

Stream periphyton response to phosphorus loading events is constrained by antecedent conditions

by

Natalie Schneider

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## **Authors Declaration**

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

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## Abstract

Phosphorus (P) loadings to streams often occur in short duration events associated with runoff from human activities. Although it has been shown that stream periphyton can uptake and assimilate event-based P, the role of antecedent P concentrations in modulating P uptake from event-based loadings and resulting effects on periphyton structure and function is not known. To assess effects of antecedent P concentration on stream periphyton response to short-term P loading events, we completed two 26-day artificial stream experiments at the Thames River Experimental Stream Sciences (TRESS) Centre in London, Canada. Experiments consisted of exposing periphyton communities in nine artificial streams to a range of 48-hour P loading event concentrations (15 to 690  $\mu\text{g P/L}$ ) under low (10  $\mu\text{g P/L}$ ) or high (50  $\mu\text{g P/L}$ ) antecedent P concentrations. Periphyton was sampled one day before, one day after and 10 days after P loading events to quantify periphyton structure (ash free dry mass (AFDM), chlorophyll *a* (chl *a*), P content) and function (P uptake, benthic metabolism, cellulose decomposition, biomass growth, chl *a* accumulation). Under low antecedent P conditions one day after the P event, P content and P uptake had a positive linear relationship with event concentration and this was similarly seen in biomass and chl *a* ten days after the P event. One day after the P event in high antecedent streams, P content and P uptake showed a positive linear response with P event concentration, but this additional P in periphyton did not lead to increases in biomass and chl *a*. Whereas, a negative linear relationship with event concentration and P uptake was seen ten days after the P event. Measures of periphyton function (benthic metabolism and cellulose decomposition) were unaffected by P event size and regardless of the antecedent condition. These findings suggest that high antecedent P concentrations caused cellular saturation of

periphyton limiting the assimilation of P from event-based P loads. Therefore, streams with high antecedent P may deliver reduced water purification benefits with regards to attenuating P transport to downstream ecosystems at risk of eutrophication. Management actions to reduce antecedent P concentrations will be needed to rehabilitate ecosystem service provision in streams chronically enriched in P.

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## List of Abbreviations

AFDM	Ash free dry mass
AI	Autotrophic index
AICc	corrected Akaike information criterion
AICw	Akaike's information criterion weight
C <sub>B</sub>	Elemental concentration in periphyton
Chl <i>a</i>	Chlorophyll a
DO	Dissolved oxygen
DUP	Dissolved unreactive phosphorus
ER	Ecosystem respiration
GPP	Gross primary production
HCl	Hydrochloric acid
ICP-OES	Inductively coupled plasma optical emission spectroscopy
KH <sub>2</sub> PO <sub>4</sub>	Potassium dihydrogen phosphate
N	Nitrogen
NH <sub>4</sub> NO <sub>3</sub>	Ammonium nitrate
P	Phosphorus
PAR	Photosynthetic active radiation
SRP	Soluble reactive phosphorus

TRESS Thames river experimental stream sciences

TN Total nitrogen

TP Total phosphorus

## Chapter 1: Introduction

Increased loading of phosphorus (P) from human activities is globally recognized as a prominent threat to streams and rivers (Mainstone & Parr, 2002). When excess P is present, streams are at risk of eutrophication, which is described as increased productivity in response to increased nutrients (Dodds, 2007). Symptoms of eutrophication include excessive algal biomass, shifts in community composition, and impairment of ecosystem services such as provision of drinking water and recreational activities (Dodds, 2007).

Once P arrives into streams, there are many compartments in the stream where it can be cycled (Withers & Jarvie, 2008). However, one important compartment where P can be taken up and processed is periphyton (Ready et al., 1999). Periphyton are multi-trophic level communities consisting of diverse assemblages of heterotrophs and autotrophs (i.e., bacteria, algae, and fungi) that are attached to substrates (Bengtsson et al., 2018). Periphyton are a major component of P cycling in streams and are the dominant contributors to primary production in many streams (Bengtsson et al., 2018).

P loadings to streams can be highly variable due to surrounding land use, changes in environmental conditions, or seasonal changes that influence nutrient transport and runoff events. Streams can receive continuous loadings from ground water inputs or from activities present in the catchment (e.g., waste water treatment plants, septic systems) (Edwards & Withers, 2008; Mainstone & Parr, 2002; Smith et al., 1999). Continuous loading of P means that streams are consistently receiving P and often streams with this loading pattern experience elevated P concentrations which can lead to the growth of nuisance algae and can pose threats to stream ecosystems (Withers et al., 2009). However, streams also can receive large P loads in

short duration loading events in association with episodes of elevated surface and subsurface runoff that transport land-based P into streams (Edwards & Withers, 2008). The biological relevance of P loading events are less understood, in part because of the difficulty in studying a phenomena that is highly variable in concentration and timing.

Previously, the capacity for streams to manage P from short term events, was not well understood and it was believed that in short duration events, P would bypass periphyton and be transported into downstream ecosystems (Wang et al., 2020). However, many studies have demonstrated that periphyton in stream ecosystems play an influential role in P uptake by efficiently removing soluble reactive phosphorus (SRP) from the water column during P loading events (Besemer, 2015; Lundsgaard-Nielsen, 2023; Pearce et al., 2020, 2023; Stevenson et al., 2008; Weigelhofer et al., 2018). In fact, studies such as Pearce et al., (2020) and Lundsgaard-Nielsen (2023) found that periphyton could assimilate excess P from the water column into biomass both from episodic and continuous P loading patterns. Pearce et al., (2023) reported that periphyton P uptake ranged from 0.17 to 0.95  $\mu\text{g P m}^{-2} \text{s}^{-1}$  and increased with rising P availability from P events. This uptake was associated with increased periphyton biomass. However, it remains unclear whether increases in biomass are driven by P uptake from P events influence ecosystem processes (e.g., stream metabolism), and whether this effect depends on the concentration of the P event, or if it is shaped by the streams antecedent conditions.

Benthic metabolism, including gross primary production (GPP) and ecosystem respiration (ER) as well as the rates of organic matter breakdown (e.g. cellulose decomposition) are widely recognized as key processes that serve as indicators of stream health. In stream ecosystems, periphyton have been found to play a key role in primary production through

photosynthetic components influencing GPP and ER, as well as influencing cellulose decomposition under various conditions (Poisson & Yates, 2022; Woodward et al., 2012). Both metabolic activity and cellulose decomposition are influenced by increases in periphyton biomass and associated microbial activity, due to nutrient enrichment (Poisson & Yates, 2022; Webb et al., 2019). Woodward et al., (2012) demonstrated that decomposition rates had a quadratic relationship in response to a gradient of instream P concentrations, with high P loadings resulting in decreased decomposition rates. Further, Woodward et al., (2012) showed that rates of decomposition can shift to have a negative response to nutrient enrichment when P concentrations are high due to the detrimental effects of eutrophic streams (i.e., oxygen depletion). Although studies have addressed how chronic enrichment affects stream health, little is known about how various short term P events affect these functional processes in periphyton.

P uptake by periphyton in stream ecosystems has well-documented consequences, including increased biomass, shifts in community composition, alterations in functional processes, and changes in P transport dynamics. Studies have shown that uptake can be modulated by the environmental conditions a stream experiences (Lock & John, 1979; Pearce et al., 2023; Steinman et al., 1995). For example, altering light availability for stream periphyton have shown corresponding changes in periphyton productivity and nutrient demand, while temperature and flow can influence metabolic rates and nutrient retention (Larned, 2010; Stutter et al., 2010). However, there is limited knowledge on how antecedent P conditions can influence the capability of stream periphyton to uptake P during short duration events.

The antecedent P condition in the stream refers to the concentration of P occurring in the undisturbed state of the stream, and the amount of antecedent P in a stream is dependent upon the

activities in the catchment (Waiser et al., 2011). For example, streams can have high antecedent P concentrations when subjected to point sources, such as discharge from wastewater treatment plants, or P-rich groundwater that consistently load P over time. Without these persistent P loadings streams in catchments with large amounts of nutrient releasing activities, such as fertilizer application and livestock husbandry, often exhibit low antecedent P availability. Streams with both low antecedent P (i.e., lack of continuous P loading) and high antecedent P (i.e., exposed to continuous P loading) can receive significant land-based P loading from human activities and transported to streams during runoff events (Banner et al., 2009; Price & Carrick, 2014). These antecedent conditions may influence periphyton responses to P loading events as under elevated antecedent P concentrations periphyton may already have access to sufficient P to attain maximum growth rates limiting the impact of additional P associated with events (Dodds, 2003; Dodds, 2006). However, the impact of high antecedent P on the uptake, assimilation and function of periphyton has not been tested.

Assessment of the impacts of P events on periphyton is challenging due to the wide array of changing conditions that periphyton in natural streams can encounter over time and space (e.g., light, temperature, substrate, and invertebrate grazing), as well as the difficulty in studying event loads that occur unpredictably. As a result, researchers often use artificial streams to examine instream processes such as P events in a controlled and replicable environment. Artificial streams refer to an experimental system where stream processes can be studied under certain conditions and are especially useful when studying P events. Many stream periphyton studies have been conducted in artificial streams as treatment levels can be easily manipulated (Lamberti & Steinman, 1993; Pearce et al., 2023). Artificial streams offer the advantage of controlled

and replicable conditions, making them valuable tools for experimental research, though they may not capture all the complexities of natural systems (Coelho et al., 2013; Lamberti & Steinman, 1993). Artificial streams are especially beneficial when looking to test hypotheses and to gain a better understanding of isolated processes, as real streams are complex systems which include a diverse set of organisms from different trophic levels that may influence stream health (Coelho et al., 2013). In some cases, the absence of certain organisms or environmental conditions in artificial streams may limit their ability to accurately reflect whole-stream processes. Although artificial streams are unable to reflect all aspects of natural streams they do provide insights into response patterns, that can be validated in target real streams.

In this study, artificial streams were used to control nutrient loading and each stream could received a controlled level of loading while all being exposed to the same conditions. The use of natural streams for a study with multiple treatment levels is extremely difficult as finding natural streams with the desired characteristics and comparable environmental conditions is very uncommon. Although variation is possible in these environments, all artificial streams are exposed to the same environmental conditions, whereas field sites may be exposed to different loading events or environmental characteristics (Filazzola & Cahill, 2021). Further, replicability of conditions in various treatments is possible with artificial streams where conditions and treatments are upon the control of the researcher.

## **1.1 Objective and goals**

The goal of this study was to determine how various P loading events impacted stream periphyton structure and function and to assess if the response is modulated by antecedent P conditions. This goal was achieved by conducting two 26-day experiments in artificial streams

with antecedent P conditions of either 10  $\mu\text{g P/L}$  or 50  $\mu\text{g P/L}$  and received a gradient of nine P loading events. The goal is addressed through the following set of objectives:

1. Assess the effect of the magnitude of P loading events on periphyton structure (periphyton biomass, chl *a*, P content) and function (P uptake, chl *a* accumulation, biomass growth, benthic metabolism, cellulose decomposition).
2. Determine if antecedent P concentration influences how periphyton structure and function respond to P loading events.

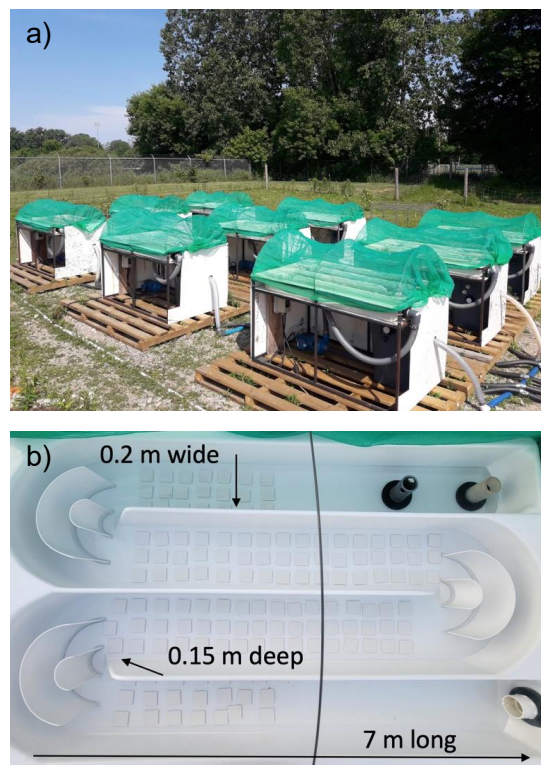
## Chapter 2: Methods

### 2.1 Experimental design and setup

Artificial stream experiments were conducted for 26 days in late July and early August in 2018 and 2020. Experiments differed in the antecedent SRP concentration with the 2018 experiment antecedent concentration at 10  $\mu\text{g P /L}$  (hereafter low antecedent) and the 2020 experiment at 50  $\mu\text{g P /L}$  (hereafter high antecedent). In both experiments streams received a 48-hr event of SRP from morning of day 13-15. Event concentrations added 15 to 690  $\mu\text{g P/L}$  (15, 40, 90, 140, 190, 240, 290, 390, 690  $\mu\text{g P/L}$ ) to the antecedent concentrations. After the 48 hr P event all streams returned to the respective antecedent P concentrations for the remainder of the experiment. Antecedent and event concentrations reflected antecedent and event-based SRP concentrations measured in agricultural stream in southern Ontario, Canada (DeBues et al., 2019).

Experiments were conducted at the Thames River Experimental Stream Science (TRESS) Centre in London, Canada. TRESS is an outdoor facility that consists of 9 artificial streams (Figure 1). Streams are 0.15 m deep, 0.2 m wide, and 7 m long. Channels have a sinuous form resulting in 4 reaches with equal length. The facility uses water from the Lake Huron Water Supply. This water supply has low nutrient concentrations (TN = 406  $\mu\text{g/L}$  and TP < 1  $\mu\text{g/L}$ ) and chemistry (e.g., pH = 7.93 to 8.08; alkalinity = 73 to 92  $\text{mg L}^{-1} \text{CaCO}_3$ ) similar to regional streams. Water and nutrients are delivered in the desired amounts to each stream through a series of tanks and metered pumps. Dosing pumps were used to attain and maintain the desired P and nitrogen (N) concentrations throughout the experiments. Antecedent and event SRP was delivered in the form of  $\text{KH}_2\text{PO}_4$ . N was delivered as  $\text{NH}_4\text{NO}_3$  at a constant concentration of

1500 ug N/L throughout the experiment. Water was delivered to streams at constant rate ( $150 \text{ cm}^3/\text{s}$ ) via diaphragm pumps linked to the common water supply. Flow rates of diaphragm pumps and dosing pumps were calibrated each day of the experiment to ensure water and nutrient delivery rates were maintained. Stream water was partially recirculated in each stream using an impeller pump, where the water in each stream had a residence time of approximately 2.5 hours.



**Figure 2.1** Nine artificial stream tables at TRESS (a) and an overhead view of a single artificial stream with dimensions (b)

In both experiments, light and stream temperature varied through time with weather conditions. Light to streams was limited using a 60% shade cloth placed overhead of each stream. Photosynthetic radiation was measured in five-minute intervals using PAR loggers

(Odyssey Submersible Photosynthetic Active Radiation Logger) placed under the shade cloth of the stream in the center of the facility; the facility experiences no shading from trees or buildings. Total PAR received by the streams averaged  $63.3 \pm 17.6 \text{ mol m}^{-2} \text{ day}^{-1}$ . Water temperature was measured at one hour intervals throughout the experiment using an Onset HOBO pendant logger placed in the second bend of each stream. Mean daily average temperature was  $21.5^{\circ}\text{C} \pm 1$  and  $22.3^{\circ}\text{C} \pm 0.7$  in the low and high antecedent experiments, respectively. Water velocity was consistent in the low and high antecedent experiment at approximately 0.1 m/s in the second and third reaches.

Low and high antecedent streams were inoculated with periphyton from two sources. First, mesh bags (2 cm x 2 cm) containing quarried river rock were placed in Medway Creek (Table 2.1) for 4.5 weeks in the low antecedent and 2.5 weeks in the high antecedent weeks prior to the experiment to allow for colonization by periphytons. Colonized river rock was brought to TRESS and evenly distributed amongst the nine streams. Second, periphyton were collected from five regional streams ranging in TP concentrations from low (i.e., 0.025 TP (mg/L)) to high (i.e., 0.191 TP (mg/L); Table 2.1). In each of the five streams periphyton was collected from 10 randomly selected cobbles into 1 L Nalgene bottles and transported to TRESS. At TRESS, large debris and invertebrates were removed from the inoculate prior to the samples being composited and homogenized into a slurry. The slurry was spilt into nine equal parts and each part poured into a randomly assigned stream. 135 unglazed square ceramic tiles (4.7 cm x 4.7 cm) were placed on top of cobbles in the second and third reaches of each stream to act as a consistent substrate for periphyton growth.

**Table 2.1** Stream periphyton inoculum collection location, Strahler order, total phosphorus and total nitrogen

<b>Stream Name</b>	<b>Location</b>	<b>Strahler Order</b>	<b>TP (mg/L)</b>	<b>TN (mg/L)</b>
<b>Waubuno Creek</b>	42.99, -81.12	4	0.025	4.39
<b>Reynolds Creek</b>	42.97, -80.95	4	0.191	3.10
<b>Middle Thames</b>	43.03, -80.99	6	0.046	4.17
<b>South Thames A</b>	43.02, -80.93	5	0.122	4.99
<b>South Thames B</b>	43.13, -80.78	5	0.158	5.38
<b>Medway Creek</b>	43.01, -81.28	3	0.020	3.30

## **2.2 Sample collection and analysis**

To assess periphyton, P content, chlorophyll *a* (chl *a*), and biomass samples were collected one day before, one day after and 10 days after the P event. To assess stream health, samples for benthic metabolism were collected one day before and 10 days after the P event and samples for cellulose decomposition were collected 10 days after the P event. The high antecedent experiment experienced pump failure, resulting in the stream receiving the 190 µg P/L to be removed from this experiment.

Periphyton samples for chl *a*, biomass and TP content were collected in triplicate and were collected by scraping a fixed area from 3 randomly selected tiles into specimen cups. All samples were frozen and stored at -20°C until analysis.

Chl *a* samples were thawed on a Whatman GF/C filters and put into 50 mL centrifuge tubes containing 10 mL of 90% ethanol. Centrifuge tubes were partly submerged in a 80°C hot water bath for 7 minutes. Fluorescence values for each sample were determined using a Turner Designs Trilogy Fluorometer (Model: 7200-000). Samples producing fluorometer readings

greater than 200 ug/L were diluted using 100 dilution factor and rerun through the fluorometer to ensure values less than 200 ug/L. If values remained above 200 ug/L a second dilution factor of 1000 was performed and the sample was rerun in the fluorometer. Once fluorometer readings were collected, chlorophyll a was then determined using Equation 1:

$$\text{Chl } a \text{ (}\mu\text{g/cm}^2\text{)} = \frac{\left(\text{Fluorometer Reading } \left(\frac{\mu\text{g}}{\text{L}}\right)\right) \left(\frac{\text{Volume of extract ml}}{\text{Volume of sample filtered}}\right) \left(\frac{\text{Volume of sample}}{1000}\right) * \text{Dilution factor}}{\text{Area Sampled (cm}^2\text{)}}$$

Chl *a* triplicates for each stream at each time point were then averaged. Chl *a* accumulation rates for intervals day 1-12, 12-16, and 16-26 were calculated by determining the change in chl *a* over each time period, which was done by dividing this value by the number of days in that time interval.

Periphyton biomass and TP content were determined following Aspila et al., (1976). In brief, samples were freeze dried for 9 days, then ashed for 3 hours in a muffle furnace at a temperature of 550°C. Biomass was determined by weighing these samples before and after ashing in the muffle furnace. To determine the biomass growth, the differences in biomass from time intervals day 1-12, 12-16, and 16-26 were calculated and divided by the amount of days in each time period. To determine TP concentration, once samples cooled from the muffle furnace, each sample was mixed with 1 M HCl and placed onto a shaker table in an incubator to complete an extraction for 16 hours. Samples were then filtered into 13 mL tubes using a 0.45 μm Supor IC syringe filter. TP content was determined using inductively coupled plasma optical emission spectroscopy (ICP-OES). TP contents are reported on a per unit area basis by dividing the measured P mass by the area sampled. P uptake was calculated by determining the change in TP

content between sampling time intervals of day 1-12, 12-16, and 16-26 and these values were divided by the number of days in each time period.

The autotrophic index (AI) was determined to assess the proportion of autotrophic to heterotrophic biomass, where changes in AI are a result in shifts in this ratio. The AI is calculated by dividing the AFDM by the chl *a*. Additionally, to determine P relative to biomass, P content per biomass ratio was determined by dividing P content and uptake by biomass.

Organic matter processing was estimated using the cotton strip assay (Tiegs et al., 2013). Cotton strips were assembled using Fredrix-brand unprimed 12-oz. heavy-weight cotton fabric, and measured to be 27 threads wide, 8 cm long with 3 mm frayed edges. Five strips were anchored to the bottom of each stream using metal washers and zip ties. At the end of the experiment, strips were removed from the streams and washers and zip ties were disconnected from each strip. Strips were then submerged in ethanol for 30 seconds to cease microbial activity and gently brushed to remove any excess algae and debris. Strips were wrapped in labelled foil packets and placed in a -20°C freezer until analysis. Prior to analysis, strips were dried in a 40 °C oven for 24 hours, then cooled in a desiccator.

Tensile loss was analyzed using a Mark-10 ESM303 tensiometer and a test stand, following (Tiegs et al., 2013). Average tensile loss per day was calculated using equation 5:

$$\% \text{ Tensile Loss/day} = \frac{(\frac{\text{Tensile Strength (reference)} - \text{Tensile Strength (treatment)}}{\text{Tensile Strength (reference)}}) \times 100}{\text{Incubation Time (days)}}$$

Where tensile strength (reference) refers to the average maximum tensile strength of 50 strips that were processed identically to field samples, but were not incubated in the field. Tensile

strength (treatment) refers to the average of tensile strength of 5 cotton strips from each treatment.

Benthic metabolism was estimated using the light and dark chamber method (Grace & Imberger, 2006). For each stream, six randomly selected tiles were placed in each of a light and a dark chamber, which each had a volume of 2L. Chambers were filled with stream water and placed into the first reach of each stream. Lids were then affixed to the chamber with a dissolved oxygen logger (D-Opto Logger, Zebratech) inserted through the lid. Loggers measured temperature, oxygen concentration and percent saturation every five minutes. Chambers were left in the stream for 195 minutes. Changes in oxygen concentrations in the dark and light chambers were used to calculate ecosystem respiration (ER) and gross primary production (GPP) following equations 7 and 8, respectively (Grace & Imberger, 2006). To determine rates of oxygen change, a linear regression was applied to the oxygen concentration data over time for each chamber. The slope of the regression line was used to quantify oxygen consumption or production, for the ER and GPP calculations.

Equation 7:

$$ER = (\text{dark slope}) \left( \frac{\text{volume (L)}}{\text{time interval}} \right) \left( \frac{\text{chamber volume (L)}}{\text{surface area (M}^2\text{)}} \right) \frac{1}{1000}$$

Equation 8:

$$GPP = (\text{light slope} - \text{dark slope}) \left( \frac{\text{volume(L)}}{\text{time interval}} \right) \left( \frac{\text{chamber volume (L)}}{\text{surface area (M}^2\text{)}} \right) \frac{1}{1000}$$

## 2.3 Data analysis

Relationships between the SRP event concentrations and the measured endpoints (i.e., chl *a*, AFDM, P content, P uptake, chl *a* accumulation, periphyton growth, benthic metabolism, and cellulose decomposition) were individually assessed for the low P and high P antecedent experiments using null, linear, and nonlinear (i.e., logistic and asymptotic) least squares regression models. Competing models were compared using Akaike Information Criterion corrected for small sample sizes (AIC<sub>c</sub>) (Burnham et al., 2011; Burnham & Anderson, 2004). Models more than 2 ΔAIC<sub>c</sub> units from the best model (i.e., model with lowest AIC<sub>c</sub> value) were considered to have no support. Models within 2 ΔAIC<sub>c</sub> units of the best model were considered plausible (Burnham et al., 2011). Regression and AIC analyses were run using R (version 4.4.1) and the packages AICcmodavg, MuMIn, lme4, nlme, and nls2 were used for analysis.

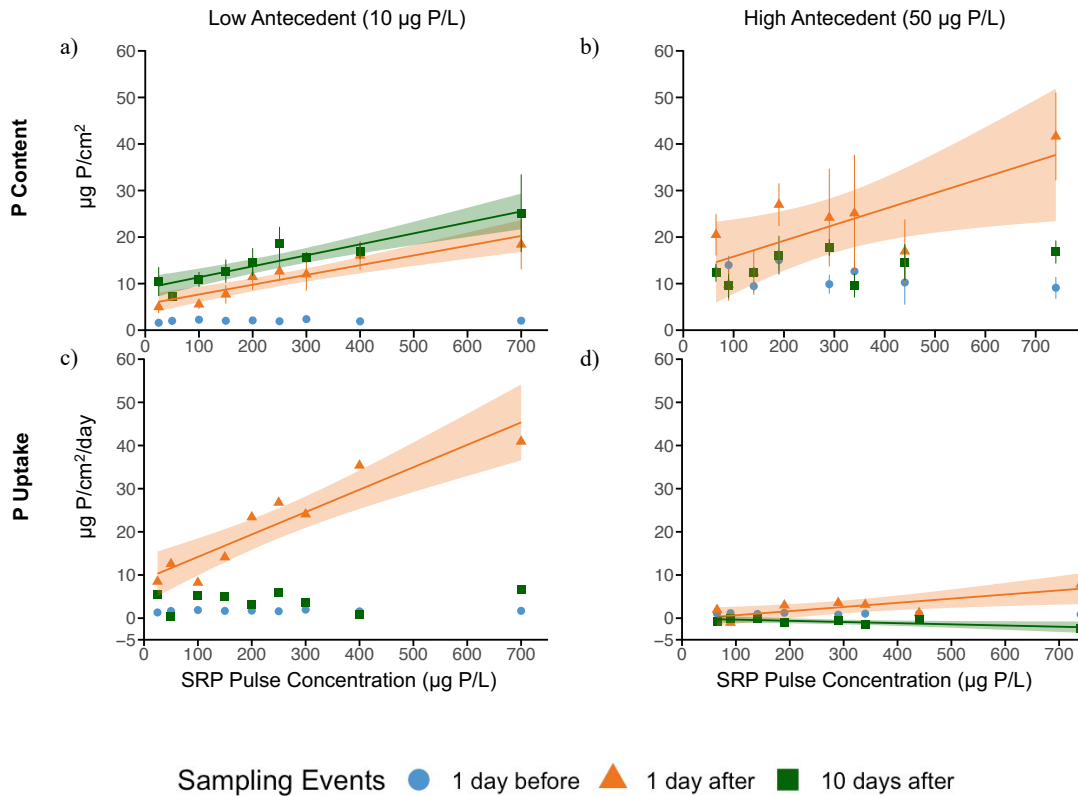
## Chapter 3: Results

### 3.1 Periphyton phosphorus content and uptake

Periphyton P content was about 6 times higher in streams with high antecedent streams with mean value of  $12.3 \pm 0.6 \mu\text{g P/cm}^2$  versus  $2 \pm 0.1 \mu\text{g P/cm}^2$  in low antecedent streams (Figure 3.1a). P content in the low and high antecedent streams was not related to P event concentration before the event. Both low and high antecedent streams displayed positive linear relationships between P content and P event concentration one day after the event, with the asymptotic model also plausible for the low antecedent experiment (Figure 3.1a; Figure 3.1b). One day after the event the magnitude of P content in the high antecedent streams was about 2 times larger (Range: 9.8 to  $41.6 \mu\text{g P/cm}^2$ ) than low antecedent streams (Range: 5 to  $18.4 \mu\text{g P/cm}^2$ ). At the end of the experiment (10 days post P event) only low antecedent streams showed an association with P content and P event concentration (Range: 7.3 to  $25.1 \mu\text{g P/cm}^2$ ), where high antecedent streams showed no associations (mean:  $13.6 \pm 1.1 \mu\text{g P/cm}^2$ ).

Similar to P content, uptake in both low and high antecedent streams before the P event was not associated with P event concentration with mean values of  $1.7 \mu\text{g P/cm}^2/\text{day} \pm 0.1$  and  $1 \mu\text{g P/cm}^2/\text{day} \pm 0.1$ , respectively (Figure 3.1c; Figure 3.1d). However, one day after the P event both low and high antecedent streams showed positive linear relationships between uptake and P event concentration, with the logistic model also being considered plausible for the low antecedent streams. One day after the P event low antecedent streams showed that uptake in streams receiving the highest P event was about 5 times higher (Range: 8.5 to  $41 \mu\text{g P/cm}^2/\text{day}$ ) than in high antecedent streams (Range: -1.1 to  $7.8 \mu\text{g P/cm}^2/\text{day}$ ). At the end of the experiment there were no associations between uptake and P event concentration in the low antecedent

streams (mean:  $4.1 \mu\text{g P/cm}^2/\text{day} \pm 0.7$ ), however, uptake was negatively and linearly related with P event concentration in high antecedent streams (range:  $-2.5$  to  $-0.2 \mu\text{g P/cm}^2/\text{day}$ ), with the null model also being plausible.



**Figure 3.1** Associations between event P concentration and periphyton total phosphorus (TP) content and phosphorus (P) uptake and in artificial streams with low (a,c) and high (b,d) antecedent P concentrations one day before, one day after and 10 days after the P event. Trend lines represent the most supported regression models and shaded areas indicate the 95% confidence interval. Error bars shown on figures represent  $\pm 1$  standard deviation.

### 3.2 Periphyton biomass & chlorophyll *a*

Both low and high antecedent streams showed no associations with periphyton biomass and chl *a* concentration and P event concentration one day before or one day after the P event.

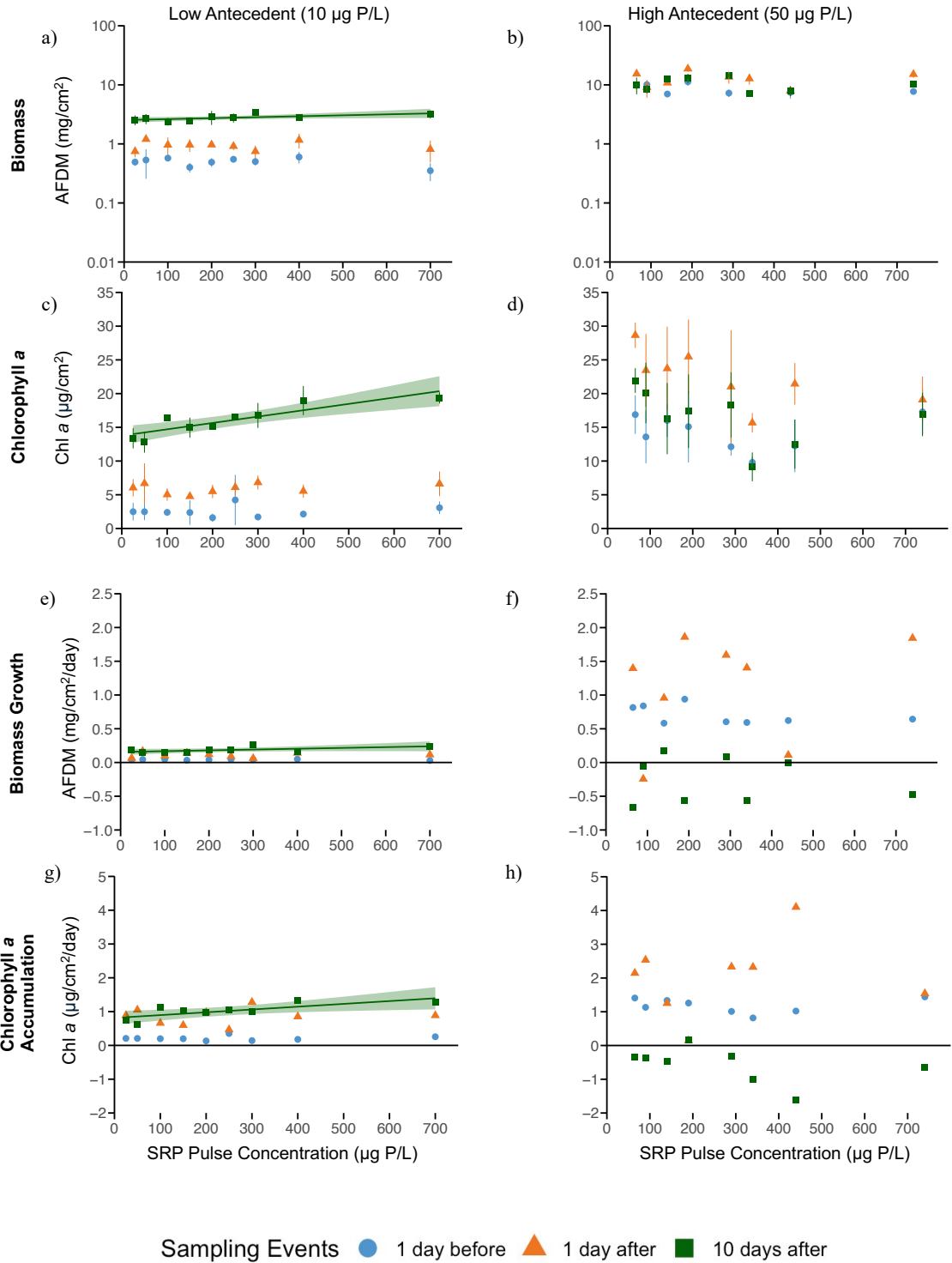
Biomass of high antecedent streams (about  $8.5 \pm 0.6 \text{ mg/cm}^2$ ) was more than an order of magnitude larger than biomass in low antecedent streams ( $0.5 \pm 0.02 \text{ mg/cm}^2$ ) one day before the

P event (Figure 3.2a; Figure 3.2b). One day after the event biomass in high antecedent streams ( $12.9 \pm 1.3 \text{ mg/cm}^2$ ) was similarly about an order of magnitude larger than in low antecedent streams ( $0.9 \pm 0.05 \text{ mg/cm}^2$ ). 10 days after the P event low antecedent streams showed positive linear associations between biomass and P event concentration (range: 2.4 to 3.4  $\text{mg/cm}^2$ ) and no associations in the high antecedent streams averaging at  $10.3 \pm 1 \text{ mg/cm}^2$ .

Chl *a* in high antecedent streams (mean:  $14.1 \pm 0.9 \text{ } \mu\text{g/cm}^2$ ) was more than 5 times higher than in low antecedent streams (mean:  $2.5 \pm 0.3 \text{ } \mu\text{g/cm}^2$ ) (Figure 3.2c; Figure 3.2d). One day after the P event there were also no associations between chl *a* and P event concentration, but chl *a* in high antecedent streams ( $22.3 \pm 1.4 \text{ } \mu\text{g/cm}^2$ ) was about 3.8 times larger than low antecedent streams ( $5.9 \pm 0.2 \text{ } \mu\text{g/cm}^2$ ). At the end of the experiment, chl *a* and P event concentration were positively and linearly related in low antecedent streams (range: 12.8 to 19.4  $\mu\text{g/cm}^2$ ), however there was no association in high antecedent streams (mean:  $16.6 \pm 1.4 \text{ } \mu\text{g/cm}^2$ ).

Results from associations between P event concentration and biomass growth as well as chl *a* accumulation are seen similarly to the relationships with P content and chl *a*. One day before the P event, biomass growth was not correlated with P event concentration in low or high antecedent streams, however biomass growth in high antecedent streams ( $0.7 \pm 0.05 \text{ mg/cm}^2/\text{day}$ ) was 17 times larger than low antecedent streams ( $0.04 \pm 0.002 \text{ mg/cm}^2/\text{day}$ ) (Figure 3.2e; Figure 3.2f). One day after the event there was also no associations between biomass growth and P event concentration, with the high antecedent streams being about an order of magnitude larger ( $1.1 \pm 0.3 \text{ mg/cm}^2/\text{day}$ ) than low antecedent streams ( $0.1 \pm 0.01 \text{ mg/cm}^2/\text{day}$ ). By the end of the experiment biomass growth was positively and linearly related with P event concentration in low antecedent streams (range: 0.1 to 0.3  $\text{mg/cm}^2/\text{day}$ ) and high

antecedent streams showed no associations and the mean value as  $0.3 \pm 0.1 \text{ mg/cm}^2/\text{day}$ . The same trends were found for chl *a* accumulation where one day before and one day after the P event there were no associations between chl *a* accumulation and P event concentration (Figure 3.2g; Figure 3.2h). Chl *a* accumulation was about 3.5 times larger (high:  $0.7 \pm 0.05 \text{ }\mu\text{g/cm}^2/\text{day}$ ; low:  $0.2 \pm 0.02 \text{ }\mu\text{g/cm}^2/\text{day}$ ) and about 1.2 times larger (high:  $1.1 \pm 0.3 \text{ }\mu\text{g/cm}^2/\text{day}$ ; low:  $0.9 \pm 0.1 \text{ }\mu\text{g/cm}^2/\text{day}$ ) in high antecedent streams compared to low antecedent streams for the day before and the day after the event respectively. By the end of the experiment there was a positive, linear relationship between chl *a* accumulation and P event concentration in low antecedent streams (range: 0.6 to  $1.3 \text{ }\mu\text{g/cm}^2/\text{day}$ ) whereas high antecedent streams showed no associations ( $-0.3 \pm 0.1 \text{ }\mu\text{g/cm}^2/\text{day}$ ).

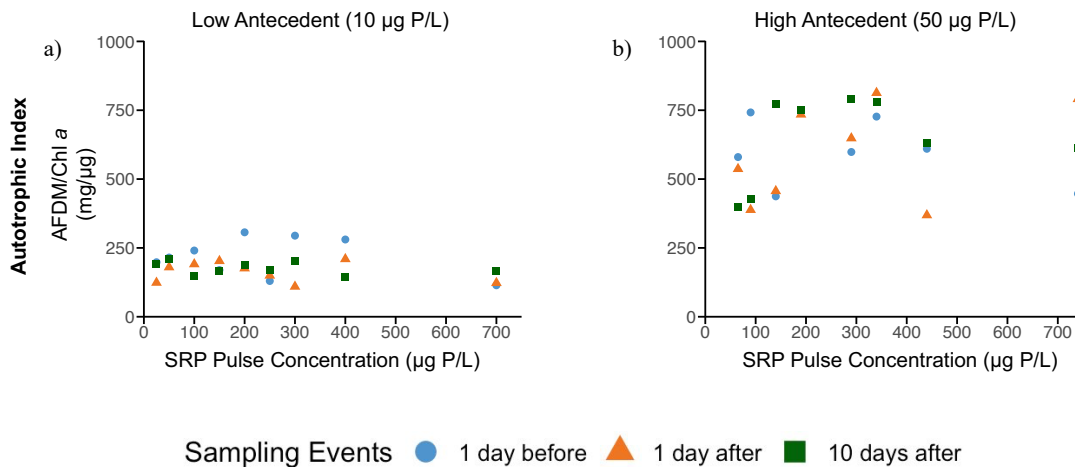


**Figure 3.2** Associations between event P concentration and (a,b) total biomass (AFDM) and (c,d) chl *a* content, (e,f) biomass growth, (g,h) chl *a* accumulation in artificial streams with low and high antecedent P concentrations one day before, one day after and 10 days after the P event.

Trend lines represent the most supported regression models and shaded areas indicate the 95% confidence interval. Error bars shown on figures represent  $\pm 1$  standard deviation.

### 3.3 Autotrophic index

There were no associations between AI and P event concentration in low or high antecedent streams at any time point in the experiment (Figure 3.3). One day before the P event AI averaged about 3 times larger in the high antecedent streams (high:  $611 \text{ mg}/\mu\text{g} \pm 44$ ; low:  $217 \text{ mg}/\mu\text{g} \pm 23$ ). One day following the P event, AI in the high antecedent streams averaged  $592 \text{ mg}/\mu\text{g} \pm 63$  compared to an average of  $163 \text{ mg}/\mu\text{g} \pm 12.4$  in the low antecedent streams. By the end of the experiment high antecedent AI was about 3.5 times greater than the low antecedent (high:  $645 \text{ mg}/\mu\text{g} \pm 56$ ; low:  $176 \text{ mg}/\mu\text{g} \pm 7.8$ ).



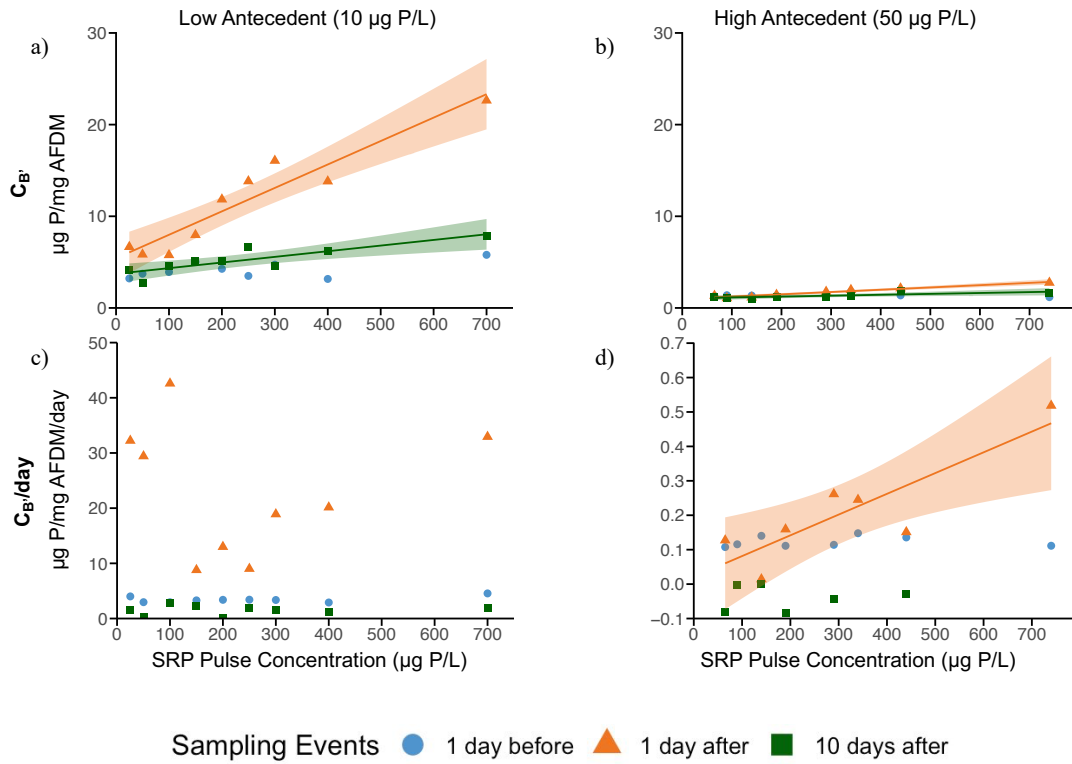
**Figure 3.3** Associations between event P concentration and autotrophic index in artificial streams with (a) low and (b) high antecedent P concentrations the day before, one day after and 10 days after a P event.

### 3.4 Biomass corrected P content and uptake

Associations between  $C_B$  (Stream Solute Workshop, 1990) and event P concentration showed no relationship one day before the P event in low and high antecedent streams when average  $C_B$  was about 3 times larger in low antecedent streams ( $4.1 \text{ } \mu\text{g}/\text{mg} \pm 0.3 \text{ mg}/\text{cm}^2$ )

compared to high antecedent streams ( $1.4 \mu\text{g}/\text{mg} \pm 0.06 \text{ mg P}/\text{g}$ ). Linear relationships between  $C_B$  and P event concentration were observed in low and high antecedent streams one day after the P event, although low antecedent streams (range: 5.772 to 22.636  $\mu\text{g}/\text{mg}$ ) had about 5 to 9 more  $C_B$  in comparison to high antecedent streams (range: 1.071 to 2.757  $\mu\text{g}/\text{mg}$ ). At the end of the experiment the difference in  $C_B$  had declined to between 2 and 5 times more in the low antecedent streams, but both low and high antecedent streams still displayed positive linear relationships.

Associations between periphyton  $C_{B'}$  (P elemental concentration in periphyton) and P event concentration showed no relationship one day before the P event, where low antecedent streams (mean:  $3.4 \mu\text{g}/\text{mg}/\text{day} \pm 0.2$ ) were about 1.5 orders of magnitude larger than high antecedent streams (mean  $0.1 \mu\text{g}/\text{mg}/\text{day} \pm 0.01$ ). One day after the P event there was no associations with  $C_{B'}/\text{day}$  and P event concentration in low antecedent streams (mean:  $23 \mu\text{g}/\text{mg}/\text{day} \pm 4$ ), however there was a linear relationship seen in high antecedent streams between  $C_{B'}/\text{day}$  and P event concentration (range:  $-0.1$  to  $0.5 \mu\text{g}/\text{mg}/\text{day}$ ) (Figure 3.4a; Figure 3.4b). By the end of the experiment similarly there was no associations seen between  $C_{B'}/\text{day}$  and P event concentration in low antecedent streams (mean:  $1.5 \mu\text{g}/\text{mg}/\text{day} \pm 0.3$ ) and was about an order of magnitude larger than high antecedent streams which also showed no associations (mean:  $-0.09 \mu\text{g}/\text{mg}/\text{day} \pm 0.03$ ) (Figure 3.4c; Figure 3.4d).



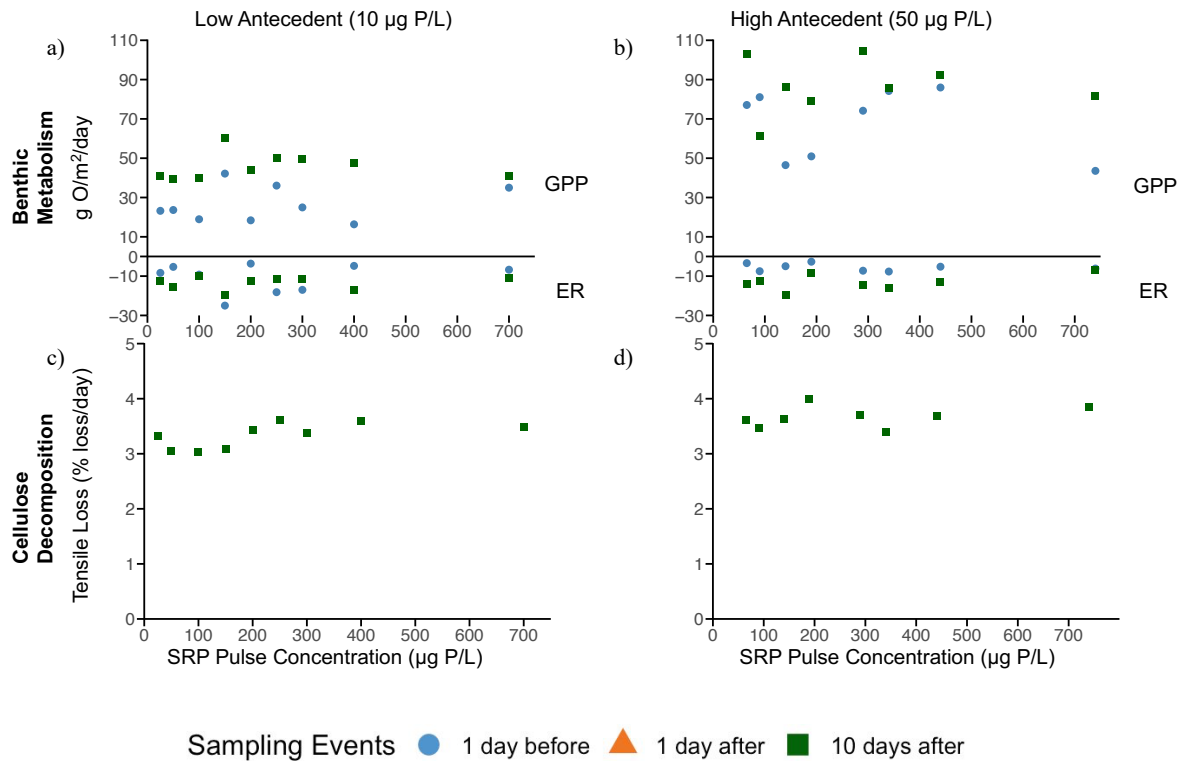
**Figure 3.4** Associations between P event concentration and C<sub>B</sub> and C<sub>B</sub>/day in artificial streams with low (a,c) and high antecedent (b,d) P concentrations the one day before, one day after and 10 days after a P event. Trend lines represent the most supported regression models and shaded areas indicate the 95% confidence interval. Error bars shown on figures represent  $\pm 1$  standard deviation.

### 3.5 Benthic metabolism and cellulose decomposition

Low and high antecedent streams showed no associations between P event concentration and either benthic metabolism or cellulose decomposition. One day before the event, GPP averaged at  $26.5 \pm 3$  g O/m<sup>2</sup>/day in low antecedent streams and was about 2.5 times larger in high antecedent streams (mean:  $68 \pm 6.3$  g O/m<sup>2</sup>/day). At the end of the experiment, GPP was  $46 \pm 2.3$  g O/m<sup>2</sup>/day in low antecedent streams and was almost double in high antecedent streams averaging at  $86.8 \pm 4.9$  g O/m<sup>2</sup>/day (Figure 3.5a; Figure 3.5b). ER in low antecedent streams was about double ( $-10.9 \pm 2.5$  g O/m<sup>2</sup>/day) of what was seen in high antecedent streams ( $-5.6 \pm 0.7$  g O/m<sup>2</sup>/day) one day before the P event (Figure 3.5a; Figure 3.5b). At the end of the experiment

ER was comparable between low and high antecedent streams averaging at  $-13.4 \pm 1 \text{ g O/m}^2/\text{day}$  and  $-13.1 \pm 1.4 \text{ g O/m}^2/\text{day}$ , respectively.

No associations were seen between cellulose decomposition and P event concentration in low or high antecedent streams. Mean values were very comparable between experiments (low:  $3.3 \pm 0.07 \text{ %/day}$ ; high:  $3.7 \pm 0.07 \text{ %/day}$  (Figure 3.5c; Figure 3.5d).



**Figure 3.5** Associations between event P concentration and benthic metabolism (GPP & ER) and cellulose decomposition in artificial streams with low (a,c) and high (b,d) antecedent P concentrations the day before a P event, and 10 days after a P event.

## **Chapter 4. Discussion and conclusions**

Pearce et al. (2023) previously established that P uptake and assimilation increase with event concentration in streams that had low antecedent P availability. However, Pearce et al., (2023) did not assess if event driven changes in periphyton P content and biomass instigated changes in periphytic function at the community or ecosystem level. Moreover, Pearce et al. (2023) did not explore how periphyton might respond to P events in environments that are already phosphorus enriched. In addressing these knowledge gaps it was determined by our study that the increased biomass resulting from increasing amounts of event P did not translate into altered periphyton function and that event P does not enhance periphyton growth when antecedent P concentrations are large.

### **4.1 P content and uptake**

Periphyton in the high antecedent streams took up P during the event despite evidence of significant cellular P content prior to the event. Such an uptake pattern is consistent with luxury uptake, when excess P is taken up beyond what is needed for immediate growth (Ferragut et al., 2022; Powell et al., 2011; Solovchenko et al., 2019). Pearce et al. (2023) also suggested that luxury uptake was occurring in the low antecedent experiment, however, based on our findings in the high antecedent conditions it is noteworthy that luxury uptake rates were on average about 5 times greater in the low antecedent than the high. This result is consistent with the findings of (Portielje & Lijklema, 1994) who observed that a large P addition initiated lower uptake rates by periphyton from a P rich ditch compared to a reference site, suggesting luxury uptake of event P may be reduced under antecedent P availability. However, as studies in wastewater stabilization ponds have been able to induce luxury uptake under levels of P enrichment seldom observed in

real streams (reviewed by (Brown & Shilton, 2014)), further evaluations of luxury uptake rates in hyper P rich streams are needed.

In an enriched environment, P uptake is expected to plateau as the internal concentration approaches the external, requiring more energy for uptake and thus slowing the rate (Dodds, 2003). The linear relationship between P event concentration and P uptake in high antecedent streams suggests that periphyton in these conditions did not reach a threshold for saturation. This result was unexpected as Price & Carrick (2016) have stated that periphyton in P enriched streams are prone to saturation. However, similar to our study, results from McCormick et al., (2001) indicated that periphyton in an enriched environment did not exhibit a clear saturation point as they found almost 100% SRP removal by periphyton across a range of SRP events (11-338  $\mu\text{g P/L}$ ). It is possible saturation was not reached in our study streams because periphyton can reduce intracellular SRP content by converting to polyphosphates (Pearce et al., 2023), enabling periphyton to maintain uptake rates at a high level throughout the event. To further understand when periphyton may become saturated by additional P events, more studies should assess how periphyton respond to a larger range of P event concentrations.

Results from our high antecedent streams showed that despite proportional increases in intracellular P content associated with the P event the additional P was not assimilated into biomass. The lack of enhanced periphyton growth despite increased cellular P content suggests that periphyton in the streams with high antecedent P already had sufficient P to attain maximum growth rates. This finding is consistent with previous studies showing that periphyton growth often saturates at SRP concentrations below the high antecedent concentrations used in our experiment (i.e., 50  $\mu\text{g P/L}$ ; (Bothwell, 1989; McCall et al., 2017). For example, Rier &

Stevenson (2006) found that growth rates saturated at 16  $\mu\text{g P/L}$ , which aligns with our results as we only found biomass growth associated with P events in low antecedent streams. Additionally, Schmidt et al., (2019) found that growth rate was found to increase up until about 10  $\mu\text{g P/L}$ , indicating that growth following a P event in high antecedent streams was unlikely. The lack of growth supports the hypothesis that the observed uptake of P during the event was indeed beyond the growth requirements of the periphyton and therefore qualifies as luxury uptake.

## **4.2 P release**

By the end of the experiment (10 days post P event), P uptake by periphyton high antecedent streams declined and showed a negative linear correlation with event P concentration, despite relatively stable periphyton biomass. The stable biomass indicates that P loss in the last ten days of the experiment was not due to periphyton senescence and associated sloughing. Instead, the decline in P suggests that dissolved P was being leaked from the cell. Cellular leakage of P has been observed in past studies (Borchardt et al., 1994; Olsen, 1989). It is likely that cells leak additional P from P events when fully saturated, and there is no further use for stored P (i.e., assimilation to biomass; Olsen, 1989; Pearce et al., 2023). Indeed, a study of P mass balance by Lundsgaard-Neilsen (2023) indicated that a significant fraction of the SRP load from a P event was not accounted for by periphyton uptake or SRP export, suggesting significant processing and subsequent leakage of SRP by periphyton. Our results build on the Lundsgaard-Neilsen (2023) result by showing that P release by periphyton scales with event size. Aside from saturation there may be other factors which influence P release as Zhao et al., (2019) showed P release by periphyton could be influenced by low light availability which was likely the condition in the high antecedent streams by the end of the experiment due to self-shading.

Further our results build on previous literature showing that P release is likely when enriched streams receive additional P from loading events, however more studies are needed to determine the fate of P that is released.

Although our results provide strong evidence that unassimilated P is released, the P species being released are unknown. It is possible that the periphyton released some of the P as the orthophosphate. However, as Lundsgaard-Neilsen (2023) reported that P export during and following an event comprised significantly less orthophosphate than the initial load it seems likely that orthophosphate was a minor component of the released P in our study. Alternatively, P may have been leaked as dissolved unreactive P as previous studies assessing luxury P uptake show that additional P is stored as polyphosphates in periphyton (Brown & Shilton, 2014; Powell et al., 2011; Solovchenko et al., 2019). Indeed, Pearce et al., (2023) found that periphyton rapidly converts orthophosphate into polyphosphates following a short duration P event (Pearce et al., 2023). Pearce et al., (2023) also found that the decline in polyphosphates in periphyton cells was greater than what could be explained by conversion to biomass, which also suggested leakage of P. If leaked P is primarily released as dissolved unreactive phosphorus (DUP) following P loading events, then elevated DUP concentrations in enriched streams may indicate that P is being processed without assimilation into biomass. In such cases, P may cycle through the stream at a faster rate, reducing retention time compared to streams where P is assimilated into biomass. This reduced retention could lengthen nutrient spiraling lengths and increase the risk of transport into downstream ecosystems in comparison to low antecedent streams. Understanding the form of P released by periphyton is therefore critical for identifying which streams can

effectively retain P and limit its export to sensitive downstream ecosystems such as the Great Lakes.

### **4.3 Benthic metabolism and cellulose decomposition**

Despite increases in periphyton P content following a P event in both low and high antecedent streams, cellulose decomposition and benthic metabolism were not associated with P event concentration. This finding was expected in high antecedent streams, where additional P inputs did not stimulate further biomass growth. However, in low antecedent streams, the fact that additional biomass did not translate to additional productivity was unexpected. Indeed, numerous previous studies have linked nutrient additions to changes in periphyton function (Hillebrand & Kahlert, 2001; Nelson et al., 2013). The lack of increase in productivity following a P loading event even when additional biomass is present may have been due to shading from abundant filamentous algae preventing light penetration to inner periphytic layers reducing photosynthesis as has been observed in other studies (Horner et al., 1990; McIntire, 1968). Respiration may not have increased in high antecedent streams because heterotrophs, dominant over autotrophs regardless of timing, were likely limited by available labile carbon and thus unresponsive to nutrient events, which may have limited decomposition from physical constraints such as cooler temperatures in periphytic inner layers caused by self-shading (Guariento et al., 2011). Previous studies have also shown thresholds or quadratic relationships with nutrient enrichment in streams, and it is possible that our data could reflect a quadratic relationship as we observed cellulose decomposition reach a peak in the mid-size event concentrations, however, the potential of a quadratic association was not tested due to our small sample size (Schmidt et al., 2019; Woodward et al., 2012). Decoupling between biomass and

function of periphyton where metabolism does not increase in response to nutrient additions has implications for the ecosystem productivity of real streams as primary producers are needed for transfer of nutrients and energy through trophic levels.

In addition to being unaffected by P event concentration, cellulose decomposition also seemed unrelated to the antecedent P concentration as average tensile loss exhibited little difference amongst experiments. This finding contrasts with numerous previous studies showing that nutrient enrichment enhances decomposition of organic matter in streams (Elwood et al., 1981; Greenwood et al., 2007; Qualls & Richardson, 2003). Our findings may be explained by the process of negative algal priming, whereby increased algal biomass supplies heterotrophic microbes with preferred, labile carbon sources (e.g., algal exudates), thereby reducing the degradation of more recalcitrant organic matter, such as the cotton strips used in our experiments (Guenet et al., 2010). Indeed, a previous mesocosm study by Ashberry et al., (2021) observed inhibited decomposition at P loads exceeded in our low and high antecedent streams. However, further studies are needed to confirm the potential for negative algal priming effects on cellulose decomposition P enriched streams by assessing carbon sources used for decomposition.

#### **4.4 Implications and applications**

Our study showed that high antecedent P, loading impacts to periphyton are not proportionately influenced by the size of a P loading event. Building off the work of Pearce et al (2023) and Lundsgaard-Nielsen (2023), our study adds to existing knowledge that periphyton can cycle P from short duration loading events however we reveal that this is dependent upon antecedent P concentrations in the stream. Since periphyton may not process additional P that is loaded in the short term to streams when already enriched with P, excess loads may be

transported downstream ecosystems as bioavailable P in these conditions. Furthermore, a stream's antecedent conditions must be considered when evaluating its capacity to cycle excess nutrients. For example, many stream management practices utilize streams as a hotspot for nutrient cycling (Essington & Carpenter, 2000), without considering the current state of the stream. However, our findings indicate the need for a shift in management actions to prioritize the prevention of streams being P enriched, and how to reduce P in high antecedent streams so that they are still able to process additional nutrient loads.

Current research on in-stream P cycling under field conditions often overlook the importance of varying both the antecedent P concentration and the short term P load, even though natural streams face a range of conditions. Studies that fail to account for the initial conditions in the stream may miss key dynamics of P cycling by periphyton, potentially leading to an incomplete understanding of this process. In fact, it is likely for managers to observe high concentrations of P in downstream ecosystems after short term nutrient loading events as we found there is potential for P leakage for stream periphyton saturated with P from the antecedent condition. Further, it was found that excess P can bypass being processed by periphyton and are transported to downstream ecosystems in high antecedent conditions. In cases where managers are hoping to use streams as a mitigation tool for excess nutrients, there may be minimal success in streams with high antecedent P. The protection of freshwater systems from eutrophication is crucial and streams which may have limited ecosystem services must be considered when putting forth regulations for these efforts. Future studies are needed to assess the form of P leakage from periphyton in enriched streams to understand the risk of eutrophic conditions in downstream environments.

## 4.5 Future work and limitations

Results from this study should be validated in real streams to gather a complete understanding of how stream periphyton respond to P loading events under various antecedent conditions. To replicate this study in a real stream, streams could be selected by antecedent conditions which could vary based on many factors or activities present in the stream catchment (ie., groundwater inputs, agriculture, wastewater treatment plants). Once streams are selected based on varying antecedent condition, tiles could be placed on the stream bed for a uniform periphyton substrate. Nutrient loading events could be stimulated by dumping nutrients upstream of sampling sites and can vary in concentration. However, other environmental factors could impact results or be inconsistent between sites such as shading, invertebrate grazers, sediment, or flow (Wellnitz & Rader, 2003). Such variables must be accounted for, and stream selection would need to factor in similar environment variables between streams as best possible for comparing results between antecedent conditions.

To extend the results from our study, an additional experiment could be done in the artificial streams or in real streams to verify the form of P that is leaked from high antecedent streams after P loading events. As discussed, it is possible that P is being released as SRP or as DUP and depending on the form of P, the threat to downstream ecosystems can differ. Understanding the form will not only fully inform land managers on how periphyton responds to P loading events in high antecedent conditions but help assess the of severity of P loading to at risk ecosystems. Additionally, it is important that the experiment is held for a longer period time after the P loading event as the amount of time that P could leak for is unknown. Knowing how long periphyton leak P after being triggered by a loading event may also help managers assess

the stability of high antecedent streams and determine the risk level of leaking and for how long downstream ecosystems may be affected.

Our results are specific to the studied stream type and may not be directly applicable to stream systems with differing physical or environmental characteristics. During a runoff event a natural stream can be exposed to a variety of inputs such as herbicides, pesticides, and pharmaceuticals along with nutrients such as P (Meyer et al., 2011). Our findings do not account for potential interactions among the various components introduced during loading events, and variables such as periphyton growth may be influenced by the composition of runoff entering the stream, with implications for nutrient cycling. Additionally, the substrate composition in natural streams can differ substantially from that used in our artificial systems, for instance, real streams can vary in sediment type and further impact P uptake dynamics (Proia et al., 2017). However, our streams used rock substrate and therefore, the results may not fully represent instream processes from streams with more diverse sediment compositions. Flows during our P events were sub scouring, meaning that periphyton remained stable on substrates, consequently, it remains uncertain how high flow events capable of disturbing periphyton communities or mobilizing sediments might influence nutrient uptake dynamics, organic matter processing, and overall stream metabolism. Overall, these findings should be validated in natural stream environments to better determine the range of stream types and conditions to which they can be applied.

## **4.6 Conclusions**

Previously, streams have been found to be good sites for nutrient cycling, and a major site within streams where P is processed is periphyton (Pearce et al., 2023). The capacity for

streams to capture nutrients from short duration loading events had not been well established until the results from Pearce et al., (2020, 2023) and Lundsgaard-Neilsen (2023) showed that periphyton are able to process P from short duration loading events. However, these studies did not alter the antecedent condition in the stream, which in natural settings can be quite variable depending upon the activities present in the stream catchment, and environmental characteristics in the area. Our results showed that periphyton response (P content, P uptake and biomass) to P loading events is influenced by the antecedent condition in the stream. These findings suggest that nutrient cycling in streams, which is an important ecosystem service, may be limited under high antecedent P. Advancing the knowledge on how streams cycle excess P under various conditions is important as there is a limited understanding of how stream process P loading events from a range of conditions. These findings highlight the need for further studies on P loading to gather a full understanding of how streams process additional P to determine the fate of lost P to important downstream ecosystems.

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## Appendix

**Table A1.** AIC table testing the null, linear, logistic and asymptotic relationships for P content, P uptake, biomass, biomass growth, chl *a*, chl *a* growth, AI, P/biomass, P uptake/biomass, cellulose decomposition and benthic metabolism one day before, one day after and 10 days after the P event for the low antecedent experiment.

<b>Chl <i>a</i></b>	Model	k	LL	AICc	$\Delta$ AICc	AICw	Residual Dev.
<b>1 day before</b>	Null	1	-10.06	26.13	<b>0.00</b>	0.90	4.93
	Linear	2	-9.90	30.61	4.48	0.10	4.76
	Asymptotic	3	-11.06	40.12	13.99	< 0.01	6.15
	Logistic	3	-11.74	41.48	15.35	< 0.01	7.16
<b>1 day after</b>	Null	1	-9.55	25.11	<b>0.00</b>	0.87	3.96
	Linear	2	-9.08	28.96	3.85	0.13	4.40
	Logistic	3	-19.12	56.24	31.13	< 0.01	36.89
	Asymptotic	3	-19.12	56.24	31.13	< 0.01	36.89
<b>10 days after</b>	Linear	2	-12.66	36.11	<b>0.00</b>	0.77	8.78
<b>R<sup>2</sup> = 0.75</b>	Logistic	3	-11.03	39.99	3.88	0.11	6.07
	Asymptotic	3	-11.00	40.06	3.94	0.11	6.11
	Null	1	-19.49	44.98	8.87	0.01	40.08
<b>Chl <i>a</i> Growth</b>	Model	k	LL	AICc	$\Delta$ AICc	AICw	Residual Dev.

<b>1 day before</b>	Null	1	-10.46	26.92	<b>0.00</b>	0.90	5.38
	Linear	2	-10.27	31.34	4.42	0.10	5.16
	Asymptotic	3	-10.47	38.93	12.02	< 0.01	5.39
	Logistic	3	-10.47	38.93	12.02	< 0.01	5.39
<b>1 day after</b>	Null	1	-12.14	30.28	<b>0.00</b>	0.91	7.82
	Linear	2	-12.10	35.01	4.73	0.09	7.76
	Asymptotic	3	-17.46	43.82	13.54	< 0.01	9.28
	Logistic	3	-12.91	52.93	22.65	< 0.01	25.54
<b>10 days after</b>	Null	1	-19.11	44.22	<b>0.00</b>	0.63	36.83
	Linear	2	-17.25	45.30	1.08	0.37	24.35
	Asymptotic	3	-19.54	56.50	12.28	< 0.01	38.00
	Logistic	3	-19.25	57.08	12.86	< 0.01	40.50
<b>Biomass (AFDM)</b>	<b>Model</b>	<b>k</b>	<b>LL</b>	<b>AICc</b>	<b><math>\Delta</math> AICc</b>	<b>AICw</b>	<b>Residual Dev.</b>
<b>1 day before</b>	Null	1	10.52	-15.05	<b>0.00</b>	0.81	0.05
	Linear	2	11.45	-12.10	2.95	0.19	0.04
	Asymptotic	3	-6.62	19.27	34.32	< 0.01	0.61
	Logistic	3	-0.64	31.24	46.29	< 0.01	2.30

<b>1 day after</b>	Null	1	4.12	-2.25	<b>0.00</b>	0.90	0.21
	Linear	2	4.27	2.25	4.50	0.10	0.20
	Asymptotic	3	3.51	10.43	12.68	< 0.01	0.23
	Logistic	3	3.78	10.97	13.22	< 0.01	0.24
<b>10 days after</b>	Linear	2	0.39	10.02	<b>0.00</b>	0.57	0.48
<b>R2= 0.37</b>	Null	1	-2.28	10.56	0.54	0.43	0.87
	Asymptotic	3	-3.99	23.39	13.37	< 0.01	0.96
	Logistic	3	-2.70	25.98	15.96	< 0.01	1.28
<b>Biomass Growth</b>	<b>Model</b>	<b>k</b>	<b>LL</b>	<b>AICc</b>	<b>Δ AICc</b>	<b>AICw</b>	<b>Residual Dev.</b>
<b>1 day before</b>	Null	1	10.52	-15.05	<b>0.00</b>	0.81	0.05
	Linear	2	11.45	-12.10	2.95	0.19	0.04
	Logistic	3	-0.64	-3.04	12.00	< 0.01	0.05
	Asymptotic	3	10.52	19.27	34.32	< 0.01	0.61
<b>1 day after</b>	Null	1	5.23	-4.45	<b>0.00</b>	0.92	0.16
	Linear	2	5.23	0.34	4.79	0.08	0.16
	Logistic	3	-2.00	9.05	13.51	< 0.01	0.20
	Asymptotic	3	4.47	22.00	26.45	< 0.01	0.82

<b>10 days after</b>	Linear	2	1.17	8.46	<b>0.00</b>	0.68	0.41
<b>R<sup>2</sup>= 0.37</b>	Null	1	-2.14	10.28	1.81	0.28	0.85
	Logistic	3	1.26	15.33	6.87	0.02	0.39
	Asymptotic	3	1.33	15.47	7.01	0.02	0.40
<b>P content</b>	Model	k	LL	AICc	$\Delta$ AICc	AICw	Residual Dev.
<b>1 day before</b>	Null	1	63.47	-120.94	<b>0.00</b>	0.83	3.95E-07
	Linear	2	63.64	-116.48	4.46	0.09	3.80E-07
	Logistic	3	43.09	-116.14	4.80	0.08	1.77E-07
	Asymptotic	3	67.07	-68.17	52.77	< 0.01	3.66E-05
<b>1 day after</b>	Linear	2	45.60	-80.41	<b>0.00</b>	0.70	2.09E-05
<b>R<sup>2</sup>= 0.8641</b>	Asymptotic	3	27.40	-78.67	1.74	0.30	1.14E-05
	Null	1	36.02	-66.05	14.36	< 0.01	1.76E-04
	Logistic	3	48.33	-36.81	43.60	< 0.01	1.19E-03
<b>10 days after</b>	Linear	2	44.61	-78.42	<b>0.00</b>	0.93	2.61E-05
<b>R<sup>2</sup>= 0.87</b>	Asymptotic	3	44.68	-72.04	6.38	0.04	2.38E-05
	Logistic	3	45.02	-71.36	7.05	0.03	2.57E-05
	Null	1	34.97	-63.95	14.47	< 0.01	2.22E-04

<b>P Uptake</b>	Model	k	LL	AICc	$\Delta$ AICc	AICw	Residual Dev.
<b>1 day before</b>	Null	1	42.75	-79.50	<b>0.00</b>	0.83	3.95E-05
	Linear	2	42.92	-75.03	4.46	0.09	3.80E-05
	Logistic	3	22.31	-74.69	4.80	0.08	1.77E-05
	Asymptotic	3	46.35	-26.63	52.87	< 0.01	3.70E-03
<b>1 day after</b>	Logistic	3	11.81	-7.95	<b>0.00</b>	0.49	0.03
	Linear	2	9.08	-7.36	0.59	0.36	0.07
	Asymptotic	3	12.98	-5.62	2.33	0.15	0.04
	Null	1	-0.50	7.00	14.96	< 0.01	0.59
<b>10 days after</b>	Null	1	20.62	-35.23	<b>0.00</b>	0.89	0.01
	Linear	2	20.89	-30.99	4.25	0.11	0.01
	Asymptotic	3	13.66	-9.33	25.91	< 0.01	0.03
	Logistic	3	13.66	-9.32	25.91	< 0.01	0.03
<b>Metabolism (ER)</b>	Model	k	LL	AICc	$\Delta$ AICc	AICw	Residual Dev.
<b>1 day before</b>	Null	1	-30.24	66.48	<b>0.00</b>	0.91	4.37E+02
	Linear	2	-30.17	71.13	4.65	0.09	4.30E+02
	Asymptotic	3	-29.89	89.64	23.15	< 0.01	1.51E+03

	Logistic	3	-35.82	77.78	11.30	< 0.01	4.04E+02
<b>10 days after</b>	Null	1	-22.49	50.98	<b>0.00</b>	0.91	78.01
	Linear	2	-22.35	55.50	4.52	0.09	75.63
	Asymptotic	3	-36.37	90.74	39.76	< 0.01	1.71E+03
	Logistic	3	-36.37	90.74	39.76	< 0.01	1.71E+03
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<b>Metabolism (GPP)</b>	Model	k	LL	AICc	$\Delta$ AICc	AICw	Residual Dev.
<b>1 day before</b>	Null	1	-33.87	74.14	<b>0.00</b>	0.93	2.23E+03
	Linear	2	-33.59	79.19	5.05	0.07	2.08E+03
	Asymptotic	3	-45.11	111.00	36.95	< 0.01	3.49E+04
	Logistic	3	-44.88	112.00	37.41	< 0.01	3.70E+04
<b>10 days after</b>	Null	3	-31.85	70.10	<b>0.00</b>	0.94	1.34E+03
	Linear	3	-31.85	75.69	5.59	0.06	1.34E+03
	Asymptotic	2	-46.97	115.00	44.79	< 0.01	5.62E+04
	Logistic	1	-46.78	115.00	45.17	< 0.01	5.89E+04
<hr/>							
<b>Decomposition</b>	Model	k	LL	AICc	$\Delta$ AICc	AICw	Residual Dev.
<b>10 days after</b>	Null	1	1.08	3.83	<b>0.00</b>	0.57	0.41
	Linear	2	3.13	4.54	0.71	0.40	0.26

	Logistic	3	-4.44	9.93	6.10	0.03	0.21
	Asymptotic	3	4.03	26.87	23.04	< 0.01	1.41
<b>Autotrophic Index</b>	<b>Model</b>	<b>k</b>	<b>LL</b>	<b>AICc</b>	<b><math>\Delta</math> AICc</b>	<b>AICw</b>	<b>Residual Dev.</b>
<b>1 day before</b>	Null	1	-50.50	107.00	<b>0.00</b>	0.89	3.94E+04
	Linear	2	-50.16	111.00	4.14	0.11	3.66E+04
	Asymptotic	3	-61.50	141.00	33.84	< 0.01	4.46E+05
	Logistic	3	-61.42	141.00	34.00	< 0.01	4.54E+05
<b>1 day after</b>	Null	1	-44.82	95.65	<b>0.00</b>	0.89	1.12E+04
	Linear	2	-44.48	99.75	4.10	0.11	1.03E+04
	Asymptotic	3	-58.70	135.00	39.53	< 0.01	2.38E+05
	Logistic	3	-58.59	135.00	39.75	< 0.01	2.44E+05
<b>10 days after</b>	Null	1	-40.59	87.18	<b>0.00</b>	0.86	4.35E+03
	Linear	2	-40.04	90.88	3.70	0.14	3.85E+03
	Asymptotic	3	-59.26	136.00	49.14	< 0.01	2.70E+05
	Logistic	3	-59.16	137.00	49.34	< 0.01	2.76E+05
<b>P/Biomass</b>	<b>Model</b>	<b>k</b>	<b>LL</b>	<b>AICc</b>	<b><math>\Delta</math> AICc</b>	<b>AICw</b>	<b>Residual Dev.</b>
<b>1 day before</b>	Null	1	50.99	-95.98	<b>0.00</b>	0.65	6.32E-06

	Linear	2	52.77	-94.74	1.24	0.35	4.26E-06
	Asymptotic	3	36.41	-54.88	41.10	< 0.01	1.60E-04
	Logistic	3	36.44	-54.83	41.15	< 0.01	1.61E-04
<b>1 day after</b>	Linear	2	44.61	-78.42	<b>0.00</b>	1.00	2.61E-05
<b>R<sup>2</sup> = 0.90</b>	Null	1	34.33	-62.65	15.77	< 0.01	2.56E-04
	Asymptotic	3	26.47	-34.96	43.46	< 0.01	1.47E-03
	Logistic	3	26.48	-34.95	43.47	< 0.01	1.47E-03
<b>10 days after</b>	Linear	2	52.09	-93.39	<b>0.00</b>	0.97	4.94E-06
<b>R<sup>2</sup> = 0.73</b>	Null	1	46.21	-86.41	6.98	0.03	1.83E-05
	Asymptotic	3	34.21	-50.47	42.92	< 0.01	2.62E-04
	Logistic	3	34.24	-50.43	42.96	< 0.01	2.63E-04
<b>P Uptake/Biomass</b>	Model	k	LL	AICc	<b>Δ AICc</b>	AICw	Residual Dev.
<b>1 day before</b>	Null	1	55.47	-105.00	<b>0.00</b>	0.73	2.34E-06
	Linear	2	56.90	-103.00	1.94	0.27	1.70E-06
	Asymptotic	3	38.22	-58.54	46.40	< 0.01	1.07E-04
	Logistic	3	38.27	-58.44	46.50	< 0.01	1.08E-04
<b>1 day after</b>	Null	1	27.65	-49.29	<b>0.00</b>	0.92	1.13E-03

	Linear	2	27.65	-44.50	4.79	0.08	1.13E-03
	Asymptotic	3	20.22	-22.45	26.84	< 0.01	5.88E-03
	Logistic	3	20.23	-22.44	26.85	< 0.01	5.89E-03
<b>10 days after</b>	Null	1	51.25	-96.51	<b>0.00</b>	0.91	5.96E-06
	Linear	2	51.30	-91.81	4.70	0.09	5.90E-06
	Asymptotic	3	44.68	-71.51	25.00	< 0.01	2.53E-05
	Logistic	3	44.75	-71.36	25.15	< 0.01	2.57E-05

**Table A2.** AIC table testing the null, linear, logistic and asymptotic relationships for P content, P uptake, biomass, biomass growth, chl *a*, chl *a* growth, AI, P/biomass, P uptake/biomass, cellulose decomposition and benthic metabolism one day before, one day after and 10 days after the P event for the high antecedent experiment.

<b>Chl <i>a</i></b>	Model	k	LL	AICc	Δ AICc	AICw	Residual Dev.
<b>1 day before</b>	Null	1	-18.57	43.55	<b>0.00</b>	0.94	48.67
	Linear	2	-18.57	49.15	5.60	0.06	48.66
	Asymptotic	3	-31.48	56.81	13.27	< 0.01	39.51
	Logistic	3	-17.74	84.29	40.74	< 0.01	1.23E+03
<b>1 day after</b>	Null	1	-21.85	50.09	<b>0.00</b>	0.62	110.28
	Linear	2	-19.58	51.15	1.06	0.36	62.52
	Asymptotic	3	-35.57	57.15	7.05	0.02	41.19
	Logistic	3	-17.91	92.48	42.39	< 0.01	3.41E+03
<b>10 days after</b>	Null	2	-22.08	50.55	<b>0.00</b>	0.88	1.17E+02
	Linear	1	-21.24	54.47	3.92	0.12	94.72
	Asymptotic	3	-33.05	85.24	34.69	< 0.01	1.38E+03
	Logistic	3	-31.95	87.43	36.88	< 0.01	1.81E+03
<b>Chl <i>a</i> Growth</b>	Model	k	LL	AICc	Δ AICc	AICw	Residual Dev.
<b>1 day before</b>	Null	1	1.31	-38.48	<b>0.00</b>	0.94	0.34

	Linear	2	1.31	-32.91	5.57	0.06	0.34
	Logistic	3	2.14'	10.61	49.10	< 0.01	0.59
	Asymptotic	3	-0.92	17.10	55.54	< 0.01	0.27
<b>1 day after</b>	Null	2	-11.88	30.16	<b>0.00</b>	0.94	9.13
	Linear	1	-11.78	35.56	5.40	0.06	8.90
	Logistic	3	-11.89	44.64	14.48	< 0.01	9.15
	Asymptotic	3	-11.65	45.11	14.95	< 0.01	8.63
<b>10 days after</b>	Null	1	-5.79	17.99	<b>0.00</b>	0.86	1.99
	Linear	2	-4.78	21.56	3.57	0.14	1.55
	Logistic	3	-9.17	39.67	21.68	< 0.01	4.63
	Asymptotic	3	-9.17	39.67	21.68	< 0.01	4.63
<b>P Content</b>	Model	k	LL	AICc	$\Delta$ AICc	AICw	Residual Dev.
<b>1 day before</b>	Null	1	40.16	-73.93	<b>0.00</b>	0.78	35.25
	Linear	2	41.68	-71.37	2.55	0.21	23.77
	Asymptotic	3	41.68	-62.04	11.88	< 0.01	23.77
	Logistic	3	41.68	-62.04	11.88	< 0.01	23.76
<b>1 day after</b>	Linear	2	-25.65	63.30	<b>0.00</b>	0.68	2.85E+02

<b>R<sup>2</sup> = 0.59</b>	Null	1	-29.20	64.81	1.51	0.32	6.94E+02
	Asymptotic	3	-35.49	93.66	29.01	< 0.01	3.34E+03
	Logistic	3	-36.16	92.31	30.36	< 0.01	3.95E+03
<b>10 days after</b>	Null	1	-20.09	46.59	<b>0.00</b>	0.85	71.17
	Linear	2	-19.03	50.05	3.46	0.15	54.49
	Logistic	3	-29.85	59.22	12.63	< 0.01	53.35
	Asymptotic	3	-18.94	81.02	34.44	< 0.01	8.15E+02
<b>P Uptake</b>	Model	k	LL	AICc	Δ AICc	AICw	Residual Dev.
<b>1 day before</b>	Null	1	60.04	-113.68	<b>0.00</b>	0.78	0.14
	Linear	2	61.57	-111.14	2.55	0.22	0.10
	Asymptotic	3	43.64	-101.80	11.88	< 0.01	0.10
	Logistic	3	61.57	-65.95	47.74	< 0.01	0.15
<b>1 day after</b>	Linear	2	40.70	-69.39	<b>0.00</b>	0.79	17.88
<b>R<sup>2</sup>= 0.64</b>	Null	1	36.56	-66.72	2.67	0.21	50.26
	Asymptotic	3	33.85	-46.37	23.02	< 0.01	35.06
	Logistic	3	33.85	-46.37	23.02	< 0.01	52.00
<b>10 days after</b>	Linear	2	45.76	-85.33	<b>0.00</b>	0.05	2.44

<b>R<sup>2</sup>= 0.52</b>	Null	1	45.76	-85.12	0.21	0.47	5.04
	Asymptotic	3	42.68	-64.03	21.30	< 0.01	10.87
	Logistic	3	42.68	-64.03	21.30	< 0.01	10.87
<b>Biomass (AFDM)</b>	Model	k	LL	AICc	Δ AICc	AICw	Residual Dev.
<b>1 day before</b>	Null	1	-14.85	36.10	<b>0.00</b>	0.85	19.18
	Linear	2	-13.82	39.65	3.55	0.14	14.84
	Asymptotic	3	-26.50	47.78	11.68	< 0.01	12.77
	Logistic	3	-13.22	74.34	38.24	< 0.01	3.53E+02
<b>1 day after</b>	Null	1	-20.98	48.36	<b>0.00</b>	0.94	88.86
	Linear	2	-20.98	53.96	5.59	0.06	88.78
	Asymptotic	3	-30.84	80.10	31.74	< 0.01	725.92
	Logistic	3	-29.38	83.00	34.64	< 0.01	1.04E+03
<b>10 days after</b>	Null	1	-18.81	44.02	<b>0.00</b>	0.94	51.62
	Linear	2	18.77	49.54	5.52	0.06	51.10
	Logistic	3	-26.72	58.87	14.85	< 0.01	51.07
	Asymptotic	3	-18.77	74.78	30.76	< 0.01	3.73E+02
<b>Biomass Growth</b>	Model	k	LL	AICc	Δ AICc	AICw	Residual Dev.

<b>1 day before</b>	Null	1	-14.85	36.10	<b>0.00</b>	0.85	19.18
	Linear	2	-13.82	39.65	3.55	0.14	14.84
	Asymptotic	3	-26.50	47.78	11.68	< 0.01	12.77
	Logistic	3	-13.22	74.34	38.24	< 0.01	3.53E+02
<b>1 day after</b>	Null	1	-20.01	46.42	<b>0.00</b>	0.92	69.72
	Linear	2	-19.68	51.36	4.93	0.08	64.16
	Logistic	3	-20.10	60.51	14.08	< 0.01	62.69
	Asymptotic	3	-19.59	61.54	15.12	< 0.01	71.35
<b>10 days after</b>	Null	1	-20.63	47.65	<b>0.00</b>	0.94	81.30
<b>R<sup>2</sup>= 0.3689</b>	Linear	2	-20.58	53.15	5.50	0.06	80.30
	Logistic	3	-22.64	66.62	18.97	< 0.01	1.35E+02
	Asymptotic	3	-22.64	66.62	18.97	< 0.01	1.35E+02
<b>Metabolism (GPP)</b>	Model	k	LL	AICc	$\Delta$ AICc	AICw	Residual Dev.
<b>1 day before</b>	Null	1	-33.87	74.14	<b>0.00</b>	0.93	2.23E+03
	Linear	2	-33.59	79.20	5.05	0.07	2.08E+03
	Asymptotic	3	-45.11	111.10	36.95	< 0.01	3.49E+04
	Logistic	3	-44.88	111.56	37.41	< 0.01	3.70E+04

<b>10 days after</b>	Null	1	-31.85	70.10	<b>0.00</b>	0.94	1.34E+03
	Linear	2	-31.85	75.70	5.60	0.01	1.34E+03
	Asymptotic	3	-46.97	114.89	44.79	< 0.01	5.62E+04
	Logistic	3	-46.78	115.26	45.17	< 0.01	5.89E+04
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<b>Metabolism (ER)</b>	Model	k	LL	AICc	$\Delta$ AICc	AICw	Residual Dev.
<b>1 day before</b>	Null	1	-15.90	38.20	<b>0.00</b>	0.92	24.93
	Linear	2	-15.60	43.20	5.00	7.60	23.12
	Asymptotic	3	-25.51	72.35	34.16	< 0.01	2.76E+02
	Logistic	3	-25.51	72.35	34.16	< 0.01	2.76E+02
<b>10 days after</b>	Null	1	-21.99	50.37	<b>0.00</b>	0.82	1.14E+02
	Linear	2	-20.72	53.44	3.07	0.18	83.27
	Logistic	3	-32.25	61.21	10.84	< 0.01	68.44
	Asymptotic	3	-19.94	85.83	35.46	< 0.01	1.49E+03
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<b>Decomposition</b>	Model	k	LL	AICc	$\Delta$ AICc	AICw	Residual Dev.
<b>10 days after</b>	Null	1	2.45	1.50	<b>0.00</b>	0.91	0.25
	Linear	2	2.91	6.17	4.67	0.09	0.23
	Asymptotic	3	-15.50	26.53	25.03	< 0.01	0.90

	Logistic	3	-2.60	52.34	50.83	< 0.01	22.58
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<b>Autotrophic Index</b>	Model	k	LL	AICc	$\Delta$ AICc	AICw	Residual Dev.
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<b>1 day before</b>	Null	1	-49.37	105.13	<b>0.00</b>	0.90	1.07E+05
	Linear	2	-48.72	109.44	4.30	0.10	9.12E+04
	Asymptotic	3	-62.79	146.86	41.72	< 0.01	3.05E+06
	Logistic	3	-62.76	146.91	41.77	< 0.01	3.07E+06
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<b>1 day after</b>	Null	1	-52.32	111.04	<b>0.00</b>	0.87	2.25E+05
	Linear	2	-51.42	114.83	3.79	0.13	1.79E+05
	Asymptotic	3	-62.70	146.69	35.65	< 0.01	2.99E+06
	Logistic	3	-62.68	146.74	35.70	< 0.01	3.01E+06
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<b>10 days after</b>	Null	1	-51.37	109.14	<b>0.00</b>	0.93	1.77E+05
	Linear	2	-51.14	114.28	5.14	0.07	1.67E+05
	Asymptotic	3	-63.29	147.86	38.72	< 0.01	3.46E+06
	Logistic	3	-63.26	147.91	38.77	< 0.01	3.48E+06
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<b>P/Biomass</b>	Model	k	LL	AICc	$\Delta$ AICc	AICw	Residual Dev.
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<b>1 day before</b>	Null	1	3.29	-0.17	<b>0.00</b>	0.94	0.21
	Linear	2	3.40	5.20	5.38	0.06	0.20
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	Asymptotic	3	1.54	14.75	14.92	< 0.01	0.21
	Logistic	3	3.29	18.24	18.42	< 0.01	0.32
<b>1 day after</b>	Linear	2	5.40	1.21	<b>0.00</b>	1.00	0.12
<b>R<sup>2</sup> = 0.95</b>	Null	1	-6.36	19.12	17.92	< 0.01	2.30
	Asymptotic	3	-6.90	26.99	25.78	< 0.01	0.95
	Logistic	3	-2.83	35.14	33.93	< 0.01	2.63
<b>10 days after</b>	Linear	2	2.92	6.16	<b>0.00</b>	6.92	0.23
<b>R<sup>2</sup> = 0.60</b>	Null	1	-0.71	7.82	1.66	3.01	0.56
	Asymptotic	3	-2.16	15.44	9.28	6.70	0.22
	Logistic	3	2.95	26.65	12.49	4.06	0.80
<b>P Uptake/Biomass</b>	Model	k	LL	AICc	Δ AICc	AICw	Residual Dev.
<b>1 day before</b>	Null	1	3.29	-0.17	<b>0.00</b>	9.36	35.26
	Linear	2	3.40	5.20	5.38	6.36	23.77
	Asymptotic	3	1.54	14.75	14.92	5.39	5.00E+02
	Logistic	3	3.30	18.24	18.42	9.38	7.76E+02
<b>1 day after</b>	Linear	2	5.40	1.21	<b>0.00</b>	1.00	0.07
<b>R<sup>2</sup> = 0.73</b>	Null	1	-6.36	19.12	17.92	< 0.01	0.24

	Asymptotic	3	-6.90	26.99	25.79	< 0.01	0.47
	Logistic	3	-2.83	35.14	33.93	< 0.01	0.48
<b>10 days after</b>	Linear	2	2.92	6.16	<b>0.00</b>	0.69	0.03
<b>R<sup>2</sup>= 0.46</b>	Null	1	-0.71	7.82	1.66	0.30	0.06
	Asymptotic	3	-2.16	15.44	9.28	0.01	0.12
	Logistic	3	2.95	25.65	19.48	< 0.01	0.12