



Influence of nutrient levels, travel time and light availability on phytoplankton chlorophyll-*a* concentrations in a neotropical river basin

Influência dos níveis de nutrientes, tempo de viagem e disponibilidade de luz nas concentrações de clorofila-*a* fitoplanctônica em uma bacia de rio neotropical

Kennedy Francis Roche^{1*} , Maria Gabriela Alves Ferreira¹  and

Débora Fernandes Calheiros² 

¹Faculdade de Engenharias, Arquitetura e Urbanismo e Geografia, Universidade Federal de Mato Grosso do Sul, Cidade Universitária, Campo Grande, 79070-900, MS, Brasil

²Empresa Brasileira de Pesquisa Agropecuária, Embrapa Pantanal, Parque Estação Biológica s/n., 70770-901, Brasília, DF, Brasil

*e-mail: kennedy.roche@ufms.br

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Abstract: Aim: Knowledge of the factors influencing the biomass of phytoplankton in rivers is important with reference to the characterization of water quality and predicting the effects of environmental change on such ecosystems. The present study quantified the concentrations of chlorophyll-*a* in the water column of the Miranda River Basin, located in western Brazil, contributing to form the Pantanal Wetland, and attempted to identify the primary environmental influences on the phytoplankton biomass. **Methods:** Temperature, depth, current speed, turbidity, Secchi transparency and concentrations of nutrients, suspended solids and chlorophyll-*a* were measured at approximate monthly intervals during the course of a year, at five upland and three lowland sites. Relationships between chlorophyll-*a* and nutrient concentrations, travel times and light availability were examined. **Results:** Nutrient levels were generally low, being oligo- to mesotrophic. High levels of suspended solids were recorded (up to approximately 250 mg.L⁻¹), especially in the rainy season at the upland sites. The latter showed low chlorophyll-*a* concentrations, while lowland sites, with the exception of one, showed two peaks, one in winter (dry season) and the other in summer (wet season), of 4.9 and 2.4 µg.L⁻¹, respectively, coincident with reduced concentrations of suspended solids. **Conclusions:** The low nutrient levels recorded may have been due to the main land use being cattle rearing. The high solids concentrations found may have been due to the degradation of native vegetation, especially riparian, that has occurred over the past decades. Travel times of approximately three to four days may have been a factor in retarding algal abundance in the upland sites, as opposed to approximately ten days in the lowland sites, where light limitation may have been a factor reducing algal growth.

Keywords: land use; erosion; water quality; Pantanal; algae.

Resumo: Objetivo: Um maior conhecimento sobre os fatores que influenciam a biomassa de fitoplâncton em rios é importante para a caracterização da qualidade da água, bem como para prever os efeitos de mudanças ambientais destes ecossistemas. Este estudo quantificou as concentrações de clorofila-*a* na coluna de água da bacia hidrográfica do rio Miranda - MS, situada na região oeste do Brasil, uma das principais formadoras do bioma Pantanal, para identificar as principais influências na



biomassa do fitoplâncton. **Métodos:** Temperatura, profundidade, velocidade de correnteza, turbidez, transparência por Disco de Secchi, e concentrações de nutrientes, sólidos em suspensão, e clorofila-*a* foram medidos a intervalos aproximadamente mensais, durante um ano, em cinco pontos do planalto e três pontos na planície. Relações entre clorofila *a* e concentrações de nutrientes, tempo de viagem e disponibilidade de luz foram examinados. **Resultados:** Os níveis de nutrientes foram geralmente baixos, sendo oligo- a mesotrófico. Altas concentrações de sólidos em suspensão foram encontradas (até aproximadamente 250 mg.L⁻¹), especialmente na época chuvosa nos pontos no planalto. No planalto ocorreram baixas concentrações de clorofila-*a*, enquanto nos pontos da planície, com exceção de um, ocorreram dois picos, no inverno (época seca) e no verão (época chuvosa), de 4,9 e 2,4 µg.L⁻¹, respectivamente, coincidindo com concentrações reduzidas de sólidos em suspensão. **Conclusões:** Os baixos níveis de nutrientes provavelmente estão relacionados ao uso da terra, principalmente para pecuária. As altas concentrações de sólidos devem estar relacionadas à degradação da vegetação nativa, especialmente da mata ciliar nas últimas décadas. O tempo de viagem de aproximadamente três a quatro dias nos pontos de planalto, comparado ao tempo de aproximadamente dez dias nos pontos da planície, podem ter sido um fator determinante na diminuição da abundância de algas no planalto, enquanto a limitação por luz poderia ter sido importante diminuindo o crescimento de algas na planície.

Palavras-chave: uso da terra; erosão; qualidade de água; Pantanal; algas.

1. Introduction

The principal primary producers in rivers are often planktonic algae (Wehr & Descy, 1998; Hilton et al., 2006), serving as the base of aquatic food webs (Delong & Thorp, 2006). Excessive growth of these organisms can cause an assortment of problems related to environmental quality and water use (Hilton et al., 2006). The quantification of the biomass of such organisms and the understanding of what environmental factors control such biomass is of importance with regard to determining human control strategies as well as predicting the impacts of environmental modification, including climate change (van Steveninck et al., 1992; Wehr & Descy, 1998; Zwolsman & van Bokhoven, 2007; Hardenbicker et al., 2014). Studies of tropical rivers are still scarce when compared to temperate systems (Santana et al., 2016; Descy et al., 2017 and references therein; Townsend & Douglas, 2017 and references therein).

Nutrient concentrations are of paramount importance in determining the growth rates and biomass of algae, and although nitrogen can be important, phosphorus is considered to be the key nutrient controlling primary production (Dodds et al., 1998; Hilton et al., 2006; Mischke et al., 2011; Bowes et al., 2012). Significant positive relationships between phosphorus concentrations and planktonic algal biomass, thus implying that this is the limiting nutrient, have been established for lotic environments (Soballe & Kimmel, 1987; Basu & Pick, 1996; Lamparelli, 2004). Although less common, significant regressions of algal concentrations versus nitrogen in rivers have also been calculated (Dodds,

2006, using the data of Basu & Pick (1996); Lamparelli, 2004).

Besides nutrient concentration, one of the most influential characteristics affecting algal biomass in rivers is residence time of the water (Soballe & Kimmel, 1987; Mischke et al., 2011). Thus, phytoplankton abundance increases with river order, this pattern being due principally to the greater residence times in lower reaches, and therefore greater time periods for algal growth to occur (Vannote et al., 1980; van Steveninck et al., 1992).

Light availability may also be important in controlling algal populations. In high order rivers, the extent of marginal vegetation shading is reduced, favouring phytoplankton production; however, increases in turbidity (consonant with increases in depth) have the opposite effect (Vannote et al., 1980; Lewis, 1988). The relationship between euphotic depth and mixing depth ($Z_e:Z_m$) has been used as an indicator of the degree of light limitation of algal growth; a value of around 0.2 or less can indicate a net primary production of zero (Grobbelaar, 1989; Cole et al., 1992; Leland & Frey, 2008; Ochs et al., 2013). In tropical environments, due to the differential impact of higher temperatures on algal respiration, this value could be higher (Lind & Davalos-Lind, 1999).

While changes in water level, associated with changes in discharge, can cause increases in plankton abundances, during both the rising and falling phases, via flushing and drainage of associated lentic habitats (Lewis, 1988; Junk & Wantzen, 2003; Ochs et al., 2013; Townsend & Douglas, 2017), greater discharge generally results in lower concentrations of plankton (Leland & Frey,

2008; Hardenbicker et al., 2014; Santana et al., 2016). Such decreases would be related to decreases in residence time, increases in light limitation (due to increased suspended solids concentrations and increased depth (Lewis, 1988; Houser et al., 2010; Descy et al., 2017; Townsend & Douglas, 2017)) and increases in dilution of both nutrients and plankton provoked by greater water volume (from rainwater) (Descy et al., 1987; Descy et al., 2017).

Landscape properties and land use, including the degree of preservation of native vegetation especially at the margins, can influence the nature and quantity of nutrients and solids entering the river (Castillo, 2010; Cunha et al., 2010; Martinelli et al., 2010; Esteves et al., 2015; Pacheco et al., 2017; Chua et al., 2019; Nobre et al., 2020). Thus, for example, areas of intensive agriculture, such as soybean and cotton, have been associated with elevated concentrations of nitrogen and phosphorus in rivers (Zeilhofer et al., 2006).

In summary, combining the River Continuum Concept (Vannote et al., 1980) and the Flood Pulse Concept (Junk & Wantzen, 2003), the traditional paradigm of changes in phytoplankton abundance with river order specified low concentrations in low order streams because of low dissolved nutrient levels, short residence times, high rates of sedimentation, riparian shading, competition with macrophytes and attached algae, and grazing by benthic organisms. Increases in phytoplankton downstream are consonant with changes in the above factors, with possible subsequent decreases in high order rivers due to light limitation caused by greater depths and higher turbidity, grazing by zooplankton, and higher rates of sedimentation due to decreased turbulence as the river enters the floodplain. This paradigm has been shown to be subject to smaller-scale influences, so that the modern consensus is that local characteristics of the river are of defining importance (Reynolds & Descy, 1996; Hilton et al., 2006; Thorp et al., 2006; Doretto et al., 2020).

The Miranda River basin forms part of the Upper Paraguay River basin. It is of economic importance with regard to agriculture and cattle rearing and its lower part forms part of the Pantanal wetland. During the last number of decades, the basin has been subjected to extensive removal of native vegetation, especially of the Cerrado (savanna) type of the uplands, to be replaced in large part by pastureland (Silva et al., 2011; Ferreira Sobrinho et al., 2012; Estevam et al., 2017). Based on these facts, we hypothesized that,

due to the reduced degree of protection against erosion, normally provided by native vegetation (see above), leading to high levels of suspended solids, associated with rainfall, in the waters of the system, phytoplankton productivity could be limited by light availability. We examined this possibility by, firstly, determining nutrient levels in the waters, and thus potential baseline phytoplankton biomass. Subsequently, we analyzed the effects of travel time in reducing algal biomass, and finally, compared our biomass:nutrient relationships, and light availability, with other studies.

In the present study, limnological characteristics of the water were analyzed during the course of one year (May 2005 to April 2006), at eight sampling points in the Miranda River Basin. Results were compared between upland and lowland sampling points and sampling dates. Relationships between nitrogen and phosphorus, and chlorophyll-*a* were examined. The objective was to attempt to identify the principal environmental characteristics influencing spatio-temporal differences in planktonic chlorophyll-*a* concentration in this neotropical river basin.

2. Material and Methods

2.1. Study area

For a detailed description of the Miranda River Basin, see Pereira et al. (2004), Ferreira Sobrinho et al. (2012), Merino et al. (2013), and Estevam et al. (2017). The two main rivers of this basin are the Miranda River and the Aquidauana River (Figure 1). Eight points were sampled during the course of a year, on nine dates, in May (between the dates of 3-14), June/July (between the dates of 30-4), July (between the dates of 27-31), September (between the dates of 15-19), October (between the dates of 4-8), December (between the dates of 5-9) of 2005, and January (between the dates of 7-11), January/February (between the dates of 27-2) and April (between the dates of 20-25) of 2006 (Figure 1, Table 1). Distances from source to the sampling points were calculated with QGIS 2.18 software using a map in vectorial form with a scale of 1:350,000 provided by the Brazilian National Water Agency (ANA), and GPS coordinates.

According to Merino et al. (2013), points 1, 2 and 3 have rocky beds. Shortly after, the river becomes alluvial, and while still dominated by the uplands, becomes meandering, with marginal lakes (Figure 5 of Merino et al., 2013). Shortly before the intersection with the Salobra River (near

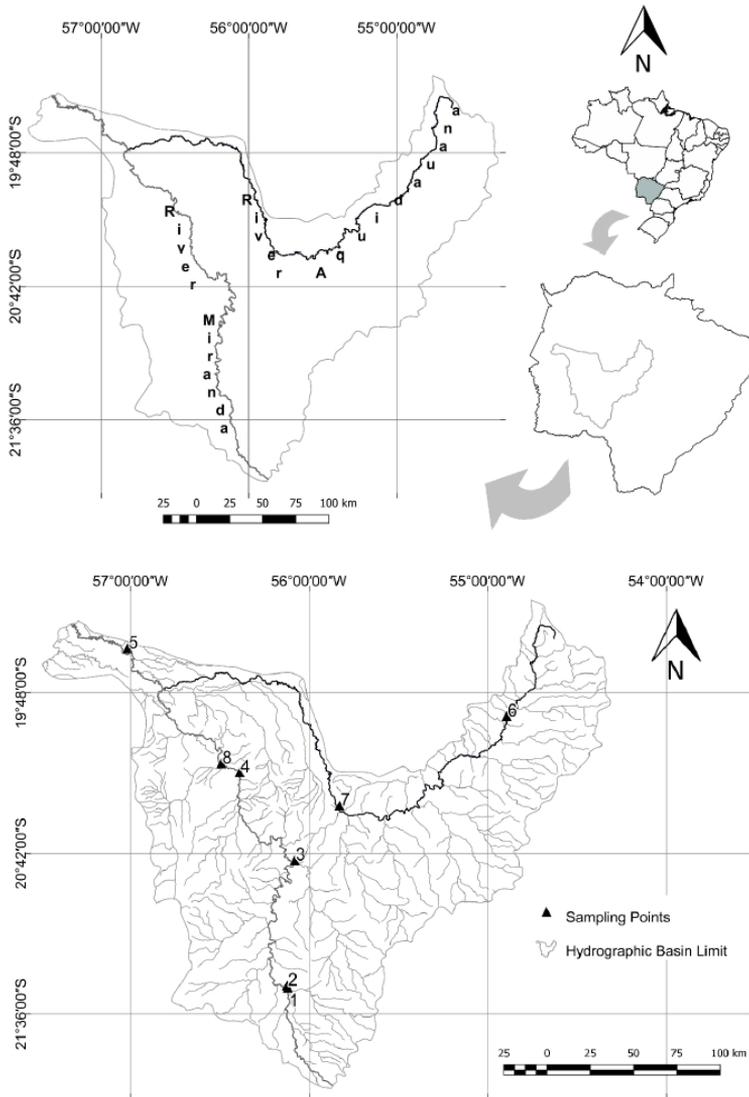


Figure 1. Location of the Miranda basin in Mato Grosso do Sul State, Brazil, with the two principal rivers (Miranda and Aquidauana) and the sampling points within the basin.

Table 1. Identification of sampling points, with geographic coordinates, altitude and distance from source. Site 5, being situated after the confluence of the River Miranda and River Aquidauana, presents two values for distance from source.

Point	Coordinates (S - W)	Altitude (m)	Distance (km)
1. Upland River Miranda	21°28'56.1" - 56°07'13.1"	224	79
2. Upland River Santo Antônio	21°28'05.9" - 56°07'29.8"	225	65
3. Upland River Nioaque	20°45'57.4" - 56°04'53.4"	151	120
4. Lowland River Miranda	20°16'21.0" - 56°23'25.9"	117	326
5. Lowland River Miranda	19°34'37.8" - 57°01'04.7"	93	482 Miranda 531 Aquidauana
6. Upland River Aquidauana	19°57'30.0" - 54°53'39.1"	252	97
7. Upland River Aquidauana	20°27'34.6" - 55°49'51.0"	142	276
8. Lowland River Salobra	20°13'21.4" - 56°29'35.0"	115	109

points 4 and 8), the river enters the floodplain proper, to form an alluvial ridge and subsequently returns to become a meander belt (Figures 6 and 7 of Merino et al., 2013).

2.2. Environmental variables

At each point, water temperature was measured *in situ* using a YSI multi-probe, transparency using a Secchi disc, and water samples collected at a

depth of 60% from the surface, using a pump. Turbidity was measured using a turbidimeter, suspended solids by filtration through cellulose filters, total phosphorus and nitrogen by persulphate digestion followed by flux injection colorimetry, and chlorophyll-*a* spectrophotometrically after extraction in 90% ethanol (Mackereth et al., 1978; Nusch, 1980; Valderrama, 1981; Wetzel & Likens, 1991; Zagatto et al., 1981).

Mean monthly rainfall was obtained from HidroWEB/ANA. Water depth and current velocity were measured using a Marsh-McBirney Flo-mate 2000 flow meter. The former was measured at a distance of 50% from the riverbank, thus the depth at the centre of the river. The latter was measured at depths of 20% and 80% from the surface, at distances of 25%, 50% and 75% from one margin, and the mean calculated. Travel time was calculated by dividing the distance from the source to each sampling point by the current velocities between intermediate points.

2.3. Data analysis

Values for the ratio between the euphotic depth (Secchi transparency multiplied by 3.3 (Koenings & Edmundson, 1991; Lee et al., 2018) and mixing depth ($Z_e:Z_m$) were calculated. Considering water depth and current speeds, it was concluded

that water flux was turbulent, with full vertical mixing, so that mixing depth was taken as total depth. Relationships between chlorophyll-*a* and nutrients were analyzed by simple regression, and compared graphically with regression lines derived from Basu & Pick (1996) and Lamparelli (2004). Selected limnological characteristics were compared between the sampling localities using the Wilcoxon signed-rank test (Table 2). Principal Components Analysis was performed on \ln transformed (with the exception of $Z_e:Z_m$) water quality characteristics for points 1-7, with the specific aim of relating chlorophyll-*a* concentrations to nutrient concentrations, travel time and light availability. Statistical analyses were carried out using Past 3.25 (Hammer et al., 2001).

3. Results

Mean monthly water temperature and rainfall were lowest in the winter months, especially July-September (Figure 2).

Chlorophyll-*a* concentrations were generally low, with somewhat elevated concentrations being found in September and January at the lowland Miranda sites (4-5) (Figure 3). There was an abrupt decrease in chlorophyll-*a* concentration from September to October, for sites 4-5.

Table 2. Wilcoxon signed-rank test p values for comparisons of limnological variables between the four groups of sites (sites 1-3 upland River Miranda, sites 4-5 lowland River Miranda; sites 6-7 River Aquidauana; site 8 River Salobra). Significant values ($p < 0.05$) are indicated in bold.

Chlorophyll- <i>a</i>	4-5	6-7	8
1-3	0.302	1	0.581
4-5		0.231	0.116
6-7			0.846
Total phosphorus			
1-3	0.571	0.131	0.014
4-5		0.113	0.014
6-7			0.076
Total nitrogen			
1-3	0.131	0.427	0.057
4-5		0.076	0.010
6-7			0.735
Travel time			
1-3	0.023	0.023	0.116
4-5		0.023	0.581
6-7			0.023
Total solids			
1-3	0.642	0.041	0.029
4-5		0.572	0.010
6-7			0.006
$Z_e:Z_m$			
1-3	0.029	0.077	
4-5		0.455	

Significantly lower values of total phosphorus were found at site 8 as compared to the Miranda River sites, while there was a significant difference in total nitrogen between the former site and the lowland Miranda sites (Figure 4; Table 2). At the beginning of the rainy season, both nutrients showed increases, tending somewhat to decrease again during the course of the study period.

Water depth was greatest in the lowland sites, increasing at all sites from winter to summer, with

peaks in December, and subsequent decreases at the upland sites (Figure 5). Current velocity was greatest at points 6-7, and lowest at point 8; comparing the Miranda River upland and lowland sites, velocity was generally highest at the latter sites. Travel time was significantly greater in the lowland sites, as compared to the upland sites (Figure 5; Table 2).

Suspended solids consisted primarily of inorganic material. Concentrations were highest at sites 6-7, notably in the second half of the study, and lowest at site 8 (Figure 6; Table 2). Values were lowest in the dry season, increasing during the initial part of the rainy season, and subsequently decreasing. Turbidity was positively related to suspended solids concentrations and Secchi transparency negatively so (Figure 7). The euphotic depth:mixing depth ratio was high for all points in July and September, and, with the exception of point 8 (the River Salobra) where the euphotic zone always extended to the river bottom, decreased at the onset of the rainy season, tending to increase again towards the end of the study period (Figure 7).

No significant relationships were found between total phosphorus and chlorophyll-*a* ($\log(\text{chlorophyll-}a+1) = 0.5264-0.1936(\log\text{TP}+1)$; $R^2 = 0.0266$; $p = 0.1591$) and total nitrogen and chlorophyll-*a* ($\log(\text{chlorophyll-}a + 1) = 0.9073-0.2661(\log\text{TN}+1)$; $R^2 = 0.0446$; $p = 0.0671$) (Figure 8).

Principal Components Analysis evidenced a positive association between chlorophyll-*a* concentrations and light availability ($Z_c:Z_m$), inversely related to suspended solids concentrations (Figure 9).

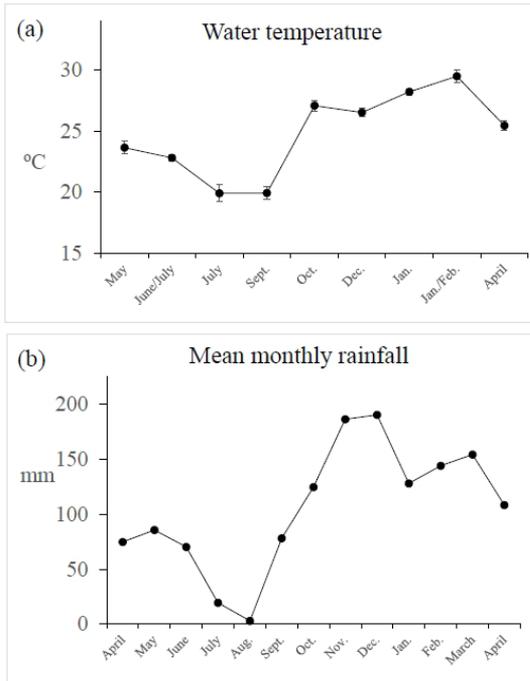


Figure 2. Monthly changes in mean monthly water temperature (a) and rainfall (b) in the Miranda River Basin between May 2005 and April 2006. Source for rainfall: HidroWEB/ANA (ANA, 2017).

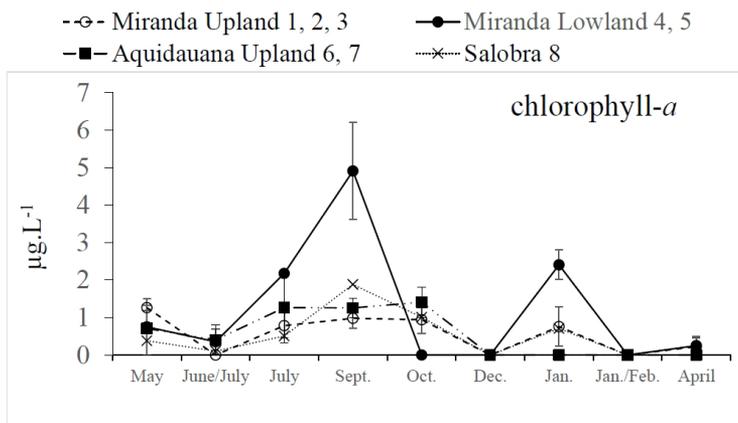


Figure 3. Monthly changes in chlorophyll-*a* in the Miranda River Basin lowland sites, between May 2005 and April 2006. Standard errors are shown.

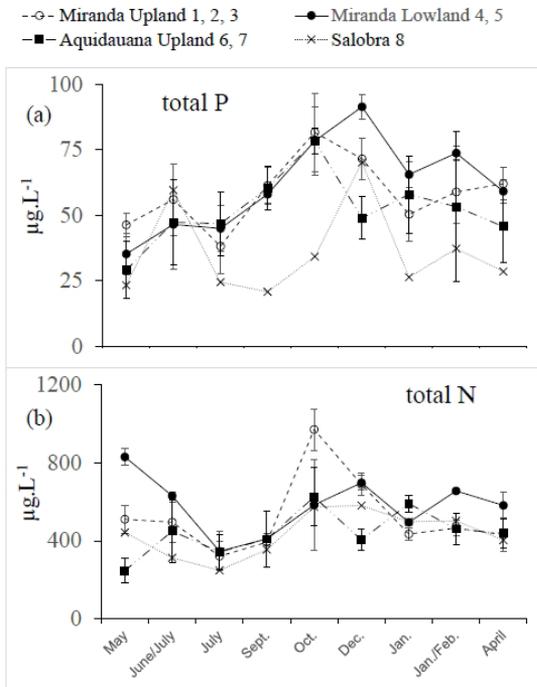


Figure 4. Monthly changes in total phosphorus (a) and nitrogen (b) in the Miranda River Basin between May 2005 and April 2006. Standard errors are shown.

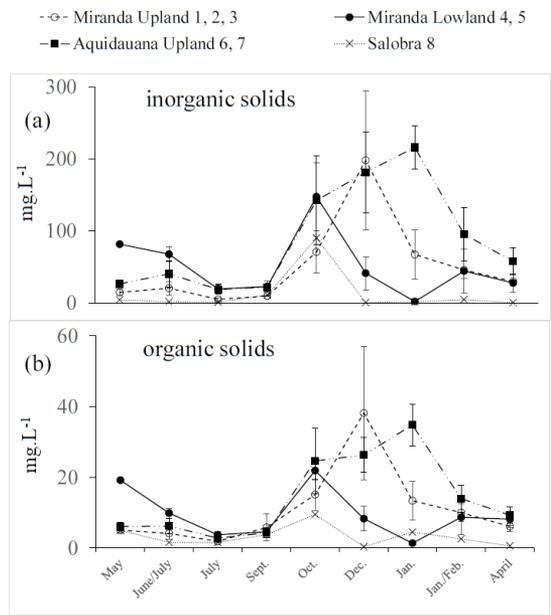


Figure 6. Monthly changes in inorganic (a) and organic (b) suspended solids in the Miranda River Basin between May 2005 and April 2006. Standard errors are shown.

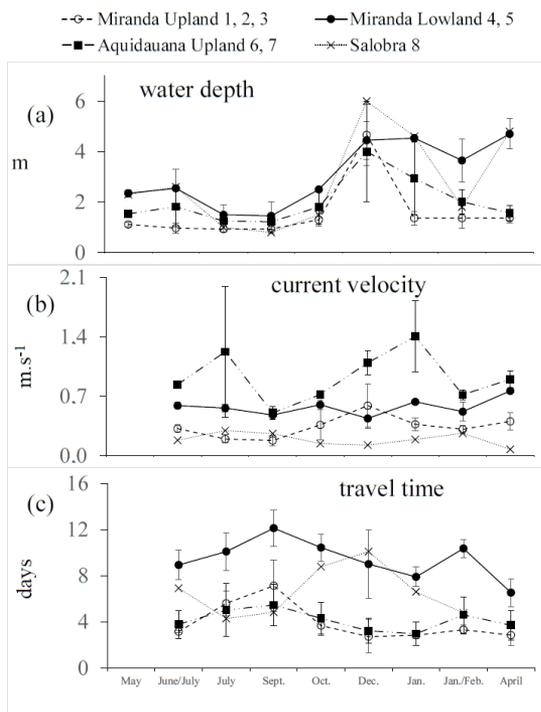


Figure 5. Monthly changes in mean water depth (a), current velocity (b) and travel time (c) in the Miranda River Basin between May 2005 and April 2006. Standard errors are shown.

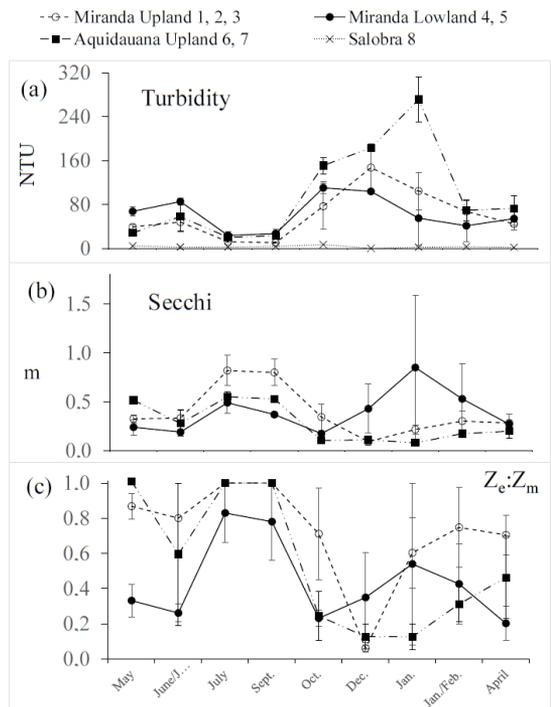


Figure 7. Monthly changes in turbidity (a), Secchi depth (excluding point 8) (b) and the ratio between euphotic and mixing water depth (excluding point 8) (c) in the Miranda River Basin between May 2005 and April 2006. Standard errors are shown.

4. Discussion

In the present study, we examined the hypothesis that the main factors affecting phytoplankton growth in the river basin would be nutrient levels,

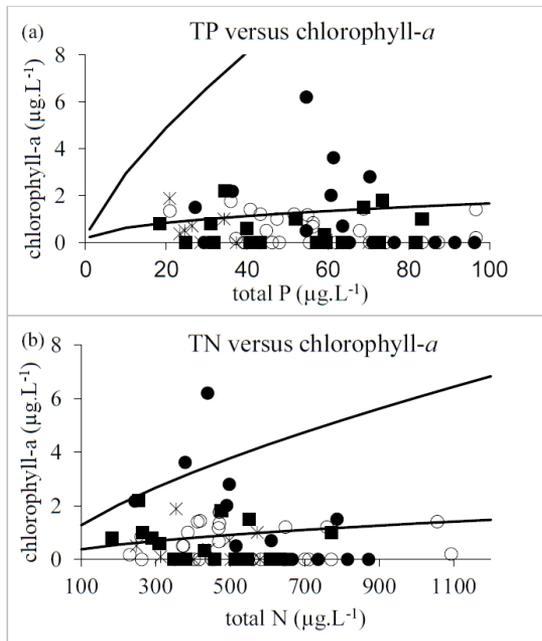


Figure 8. Relationships between chlorophyll-*a* and total phosphorus (a) and total nitrogen (b), for the sampling points of the Miranda River Basin, between May 2005 and April 2006. The relationships between chlorophyll-*a* and phosphorus derived by Basu & Pick (1996) (upper line) and Lamparelli (2004) (lower line), and between chlorophyll-*a* and nitrogen derived from Basu & Pick (1996) (upper line) and by Lamparelli (2004) (lower line) are shown. Symbols as in previous figures.

travel time and light availability; our sampling programme was designed to attempt to elucidate which factors were most important and whether these factors evidenced seasonal and spatial patterns in relative importance. Firstly, we consider the changes in phytoplankton biomass (represented as chlorophyll-*a*) in the system, and then consider the influencing roles of nutrient concentrations, travel time (reflecting the time available for algal growth with the passage of water through the system), and light availability. In order to demonstrate that nutrient levels were not paramount in determining algal biomass, thereby suggesting the importance of other factors, we compared the relationships of phosphorous and chlorophyll-*a* and nitrogen and chlorophyll-*a* derived here, with those of other studies.

Chlorophyll-*a* concentrations were generally low, the values recorded allowing the waters to be classified as oligotrophic (Dodds et al., 1998; Lamparelli, 2004). The highest concentration of chlorophyll-*a* was found in the dry season at the lowland sites of the River Miranda, as also found by Oliveira & Ferreira (2003).

The decrease in chlorophyll-*a* at the lowland sites from September to October could have been caused by the rainfall at the beginning of the wet season (Lewis, 1988; Junk & Wantzen, 2003; Leland & Frey, 2008; Santana et al., 2016; Ochs et al., 2013; Townsend & Douglas, 2017). This decrease could have been due to increased light limitation (see below) and dilution (Descy et al., 1987).

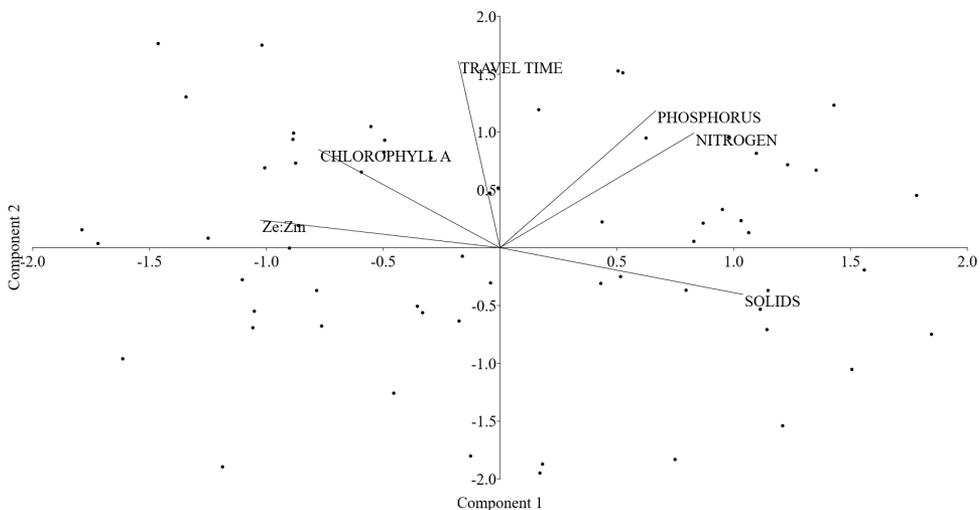


Figure 9. Principal components analysis for selected environmental variables, for all sampling points, except the Salobra River, in the Miranda River Basin, sampling between May 2005 and April 2006. Axis 1 and axis 2 explained 43% and 28%, respectively, of the variance.

The values of phosphorus and nitrogen recorded would allow the waters to be classified as generally mesotrophic with regard to phosphorus (with the Salobra River tending to be borderline between oligotrophic and mesotrophic for this nutrient for some dates), and oligotrophic with regard to nitrogen (Dodds et al., 1998; Lamparelli, 2004). Such relatively low concentrations of nutrients could be due to the predominance of pastureland in the region (Zeilhofer et al., 2016; Estevam et al., 2017; Oliveira et al., 2019), as opposed to other more intensive land uses (Zeilhofer et al., 2006; Taniwaki et al., 2017). The greater conservation of native vegetation in the watershed of point 8 (Ferreira Sobrinho et al., 2012) could have contributed to the lower phosphorus concentrations recorded at the latter point (Castillo, 2010; Cunha et al., 2010; Martinelli et al., 2010; Esteves et al., 2015).

In the present study, the time it would take for a quantity of water to travel from the source to each sampling point was determined according to water current speed and the distance from the source, and thus termed “travel time”. Leland (2003) and Leland & Frey (2008) calculated “travel time” by regressing current speed on discharge. Values of 3.6, 2.8, 2.2, 1.2 and 0.2 days were obtained through regression by Leland (2003) while the corresponding values calculated by simply dividing the distance by the current speed (as done in the present study) were 4.3, 2.8, 1.8, 2.5 and 0.3, respectively; thus, the two methods gave similar results. Analogous to this is the “age” or the time the water has spent in the system, being calculated by using the area of the hydrographic basin upstream of the sampling point and mean annual flow, with the term “residence time” being used (Soballe & Kimmel, 1987; Basu & Pick, 1996). Bowes et al. (2012) used the downstream distance as a proxy for residence time, while the terms “transport time” by van Steveninck et al. (1992) and “transit time” (Bukaveckas et al., 2011) would be most equivalent to our approach.

The reduced travel times (around 3-4 days) of the upland sites could have contributed to the low levels of chlorophyll-*a* recorded (Soballe & Kimmel, 1987; Hilton et al., 2006; Mischke et al., 2011). Nevertheless, other studies have found large increases in chlorophyll-*a* at reduced residence times. Thus, Basu & Pick (1996) suggested that for times greater than three days, nutrient availability would be more important; the latter authors found that chlorophyll-*a* levels could reach about 11 µg.L⁻¹

after only three and a half days and up to 23 µg.L⁻¹ after four and a half days.

The high concentrations of solids recorded in the present study, especially during the rainy season at the upland sites, and during the high water periods of 1996-1999, in the rivers Santo Antonio, Nioaque and Aquidauana, equivalent to upland sites of the present study (Oliveira & Calheiros, 1999), could have been due to degradation of the native vegetation (Oliveira & Ferreira, 2003; Ferreira Sobrinho et al., 2012; Estevam et al., 2017). For example, Pereira et al. (2004) concluded that, in the superior part of the River Aquidauana basin, an intense degradation of marginal vegetation has occurred, with pastureland reaching the margins of the river. This scenario reveals an accentuated need for restoration of such vegetation, especially on the river margins (Taniwaki et al., 2017; Yang et al., 2018; Chua et al., 2019).

In the middle to lower reaches of the River Miranda, during the years 1987-1989, Oliveira & Ferreira (2003) found higher values of suspended solids at the beginning of the rainy season, but lower values at the height of this season, as found in the present study, especially at the lowland points, most notably in January. Lewis (1988) recorded a similar pattern of change, with highest values of transparency at low discharge (and low water depth), a decrease with increasing discharge, and a subsequent increase at high discharge. Thus, in the present study, increases in nutrients and solids at the beginning of the rainy season would have been due to increased soil runoff (so-called “first flush” (Chen et al., 2012; Zeilhofer et al., 2016)), while dilution would have contributed to the decreases during the remainder of the wet season (Descy et al., 1987; Everbecq et al., 2001).

Although comparing light availability to chlorophyll-*a* concentrations at a particular point in a river can be confounded by different light availabilities upstream (for example, by discontinuous variations in water depth along the course of the river) (Cole et al., 1992; Bukaveckas et al., 2011), the low values of the euphotic depth to mixing depth found here associated with the rainy period would imply unfavorable conditions for algal production (Ochs et al., 2013; Townsend & Douglas, 2017). In the study of Leland & Frey (2008), the euphotic zone was generally less than 15% of total water depth, due to the high concentrations of suspended solids present (generally approximately 50 to 300 mg.L⁻¹) and the authors concluded

that the populations of algae were limited by light availability. Similarly, Leland (2003) stated that concentrations of greater than 50 mg.L⁻¹ of suspended solids would be expected to prohibit net primary production. In the Lower Mississippi River, where phytoplankton was consistently light limited, turbidity values were recorded of around 20-60, up to 80 NTU, with total suspended solids reaching values of approximately 250-350 mg.L⁻¹, comparable to our values (Ochs et al., 2013).

The absence of linear relationships between nutrients and chlorophyll-*a* in the present study means that for an increase in nutrient concentration, there was no increase in chlorophyll-*a*, in contrast to other studies (Soballe & Kimmel, 1987; Basu & Pick, 1996). Much larger increases in chlorophyll-*a* in relation to total phosphorus and total nitrogen were found by Basu & Pick (1996) for rivers where light limitation was not considered to be an important factor. Our results resemble most closely those of Lamparelli (2004). In the latter study, the rivers (in the São Paulo State region of Brazil) were found to be generally turbid, with only five of the 17 Secchi Disc readings provided being greater than 0.4 m, similar to found here. This low transparency would have been caused by suspended solids, and resulted in the lack of any linear relationship between chlorophyll-*a* and nutrient concentrations due to light limitation (with, as discussed above, another factor possibly being short travel time in the upland sites).

Studies have recorded declines in fish populations in rivers of the region, attributing this to over-fishing; however, environmental degradation could also be an important factor (Mateus et al., 2011; Calheiros et al., 2012; Alho & Reis, 2017). The high sediment concentrations recorded here could lead to decreases in macroinvertebrate abundances via smothering and scouring (Wantzen, 1998) and in fish habitat availability and even direct physical harm, with typical values of 100 mg.L⁻¹ or more being potentially deleterious for fish (Kjelland et al., 2015). Fish larvae have been found in the channels of the Miranda river, with reproduction during the summer months occurring in the upper and middle parts of the river (Nascimento & Nakatani, 2005), thus coincident with the highest concentrations of suspended solids recorded in the present study. Additionally, while low concentrations of algae can be beneficial in the sense of diminished water treatment problems, these organisms serve as food for zooplankton and benthos (DeLong & Thorp, 2006), which in turn are consumed by fish; thus,

depressed algal production could eventually hamper fish production.

To summarize, chlorophyll-*a* concentrations were generally low throughout the entire basin, with low nutrient levels and low light availability likely being most responsible for this pattern. Chlorophyll-*a* peaks were recorded at the lowland sites when light availability was greatest. No such peaks were recorded at the upland sites when light availability was high (especially in the May to September sampling dates), thus suggesting that short travel times could have been important for retarding phytoplankton growth at the latter sites. The Salobra River site (site 8) was atypical, with lowest phosphorus concentrations and consistently high transparency; low chlorophyll-*a* values here were most probably due principally to low phosphorus concentrations. Future studies should include analyses of the phytoplankton and zooplankton communities, and estimation of the rates of such processes as algal growth and production, sedimentation, and grazing losses, leading eventually to the development of a model of phytoplankton dynamics (Garnier et al., 1995; Everbecq et al., 2001; Schöl et al., 2002).

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