The Effect of DOC and Hydraulic Residence time on Primary Production in Lake Ecosystems

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Abstract

Productivity in lake ecosystems is limited through either light or nutrient availability, and understanding what factors cause these limitations to occur is important to understanding how lake systems function. In my experiment I investigated the roles that hydraulic residence time and DOC have on primary production rates in lakes, and therefore, whether production in these lakes is limited by light or nutrients. Phosphorus uptake assays were conducted in lakes with various hydraulic residence times and DOC concentrations to quantify rates of primary production after nutrient injection. It was found that higher rates of phosphorus uptake were correlated with both lower DOC concentrations and higher hydraulic residence times. These results indicated that productivity in the sample population was controlled by both light limitation and nutrient limitation. The DOC and phosphorus uptake correlation was particularly strong, indicating that DOC is an important factor in controlling productivity across a variety of lakes.

Introduction

Understanding the factors which control primary production in lakes is essential to discerning how these systems function. Productivity in lake ecosystems is limited primarily through nutrient or light availability. The productivity of clear lakes that have low levels of dissolved organic carbon (DOC) has been shown to be controlled primarily by nutrient availability, while productivity in lakes with high DOC levels depends on light availability (Seekell et al 2015). In lakes that are nutrient limited previous studies have demonstrated that in the majority of these lakes phytoplankton are limited in phosphorus. (Schindler et al 1977). Further, phytoplankton biomass is more clearly correlated to changes in phosphorus rather than nitrogen, another possible limiting nutrient (Søndergaard et al 2017).

One factor that influences the total phosphorus levels in lakes is hydraulic residence time (HRT), the amount of time that water remains in a lake. Lakes with longer hydraulic residence times exhibit higher C:P ratios, and are therefore more nutrient limited than lakes with shorter residence times (Hecky et al 2013). This occurs because lakes with a high residence time have
less water from the watershed coming in, so the phosphorus in the water is used up and not
replaced as quickly. Further, studies have demonstrated that a longer HRT leads to a larger
proportion of phosphorus in the water being lost to the sediment (Duras and Hejzlar 2001).
Therefore, HRT can act as a control on primary production, as it influences nutrient availability.
However, it is important to note that in systems where there is a high and continuous input of
nutrients, variation in hydrologic residence time does not appear to effect primary production
levels (Soares et al 2012). Hydrologic residence time is also unlikely to have a strong effect on
productivity in high DOC lakes, which are more likely to be limited by light rather than
nutrients.

A previous study argues that production in the majority of the nutrient poor lakes in the
world is controlled by light, while nutrient supply is only the main controlling factor in lakes
dominated by pelagic production (Karlsson et al 2009). DOC can also affect the light and
temperate profile of lakes in a variety of ways. At low concentrations in nutrient limited lakes
DOC can increase primary production by releasing nutrients through photolysis (Seekell et al
2015). However, at higher levels, DOC reduces the ability of light to penetrate through the water,
which causes faster light extinction and reduces primary production as a result of reduced light
levels. High DOC levels also cause heat in lakes to be concentrated at the surface and create
steeper thermal gradients between oxygenated surface water and deoxygenated deeper water
(Solomon 2015). Further, studies have demonstrated that the enrichment of phosphorus has a
weaker effect on primary production at higher levels of DOC (Carpenter et al. 1998). Therefore,
the effect that DOC has on a lake system varies under different conditions. These differences are
exacerbated by the variability in DOC composition, which is based upon terrestrial inputs that
may be location specific (Seekell et al 2015). Overall, DOC is an important factor in primary
production, thus, it is important to understand how DOC influences productivity across a wide range of concentrations and lake conditions.

In this study I investigated the effects of nutrient and light limitation on phosphorus uptake rates across lakes with a wide DOC and HRT gradient. Phosphorus uptake rates were used as a proxy for primary production, as phosphorus uptake rates are higher after a spike of nutrients, indicating nutrient limitation. I hypothesized that a negative linear relationship would exist between DOC and phosphorus uptake rates because of the decrease in light penetration that results from higher DOC concentrations. Drainage ratio was used a proxy to hydraulic residence time, which it has an inverse relationship with. My second hypothesis was that phosphorus uptake rates would increase as drainage ratio decreased, because lakes with a lower drainage ratio are typically nutrient poor. I expected this trend to be particularly significant in clear, low DOC lakes, as productivity in those lakes tends to be nutrient mediated. Finally, I hypothesized that the depth at which the assays are conducted will have an effect on the phosphorus uptake rate, because deeper water has less light penetration. Therefore, I expected that the top level would have the highest the rate of productivity because it is exposed to the most light.

Methods

Sample area

10 lakes were sampled from June-July of 2018 on the University of Notre Dame Environmental Research Center (UNDERC) property, which is located outside of Land O’Lakes Wisconsin. Specific lakes and bogs were selected to create a wide DOC and HRT gradient. The lakes and bogs included in the study are Cranberry bog, Tenderfoot, Bay, Morris, Tuesday, Ward, Brown,
Phosphorus Uptake Assay

Microcosms were created by filling 1000 mL bottles with 1000 mL of lake water. 1 mL of a nutrient mix consisting of 0.05 mg of phosphorus and 0.95 mg of nitrogen was added to each microcosm. An initial phosphorus level was taken by filtering samples using small Chlorophyll filter paper and storing the filtered samples in pobiocups immediately after phosphorous addition. The remaining microcosms were then suspended at three different depth levels in the middle of the lake and incubated for 6 hours. All of the microcosms, including the initial phosphorus level ones, were conducted in triplicate. The levels at which the microcosms were suspended were determined by the depth of the epilimnion at each individual lake. The epilimnion depth was established through DO (dissolved oxygen) and temperature data collected using a YSI Pro20 profiler in 0.5 m intervals. The edge of the epilimnion was defined by the depth preceding a 1.0 °C or higher change in temperature relative to the previous reading. A bottom, middle and top depth level for each site was then determined using the depth marking the bottom edge of the epilimnion as the bottom level, the distance halfway between the bottom edge and the surface as the middle level, and then the surface level as the top depth. After the 6-hour incubation, samples from each of the microcosms were filtered using small Chlorophyll filter paper and stored in pobiocups. The filtered samples were placed in the freezer until lab analysis.

Light meter

A Li-COR light meter was used to measure light penetration at 0.5 M intervals in each of the lakes.
*Lab analysis*

Samples were thawed 1-2 hours before the start of the analysis. 3 mL of a mixed reagent containing ammonium molybdate, 15% sulfuric acid, ascorbic acid and potassium antimony tartrate in the 2:5:2:1 ratio was added to 30 mL of each sample. After 10 minutes, the absorbance of each sample was read on a spectrophotometer on a 10 cm path at 885 nm. The concentration of each sample was determined using a standard curve analysis. The standard curve was created using dilutions of a 10 mg/L stock of KH₂PO₄. Standard curves were only used for calculations if they had a linear R-squared value between 0.95 and 1.

*Statistical analysis*

Linear regressions were run in R studio between DOC and phosphorus uptake at each of the different depth levels, along with DOC and phosphorus uptake across all of the depth levels. The same regressions were run with drainage ratio and phosphorus uptake. A one-way ANOVA was run on the average phosphorus uptake rates between each of the different depth levels. A linear regression was also run on total phosphorus levels in the lakes and DOC, total phosphorus levels and phosphorus uptake rates, and DOC and the light extinction coefficient (Kₜ). All data points outside of 2 standard deviations from the mean were considered outliers and excluded from the statistical analyses.

**Results**

*Phosphorous Uptake Assay*
There was no significant relationship between drainage ratio and the phosphorus uptake rates at the top depth level or the bottom depth level (Top: R-squared= 0.1021, DF=7, p-value=0.4019, Bottom: R-squared=0.2142, DF=7, p-value=0.2096; Figure 1). There was a significant, negative, linear relationship between drainage ratio and phosphorus uptake rates at the middle depth level, and drainage ratio and phosphorus uptake rates across all depth levels (Middle: R-squared=0.756, DF=7, p-value=0.002322, Overall: R-squared=0.3432, DF=7, p-value=0.09741; Figure 1; Figure 2).

A significant, negative, linear relationship exists between DOC concentration and phosphorus uptake rates at the top, middle and bottom depth level (Top: R-squared= 0.761, DF=7, p-value=0.002154, Middle: R-squared=0.2909, DF=7, p-value=0.134, Bottom: R-squared=0.3444, DF=7, p-value=0.09668; Figure 3). There is also a significant relationship between DOC concentration and phosphorus uptake rates across all depth levels (Overall: R-squared=0.618, DF=7, p-value=0.012; Figure 4).

No significant difference in phosphorus uptake rates was found between the top, middle and bottom depth levels (F-value=0.445, DF=3, p-value= 0.723; Figure 5).

*Total Phosphorus Levels*

There is no significant relationship between DOC concentration and total phosphorus levels of surveyed lakes (R-squared=0.009868, DF=9, p-value=0.7714; Figure 6). There is also not a significant relationship between total phosphorus levels and P Uptake rates (R-squared=0.05093, DF=8, p-value=0.5307; Figure 7).

*DOC and Kd*
There is a statistically significant, positive, linear relationship between DOC and $K_d$. ($R^2=0.80014$, $p$-value= 0.001131, DF=7; Figure 8).

**Discussion**

The experimental results support both the hypothesis that increasing DOC concentrations leads to a reduction in phosphorus uptake and the hypothesis that larger drainage ratios lead to a decrease in phosphorus uptake. These trends are clear when looking at the overall data from each of the lakes, rather than the data from each of the individual depth levels. While it may appear these two trends contradict, as one suggests that productivity in lakes is controlled by phosphorus limitation and the other one light limitation, this is not necessarily the case because both high and low DOC lakes were sampled. Therefore, some of the clearer, low DOC lakes may be responsible for the trend seen across hydraulic residence times, as these lakes are most likely limited by nutrients rather than light. It is interesting to note that P uptake at all three of the depth levels correlated significantly with DOC concentration, while P uptake at only the middle depth level correlated with hydraulic residence time. This could indicate that DOC is correlated more strongly with phosphorus uptake in the lakes sampled than HRT did. Additionally, the majority of the lakes utilized had DOC levels on the higher end, and it has been shown that past a particular DOC threshold primary production is controlled through light limitation (Karlsson et al 2009).

However, an ANOVA run across the three different depth levels indicated that depth was not a significant factor in P-uptake. While the current data shows no significance, a larger sample size could possibly reveal differences between the depth levels. Looking at the graph for DOC vs. P. Uptake the top, middle and bottom depth level indicate a trend that initially begins with the
top level having the highest productivity, and the bottom level having the lowest productivity. Depth is major factor in determining light availability, and light declines with increasing depth, so the presence of this trend is logical (Yvonne 2014). DOC concentrations are higher towards the surface of a lake, which supports the data that shows P Uptake at the top decreases more intensely with increasing DOC than P Uptake at the lower two levels (Sugiyama 2004).

Further confirmation that light availability limits productivity in the lakes that were sampled is the positive, linear relationship that was found between the light extinction constant and DOC. The existence of this relationship supports the claim that high DOC concentrations correlate with lower levels of phosphorus uptake because of the reduced light penetration at high DOC concentrations. Interestingly, there was no relationship found between total phosphorus levels and DOC concentration, which contradicts past studies which have shown that DOC increases nutrient concentrations in lakes as it is a carrier of nitrogen and phosphorus (Seekell 2015 et al). However, additional studies have also found that DOC and phosphorus levels change independently of each other, which suggests that DOC does not have the same properties across all lakes (Persson and Broberg 1985).

Our results indicate that there is no significant correlation between total phosphorus levels in the lakes sampled and P uptake. It is expected that lower levels of total phosphorus would lead to a higher P uptake rate because those lakes are more nutrient deficient. These results suggest that primary production in the sample areas may not be limited by phosphorus, but another factor such as nitrogen or light (Karlsson et al 2009). Shallow lakes have been demonstrated to be primarily phosphorus limited in the spring, and to shift to being nitrogen or light limited later in the year (Kolzau 2004). Additionally, in unpolluted lakes N and P are
equally likely to explain nutrient limitation of phytoplankton (Evans et al 2006). However, since P uptake had a strong negative correlation with DOC and the majority of the lakes have a high DOC concentration, it appears that production in these lakes is controlled by light availability rather than nitrogen or phosphorus.

Studying the impacts that DOC has on primary production is particularly relevant as lakes in boreal and north temperate climates are undergoing “browning”, which is the result of a large increase in DOC concentration (de Wit et al 2016). Browning is likely to continue into the future as global warming may lead to increases in terrestrial and wetland production, along with higher levels of enzymatic activity in soils, which in turn produces more DOC than can enter aquatic systems. Increased precipitation is also another factor to consider, as it can lead to more terrestrial organic material entering into aquatic ecosystems (Evans et al 2006). Changes in DOC concentration within a lake can greatly alter the vertical temperature and light structure of lakes and affect organisms ranging from phytoplankton to fish (Solomon et al 2015). Higher levels of DOC may also serve as a defense against eutrophication, as the effects of an increase in nutrient is reduced in lakes controlled through light limitation (Deiningere al 2017). Understanding the impact that DOC and other factors which affect primary production have on lake ecosystem is essential to managing and protecting healthy systems.

Figures
Figure 1: Relationship between drainage ratios and phosphorus uptake rates at three different depth levels. There is a negative, linear relationship between drainage ratio and P uptake at the middle depth level. (For the middle depth level; trend line equation: \( y = -0.0644x + 4.4287 \), R-squared: 0.3432).

Figure 2: Relationship between drainage ratio and overall P uptake rates. There is a negative, linear relationship between drainage ratio and phosphorus uptake rates across all depth levels. (Trend line equation: \( y = -0.0465x + 3.9511 \), R-squared: 0.34309, 0.09741).
Figure 3: Relationship between DOC concentration and phosphorus uptake rates at three different depth levels. There is a negative, linear relationship between DOC concentration and phosphorus uptake rates at all three depth levels. (For the top depth level; trend line equation: $y = -0.1603x + 5.5605$, R-squared: 0.76094, p-value: 0.002154. For the middle depth level; trend line equation: $y = -0.0657x + 4.3985$, R-squared: 0.29096, p-value: 0.134. For the bottom depth level; trend line equation: $-0.0812x + 4.2023$, R-squared: 0.34426, p-value: 0.09668.)

Figure 4: Relationship between DOC and overall P uptake rates. There is a negative, linear relationship between DOC and P Uptake rates. (Trend line equation: $-0.1027x + 4.7229$, R-squared: 0.61791, p-value: 0.012.)
Figure 5: Average phosphorus uptake rates at three different depth levels. No significant difference was found between the phosphorous uptake rates at the different depth levels. The top depth level had the lowest average uptake rate, while the middle had the highest.

Figure 6: Relationship between DOC and total lake phosphorus concentrations. No significant relationship was found between DOC and total phosphorus concentration. (R-squared: 0.009868, p-value: 0.7714.)
Figure 7: Relationship between total lake phosphorus concentrations and P uptake rates. There is no significant relationship between total phosphorus concentration and P uptake rates. (R-squared: 0.05093, p-value: 0.5307).

Figure 8: Relationship between DOC the light extinction constant $K_d$. There is a positive, linear relationship between DOC concentration and the light extinction constant value. (Trend line equation: $0.2186x - 0.4903$, R-squared: 0.80014, p-value: 0.001131).
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Literature Cited


