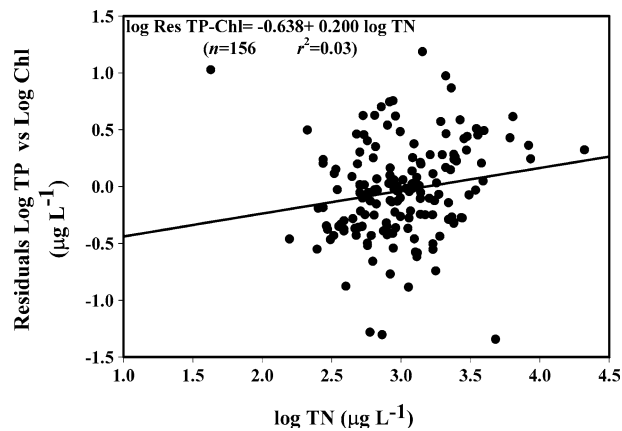

Figure 3. Residuals of total phosphorus–chlorophyll relationship in tropical and subtropical lakes vs. log total nitrogen (µg l⁻¹).

Table 2. Nutrient–chlorophyll and chlorophyll–Secchi depth regressions for the 192 tropical–subtropical lakes.

Regression models	n	r^2	p
log Chl = −0.152 + 0.703 log TP	192	0.42	<0.0001
log Chl = −1.753 + 0.936 log TN	156	0.39	<0.0001
log Chl = −0.059 + 0.615 log TP (low TN:TP)	71	0.26	<0.0001
log Chl = −0.262 + 0.789 log TP (high TN:TP)	85	0.37	<0.0001
log Chl = −1.188 + 0.413 log TP + 0.504 log TN	156	0.47	<0.0001

Discussion

This paper represents the largest compilation of nutrients and Chl data from a broad range of tropical and subtropical systems and analysis of their relationship. Although conclusions may be changed by future analyses that include more data particularly from Asia, Oceania and Africa our analyses does suggest several similarities and some differences to temperate studies to the relationship between nutrients and Chl. First our data show that, tropical lakes, like temperate ones, vary dramatically not only in morphometry, light extinction and trophic status. Using Chl concentrations, as a criterion (Wetzel 2001), 15% of systems were oligotrophic (<3 μ g l^{-1} Chl-*a*), 35% were mesotrophic, 50% were eutrophic (>11 μ g l^{-1} Chl-*a*). Further, a full 25% have average annual chlorophyll concentrations greater than 50 μg l^{-1} Chl-*a*, suggesting hypereutrophic conditions. The, high chlorophyll concentrations are related to both high nitrogen and phosphorus concentrations in tropical as for temperate systems. Like temperate systems N:P ratios are generally greater than the 7:1 ratio (by weight) required for balanced phytoplankton growth (Wetzel 2001) and phosphorus relates somewhat better to chlorophyll concentration than does nitrogen. There are, however, substantial differences in the quantitative relationship between chlorophyll and nutrients in comparison to temperate regions and to some studies from relatively narrow geographic regions in tropical areas (e.g., Sarnelle et al. 1998). Our analysis suggests both a more variable relationship between log TP and log Chl and a somewhat lower chlorophyll yield per unit TP than do regressions from the temperate zone (Table 3).

The differences we found between tropical and temperate TP–Chl relationships could have several causes. It is possible that the lower Chl yield is related to differences in sampling. Many studies in temperate systems are based on only summer growing season sampling, when Chl is likely higher than the annual average, while the tropical samples are based on year round sampling (Lewis 1990). We do not believe, however, that this would explain the higher between system variance between TP and Chl in the tropical systems. This higher variation could occur, if TP had a low dynamic range as compared to temperate studies. Our TP data, however, range by nearly 500-fold between systems, a range as large as seen in the better-fitting temperate data sets.

Table 3. Selected regression equations for selected temperate lakes used in comparisons with our tropical–subtropical data.

	n	r^2	p	Distribution
TP vs. Chl				
(a) log Chl $= -0.35 + 0.94$ log TP	367	0.71	<0.0001	North American and European lakes[a]
(b) log Chl $= -0.25 + 0.799$ log TP	180	0.64	<0.0001	Worldwide lakes[b]
(c) log Chl $= -0.390 + 0.874$ log TP	133	0.69	<0.0001	North American and European lakes[c]
TP and TN vs. Chl				
(d) log Chl $= -0.83$ log TP $+ 0.34$ log TP$^2 - 0.12$ log TP$^3 + 0.43$ (log TP×log TN) $+ 0.03$	875	0.71	<0.01	USA lakes[d]
(e) log Chl $= -2.213 + 0.517$ log TP $+ 0.838$ log TN	133	0.81	<0.0001	North American and European lakes[c]
(f) log Chl $= -1.517 + 0.653$ log TP $+ 0.548$ log TN	127	0.76	<0.01	North temperate lakes[e]

[a]Mazumder (1994).
[b]Nürnberg (1996).
[c]Prairie et al. (1989).
[d]McCauley et al. (1989).
[e]Smith (1982).

Another possible cause for the relatively poor linear relationship between log TP and log Chl is that systems are outside the range of linearity between TP and Chl relationships (McCauley et al. 1989), however, 85% of the data have TP between 10 and 300 µg l^{-1}, a range where log TP relates nearly linearly to log Chl (McCauley et al. 1989).

Widespread N limitation in tropical–subtropical systems could explain both the lower Chl yield and higher variance in TP–Chl relationship. It has also been suggested that while N limitation occurs in temperate freshwater systems (Smith 1982) and P limitation occurs in tropical systems (Fisher et al. 1995; Sarnelle et al. 1998; Kalff 2002) for tropical systems N limitation may be more prevalent (Lewis 1996, 2002). Our studies do not suggest, however, widespread N limitation. For our tropical–subtropical lakes, TN:TP ratios were generally high and exclusion of those systems with relatively low TN:TP ratios (Figure 1) did not improve the predictability of Chl from TP. Similarly, TN did not explain well residuals of the TP–Chl relationship and a multiple regression with TN and TP did not explain substantially better the variance in Chl to TP. Further, inorganic nutrient concentrations, which may be a better indication of this limitation that are TN:TP ratios, were also on average far above 16:1 (Redfield et al. 1963) in a subset of Brazilian lakes.

In agreement with our results based on nutrient ratios and nutrient–Chl relationships, nutrient addition experiments in tropical systems as for temperate systems (Elser et al. 1990) do not show uniform N limitation but rather suggest that systems can vary between N limitation, P limitation and co-limitation of N and P. Reviewing experimental nutrient enrichment studies in 10 Brazilian lakes and reservoirs, Arcifa et al. (1995) did not find clear cut N limitation, rather limitation varied both between systems and seasonally within single systems. Similarly, nutrient limitation in other tropical areas as inferred from nutrient additions, physiological indicators, or dissolved N:P ratios do not show uniform N or P limitation but rather show seasonal and between system variance (Fisher et al. 1995). Thus, the total weight of evidence does not support the view that N limitation is necessarily the norm in tropical to subtropical systems or even that it is more prevalent than in temperate systems (Elser et al. 1990). Other factors may explain the somewhat lower Chl yield per unit TP and more variable Chl–TP relationsip that we observed.

In temperate systems, in addition to TN or TN:TP ratios, it has been suggested that variable light limitation could explain variance in the TP to Chl relationships (Canfield and Bachman 1981). While the tropical–subtropical database, as a whole, had high light extinction (K) that was dominated by color or turbidity (K_r), neither K nor K_r were negatively related to the residuals of the Chl–TP relationship. It is possible that a better indicator of light availability (e.g., the amount of light in the mixed layer) would relate well to residuals of the TP to Chl relationship, however, we did not have information on thermal stratification for most of the 192 systems in the data set.

There is also evidence that in temperate systems grazing, especially by large zooplankton, can regulate the empirical relationships between nutrients and

phytoplankton biomass (Pace 1984; Quirós 1990; Mazumder 1994). However, tropical and subtropical lakes are frequently dominated by small cladocerans, rotifers, and by juveniles and small copepodites (Lewis 1996; Branco et al. 2002; Jeppesen et al. 2005). While the classic control of phytoplankton by large zooplankton may not hold in tropical systems, more complex food web interactions could be responsible for the tropical–subtropical vs. temperate differences in the predictive power of the log TP vs. log Chl relationship (Lazzaro 1997).

In summary, our analysis showed some differences to expectations based on N limitation in tropical systems and to similar empirical studies from both broad temperate regions and narrow tropical areas. A number of possible mechanisms could explain these differences and different mechanisms could be operating across different regions of the tropics and subtropics. Further empirical as well as experimental studies on a diverse set of tropical systems are needed to elucidate these differences.

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