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Light and dissolved nutrients mediate recalcitrant organic matter decomposition via microbial priming in experimental streams

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Abstract

1. Environmental factors such as nutrient and light availability may play important roles in determining the magnitude and direction of microbial priming and detrital decomposition and, therefore, the relative importance of microbial priming in carbon (C) dynamics in freshwater ecosystems.
2. We integrated light availability with an existing conceptual model predicting the magnitude of the priming effect (PE) along a dissolved nutrient gradient (i.e. *nutrient* PE model). Our modified *light-nutrient* PE model hypothesises how light may mediate priming at any given nutrient concentration and provides a calculation method for quantitative PE values (i.e. light effect size at a given nutrient concentration).
3. We used recirculating stream mesocosms with *Quercus stellata* (post oak) leaf litter as an organic matter (OM) substrate in a 150-day experiment to test our model predictions. We manipulated light levels [ambient (full light), shaded (*c.* 19% of ambient)] and phosphorus (P) concentration (10, 100, 500 μg PO_4-P/L) in a fully factorial design. We also supplied all mesocosms with 500 μg/L dissolved inorganic nitrogen. Microbial biomass, water column dissolved organic C, and leaf litter dry mass and recalcitrant OM [i.e. the fibre (cellulose + lignin) component of post oak substrate] were measured. Recalcitrant OM (ROM) *k*-rates (day^{-1}) were used to calculate the light effect size within P treatments as a log response ratio (*ln*[ambient *k*-rate/shade *k*-rate]) to ascertain PE magnitude and direction (positive or negative).
4. Light was an important driver of dissolved organic C, a potential source of additional labile organic matter essential for priming heterotrophic microbes. There were weak PEs in total leaf litter dry mass remaining, but PEs were more pronounced in leaf litter ROM remaining. The strongest positive PEs (specific to litter ROM pools) occur in the highest P treatment, presumably due to a change in which nutrient, nitrogen versus P, was a limiting factor for microbes based on nutrient ratios rather than P concentration alone. These results illustrate the importance of considering light levels, nutrient ratios (rather than individual nutrients), and detrital ROM components in further PE model development.

KEYWORDS
freshwaters, fungi, nutrient cycling, primary production, stoichiometry

1 | INTRODUCTION

The priming effect (PE) was first described by soil scientists and can be thought of as an alteration of the rate of carbon (C) turnover; specifically the PE is a change in the rate of recalcitrant organic matter (ROM) decomposition by heterotrophic microbes when labile organic matter (LOM) is added (Guenet, Danger, Abbadie, & Lacroix, 2010; Jenkinson, Fox, & Rayner, 1985; Kuzyakov, 2010). Although evidence for the PE primarily comes from terrestrial ecosystems, it is thought to occur in aquatic systems as well (Guenet et al., 2010). The direction of PEs can either be positive or negative, where a positive PE is an increase in the rate of ROM degradation in the presence of additional LOM and a negative PE is the decrease in the rate or lack of ROM degradation in the presence of additional LOM (Blagodatskaya & Kuzyakov, 2008; Guenet et al., 2010; Kuzyakov, Friedel, & Stahr, 2000). Priming has implications for altering aquatic ecosystem C flux; however, the factors determining the relative magnitude and direction of the PE in aquatic ecosystems are not well known and methods for calculating quantitative values for PEs remain elusive (Bengtsson, Attermeyer, & Catalán, 2018).

As the environment is continually altered by anthropogenic activities, it is important to consider how these activities may affect conditions in forested headwaters and how various factors influence the aquatic PE hypothesis. Nutrients are among the major limiting factors for heterotrophic microbial (fungal and bacterial) growth and metabolism in unaltered, fresh headwater streams (Elser, 2012; Elwood, Newbold, Trimble, & Stark, 1981; Strickland, Osburn, Lauber, Fierer, & Bradford, 2009; Vitousek et al.., 2008). Heterotrophic microbes are capable of assimilating nutrients from the water column, but they also liberate C and nutrients from leaf litter detritus through enzymatic degradation to help support their energetic and dietary needs (Cheever, Webster, Bilger, & Thomas, 2013; Gauthier, Flatau, & Clément, 1990). Energy released from metabolising LOM (i.e. dissolved organic C [DOC]) in the water, such as from algal exudates, may prime heterotrophic microbes toward greater decomposition (mining) of ROM to obtain limiting nutrients (a positive PE; Danger et al., 2013; Lagrue et al., 2011; Rier, Kuehn, & Francoeur, 2007; Rier, Shirvinski, & Kinek, 2014), especially in low-nutrient environments (Blagodatskaya & Kuzyakov, 2008; Guenet et al., 2010; Jenkinson et al., 1985; Kuzyakov, 2010).

Algal production is usually low in forested headwaters, due firstly to low light levels (Hill, Ryon, & Schilling, 1995; Mosisch, Bunn, & Davies, 2001) and secondly to nutrient limitation (Hill & Knight, 1988). Anthropogenic activities that alter riparian zones and open canopy cover remove light constraints on algal growth (Justus, Petersen, Femmer, Davis, & Wallace, 2010; Mosisch et al., 2001; Von Schiller, Martí, Riera, & Sabater, 2007) and may lead to microbial priming under low-nutrient conditions. Agriculture and urbanisation can contribute to nutrient loading of aquatic environments via nutrient-enriched runoff from increased use of impervious surfaces, inefficient municipal waste handling, use of fertilisers, etc. (Carpenter et al., 1998; Elser, 2012; Smith, 1998). Studies show that as microbial growth is released from nutrient limitation, an increase in decomposition occurs (Scott et al., 2013). However, under high light conditions (i.e. unshaded conditions), nutrient enrichment may result in decreased ROM decomposition and potentially no or negative PE (Halvorson, Scott, Entrekin, Evans-White, & Scott, 2016). The recent study by Halvorson et al. (2016) found that nutrients (specifically P) and light interacted to influence detrital conditioning and decomposition by microbial communities, where light was observed to magnify effects of P on decomposition. This was especially true at lower nutrient concentrations, but at higher concentrations, high light suppressed decomposition slightly compared to lower light treatments at the same nutrient concentration, suggesting a PE. Under nutrient and light enrichment, heterotrophic microbes may use excess nutrients and LOM additions (DOC, potentially from algal exudates) from the surrounding environment rather than mining ROM for these resources (Blagodatskaya & Kuzyakov, 2008; Guenet et al., 2010; Jenkinson et al., 1985; Kuzyakov, 2010). Consequently, factors such as dissolved nutrients and light that control heterotrophic microbial activity and algal abundance may determine the magnitude and direction of PEs (Halvorson et al., 2016; Rier et al., 2014).

Calculating quantitative values for PEs has been difficult up to this point. It is common for decomposition studies to measure decomposition rates (*k*-rates); however, these measures often do not differentiate between LOM and ROM components of leaf litter and instead focus only on changes in measures such as total dry mass (TDM) or ash-free dry mass. At the heart of the PE hypothesis is the idea of changes in the rate of ROM degradation, so separating out ROM decomposition patterns in leaf litter is vital and may offer a way to calculate quantitative PE values.

The objectives of this work were: (1) to improve the current conceptual model of the PE hypothesis by integrating a light level component; (2) to provide a potential method of deriving quantitative values for PEs; and (3) to directly test the PE hypothesis according to our model modifications and suggested calculations. We postulate a modified conceptual model (i.e. *light-nutrient* PE model, Figure 1) of the effects of light and nutrient availability on the potential presence and magnitude of aquatic PEs, which provides a means of calculating quantitative values for potential PEs, and we then used a manipulative experiment to test the PE hypothesis based on our conceptual model.

We used the existing conceptual model (i.e. *nutrient* PE model) presented by Guenet et al. (2010) as a beginning frame of reference, but our *light-nutrient* PE model (Figure 1) differs from Guenet et al.'s (2010) *nutrient* PE model in a few key ways. Guenet et al.'s (2010) *nutrient* PE model shows the response variable (algal density) to be

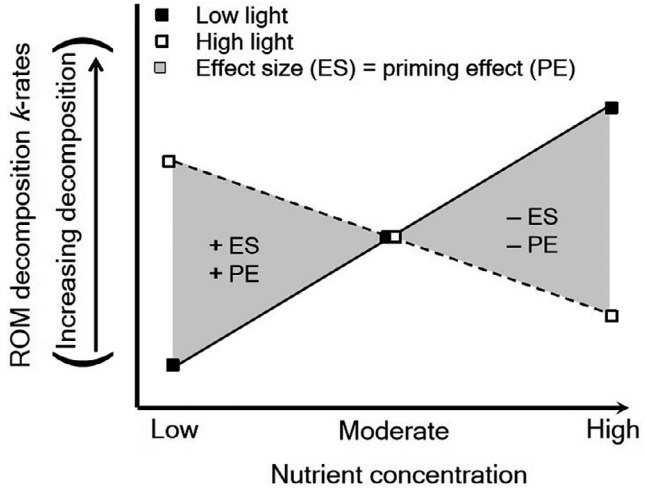

FIGURE 1 Aquatic *light-nutrient* priming effect (PE) model modified from Guenet et al.'s (2010) *nutrient* PE model. Recalcitrant organic matter (ROM) decomposition *k*-rates (day^{-1}) are presented on the *y*-axis. Nutrient concentrations presented on the *x*-axis increase from left to right. Our model assumes additional labile organic matter (LOM) inputs in the form of dissolved organic carbon (DOC), presumably from algal exudates. The filled boxes connected by a solid line show *k*-rates along an increasing nutrient gradient under low light conditions and the open boxes connected by a dashed line show *k*-rates along an increasing nutrient gradient under high light conditions. (Note: The purpose of the trend lines is to help conceptually illustrate PEs, not to imply that ROM decomposition trends are linear in nature.) As with Guenet et al.'s (2010) *nutrient* PE model, our *light-nutrient* PE model predicts the greatest positive PE when nutrients are most limited. The shaded wedges between trend lines indicate a light effect size (ES) as a method for quantifying the magnitude and direction of PE within a given nutrient concentration. Under low light, increased nutrients stimulate ROM decomposition by permitting greater heterotrophic growth and investment in nutrient-rich ROM degradative enzymes. Under high light, algae shift from positively priming decomposition (insufficient algae to allow preferential use of labile algal C), to negative priming decomposition (heterotrophs switch to reliance on labile algal C instead of ROM for growth)

a sigmoidal function of the independent variable (nutrient concentration) where algal density increases with increases in nutrient concentration. PE intensity is hypothesised to be a mirrored sigmoidal function of those two conditions, where positive PE intensity decreases with increases in nutrient concentration and algal density. Our *light-nutrient* PE model (Figure 1) expresses ROM decomposition *k*-rates (rather than algal density) as a function of nutrient concentration and we present separate, superimposed regression lines illustrating how differing light levels within a given nutrient concentration may affect ROM decomposition *k*-rates. While methods for calculating quantitative values for PEs were obscured in Guenet et al.'s (2010) model, the light regression lines in the new model suggest an effect size for light as a method for deriving quantitative values of potential PEs for specific concentrations of nutrients and light levels (Figure 1).

Our model modifications were based on the following rationale: PEs are characterised by changes in ROM decomposition rates specifically after LOM additions (Jenkinson et al., 1985), algal exudates may contribute to the LOM pool to prime heterotrophs (Danger et al., 2013), especially in nutrient-limited environments (Guenet et al., 2010), and increases in the amount of algal exudates would depend on greater photosynthetic activity (Rier et al., 2007, 2014). It should be noted that we do not intend to imply that the shapes of our *light-nutrient* PE model (Figure 1) regression lines are a steadfast rule; rather, our model conveys a conceptual idea of light and nutrient mediated PEs.

Our experimental approach to testing our *light-nutrient* PE model (Figure 1) included measurement and testing of algal biomass, water column DOC concentrations, and fungal biomass responses to light levels and nutrient amendments, for which we formulated the following sub-hypotheses: (1) increasing light will increase algal biomass within a given nutrient concentration due to relief of light-related growth limitations (except perhaps in the lowest P concentration where nutrient concentrations may limit algal growth); (2) as P concentrations increase, algal biomass and fungal biomass will increase due to relaxed P constraints on growth; and (3) water column DOC will increase with increasing algal biomass due to increased photosynthetic activity. We measured leaf litter ROM (i.e. fibre [cellulose + lignin] mass) decomposition over time and calculated *k*-rates (our model's primary response variable), which we predicted would increase with increasing P concentrations in shade and decrease with increasing P concentrations under increased light (Figure 1). Finally, we calculated light effect size as a log response ratio (LRR, *ln*[ambient *k*-rate/shade *k*-rate]) to ascertain PE magnitude and direction (positive or negative) and predicted the greatest positive PE in the lowest P concentrations.

2 | METHODS

A manipulative experiment was carried out in a temperature-controlled, greenhouse environment where recirculating stream mesocosms were exposed to normal day/night cycles from July 2015 to December 2015 for the duration of 150 days. Average daytime greenhouse temperatures ranged from 17.7 to 25.4°C and nighttime temperatures ranged from 12.4 to 21.0°C over the course of the experiment (Table S1). Mesocosms were constructed from 7-L oil pans, each maintained at a volume of 4 L of dechlorinated water for the duration of the study and each supplied with *c.* 15 g (dry mass) of leached post oak (*Quercus stellata*) leaf litter (hereafter, litter), on day 1. Post oak was chosen because it is known to be a recalcitrant species and commonly used in litter studies (Halvorson et al., 2015; Scott et al., 2013). Mesocosms were also given miniature fountain pumps that were regularly maintained by clearing any algae or debris to encourage optimal flow. On day 1, mesocosms were inoculated with a small amount (5 ml) of slurry made from mixed litter and stream water collected from a local, second-order stream known to be low in nutrient concentrations to provide a naturally occurring consortium of microbes (Halvorson et al., 2015). Average mesocosm water temperatures

ranged from 14.9 to 29.9°C over the course of the experiment as shown in Table S2. Peak mesocosm water temperatures occurred during the month of July and, although they were higher than peak air temperatures, these temperatures are within the range of warmer water temperatures occurring in surface waters and isolated pools in Arkansas during the summer.

A full-factorial cross of two factors (light and phosphorus [P]) was used in a randomised layout. There were two levels of light (ambient [full light as determined by the time of year] and shade [*c.* 19% of full light]) and three levels of P (10, 100, 500 μg PO_4-P/L). Light treatments were continuous for the duration of the experiment where shade treatments were achieved by triple-layering 1-mm mesh on top of the appropriate mesocosms and ambient treatments were left uncovered. Dissolved inorganic phosphorus was added directly to the water column weekly to maintain target P concentrations. We provided the same amount of dissolved inorganic nitrogen (N) across treatments by direct addition to each mesocosm weekly to maintain an N concentration of 500 μg/L. There were 10 replicates per unique treatment combination resulting in 60 experimental mesocosm units. Additionally, water was completely changed monthly for all mesocosms to prevent filamentous algal overgrowth, which may have resulted in self-shading and confound light treatment responses had it been allowed to remain.

A monthly sample plan was implemented where litter and suspended (i.e. planktonic) algae chlorophyll *a* were estimated as measures of algal biomass, water column samples were taken for DOC measures, litter ergosterol was estimated as a measure of fungal biomass, and litter was sampled for dry mass. Discs were cut with a cork borer (area = 1.496 cm^2) from randomly selected litter from each mesocosm and algal biomass, fungal biomass, and litter dry mass were estimated. Suspended algae sampling was accomplished by pressure filtering (0.45 μm membrane filter pore size) a known volume from the water column of each mesocosm and DOC samples were taken as grab samples of the water column and were filtered prior to processing. Suspended algae and DOC samples were always taken prior to the monthly water change in mesocosms.

Suspended and litter algal biomass were estimated using 95% ethanol extraction of chlorophyll *a* and standard spectrophotometric methods (Clesceri, Franson, Rice & Greenberg, 2005). Fungal biomass on litter was estimated by solid phase extraction of ergosterol and high-performance liquid chromatography analysis (Gessner & Schmitt, 1996). Water column samples were analysed for DOC by standard combustion catalytic oxidation methods (Eaton, Franson, American Public Health Association, American Water Works Association, & Water Environment Federation, 2005).

Total dry mass was measured initially and at termination for each mesocosm by placing leaf litter in a drying oven at 48°C for at least 2 hr and bringing to room temperature in a desiccator for at least 30 min before weighing. A subset of litter was taken initially, dried (48°C, ≥2 hr), and sent for processing to the University of Arkansas Altheimer laboratory where the Ankom method (Ankom, 2013) was used to estimate the ROM or fibre (cellulose + lignin), portion of the leaf litter being supplied as substrate for the mesocosms. The analysis of the initial subset of litter showed the beginning fibre (cellulose + lignin) content to be *c.* 43.5% of the initial TDM. This value was used along with the initial TDM values to calculate an initial fibre mass (g) of the litter substrate provided to each mesocosm. The same methods were used at termination to determine the remaining fibre content for each mesocosm. The final litter fibre content for each mesocosm was also given as a percentage (%), which we used along with final TDM values to derive final fibre mass (g) remaining of the original input.

Litter TDM and fibre mass values were used to calculate decomposition *k*-rates (day^{-1}) for each mesocosm. The exponential decay equation (Equation 1) used for these calculations is as follows:

$$k = \frac{\ln\left(\frac{M_f}{M_i}\right)}{t} \quad (1)$$

In Equation 1, M_f = final mass, M_i = initial mass, and t = time in days (in this case, 150 days). Next, *k*-rates were used to calculate a light effect size as the LRR within each P concentration as indicators of PE magnitude and direction (positive or negative) (Halvorson, Francoeur, Findlay, & Kuehn, 2019; Rosenberg, Rothstein, & Gurevitch, 2013). The LRR equation (Equation 2) used for these calculations is as follows:

$$\mathrm{LRR} = \ln\left(\frac{k_a}{k_s}\right) \quad (2)$$

In Equation 2, k_a = ambient *k*-rate and k_s = shade *k*-rate. Variance (*V*) around each LRR point (Halvorson et al., 2019; Rosenberg et al., 2013) was calculated as follows:

$$V = \left(\frac{s_{k_a}^2}{n_a\left[x_{k_a}^2\right]}\right) + \left(\frac{s_{k_s}^2}{n_s\left[x_{k_s}^2\right]}\right) \quad (3)$$

In Equation 3, s = *SD*, x = mean, n_a = ambient sample size, n_s = shade sample size, and *k*-rates are denoted the same as in Equation 2. The square root of VAR was taken to calculate *SE* around each LRR point and used to estimate the 95% confidence interval (95% CI).

Repeated measures two-way analysis of variance (α = 0.05) was used to analyse data for suspended and litter algal biomass, water column DOC, and litter fungal biomass. Two-way analysis of variance (α = 0.05) was used to analyse data for litter TDM remaining, fibre mass remaining, and decomposition *k*-rates data. Data were log-transformed where necessary to meet test assumptions and Tukey's HSD post hoc analysis was used when appropriate to discern significant pairwise comparisons. All data analyses were carried out using R statistical software, version 3.4.2 (R Core Team, 2017).

3 | RESULTS

Light and time interacted to drive differences in suspended algal biomass (Table 1). Suspended algal biomass was similar across all

TABLE 1 Repeated measures two-way analysis of variance (α = 0.05) output for suspended (i.e. planktonic) and litter algal biomass estimated as chlorophyll a (Chl *a*; mg/L and mg/cm^2, respectively), dissolved organic carbon (DOC; mg/L) in the water column, and detrital fungal biomass estimated as ergosterol (mg/cm^2)

Response variable	Factor	df	F	p
Suspended Chl *a* (mg/L)	L	1	3.830	0.052
	P	2	2.301	0.102
	T	4	8.683	**<0.001**
	L × P	2	0.246	0.782
	L × T	4	4.833	**0.001**
	P × T	8	1.275	0.257
	L × P × T	8	0.332	0.953
Litter Chl *a* (mg/cm^2)	L	1	3.623	0.058
	P	2	1.763	0.174
	T	4	1.349	0.252
	L × P	2	3.369	**0.036**
	L × T	4	1.204	0.310
	P × T	8	1.139	0.337
	L × P × T	8	1.397	0.200
DOC (mg/L)	L	1	12.770	**<0.001**
	P	2	0.541	0.583
	T	3	241.261	**<0.001**
	L × P	2	0.120	0.887
	L × T	3	3.077	**0.029**
	P × T	6	0.844	0.537
	L × P × T	6	0.411	0.872
Ergosterol (mg/cm^2)	L	1	1.225	0.271
	P	2	5.051	**0.008**
	T	4	5.992	**<0.001**
	L × P	2	0.311	0.734
	L × T	4	2.146	0.795
	P × T	8	1.739	0.097
	L × P × T	8	1.808	0.082

Note: All data were log-transformed to meet the assumption of normality. Significant *p* values are shown in bold. Tukey's HSD was conducted post hoc as necessary to discern significant comparisons. Factor abbreviations are as follows: L, light treatment; P, phosphorus treatment. Column header key: *df*, degrees freedom; *F*, ANOVA test statistic; *p*, probability value.

sampling months for shaded treatments and these were similar to ambient treatments for the month of November (Figure 2). Suspended algal biomass was similar for ambient light treatments during August, September, October, and December (Figure 2). During August, suspended algal biomass was significantly lower in ambient treatments as compared to shaded treatments and was significantly higher in ambient treatments during September, October, and December as compared to shaded treatments (Figure 2). Variation was similarly small from August to November for shaded and ambient light treatments, but much greater variation was observed in December for

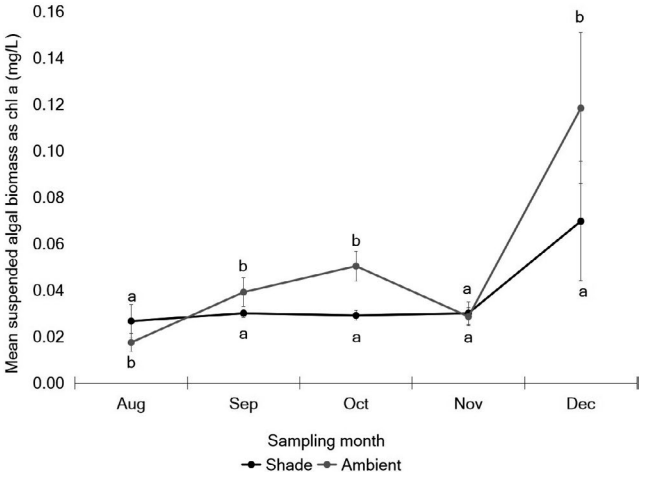

FIGURE 2 Mean ± 1 *SE* suspended (i.e. planktonic) algal biomass estimated as chlorophyll a (Chl *a*; mg/L) across repeated measures increments in months abbreviated as follows: Aug, August; Sep, September; Oct, October; Nov, November; Dec, December. Shaded treatments = black line and ambient light treatments = grey line. Data were log-transformed for statistical analyses. Significant differences due to a light × time interaction as per repeated measures two-way analysis of variance (α = 0.05) and Tukey's HSD post hoc analyses are indicated by letters

both light treatments (Figure 2). In general, suspended algal biomass tended to increase with increasing light (Figure 2), where time-pooled values showed suspended algal biomass concentrations under ambient conditions to be 0.062 and 0.037 mg/L under shaded conditions. Plot data are given in Table S3.

Detrital algal biomass was statistically similar across low, moderate, and high P/shaded treatments and these were similar to low and moderate P/ambient treatments (Figure 3). Detrital algal biomass in the high P/ambient treatment was significantly greater than all other treatments (Figure 3) due to an interaction between light and P (Table 1). Variation tended to increase with increasing P/shaded conditions but was similar across all P/ambient conditions (Figure 3). There was a general trend of increased algal biomass with increased light, except in the lowest P concentration (Figure 3). Plot data are given in Table S4.

Light and time interacted to yield significant differences between treatments over time for DOC (Table 1). No significant differences between DOC concentrations were found when comparing ambient and shaded treatments within any given sampling months except October where ambient treatments were significantly greater than shaded treatments (Figure 4). Ambient treatments differed from each other across all sampling months (Figure 4). Shaded treatments were only statistically similar during the months of October and November and these were similar to the ambient treatments during November (Figure 4). There was a trend of increasing DOC in the water column under both light treatments across time, but DOC was generally greater under ambient light as compared to shaded treatments (Figure 4). In fact, over the full duration of the study, DOC concentrations were significantly greater in the ambient treatments as compared to the shade treatments (Table 1), where time-pooled

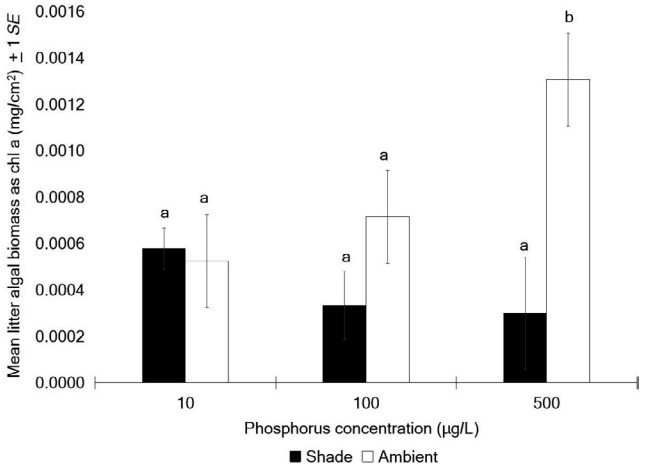

FIGURE 3 Mean ± 1 *SE* detrital-associated (litter) algal biomass estimated as chlorophyll a (Chl *a*; mg/cm^2) across low, moderate, and high (10, 100, and 500 µg/L) phosphorus (P) treatments. Shaded treatments = black bars and ambient light treatments = white bars. Data were log-transformed for statistical analyses. Significant differences due to a light × P treatment interaction as per repeated measures two-way analysis of variance (α = 0.05) and Tukey's HSD post hoc analyses are indicated by letters

values showed DOC concentrations under ambient conditions to be 60.34 and 45.23 mg/L under shaded conditions. Variation decreased over time but was small for all treatments (Figure 4). Plot data are given in Table S5.

There were no significant interactions driving fungal biomass changes and light treatment effects were weak, but time and P treatments had independent main effects (Table 1). The P main effect

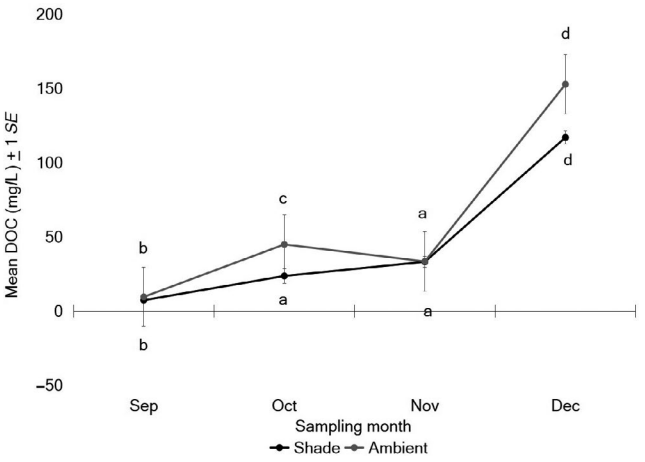

FIGURE 4 Mean ± 1 *SE* water column dissolved organic carbon (DOC, mg/L) across repeated measures increments in months abbreviated as follows: Sep, September; Oct, October; Nov, November; Dec, December. Shaded treatments = black line and ambient light treatments = gray line. Data were log-transformed for statistical analyses. Significant differences due to a light × time interaction as per repeated measures two-way analysis of variance (α = 0.05) and Tukey's HSD post hoc analyses are indicated by letters

was a significant increase in fungal biomass with increasing P, where moderate and high P treatments were similar but greater than low P treatments (Figure 5A). Fungal biomass fluctuated across time, but was statistically similar during August, November, and December (Figure 5B). Fungal biomass was greatest during October (Figure 5B). Fungal biomass in September was similar to fungal biomass in all other sampling months (Figure 5B). Variation was similarly small for all P treatments and across time (Figure 5A,B). Plot data are given in Table S6.1,S.6.2.

Total dry mass remaining did not differ across treatments and variation tended to decrease with increasing P and increasing light (Table 2 and Figure 6A). About 46.57%–50.99% of initial TDM remained at termination (Table S7). However, light and P interacted to drive differences in litter fibre (cellulose + lignin) mass remaining (Table 2). Litter fibre mass remaining was similar across all P/shaded treatments and these were similar to low and moderate P/ambient light treatments (Figure 6B). High P/ambient light had less fibre mass remaining than all other treatments (Figure 6B). There was a weak trend of more fibre mass remaining with increasing P/shaded conditions (Figure 6B). Although low and moderate P/ambient treatment fibre mass remaining were similar, there was a trend of increase before significantly dropping below all other values in the highest P concentration (Figure 6B). Fibre mass remaining was usually less under ambient light as compared to shaded conditions, except in the low P treatments where the opposite was true (Figure 6B). Variation was similarly small across all treatments for fibre mass remaining (Figure 6B). Overall, *c*. 66.7–79.7% of initial fibre mass remained at termination (Table S8). Plot data are given in Table S7.

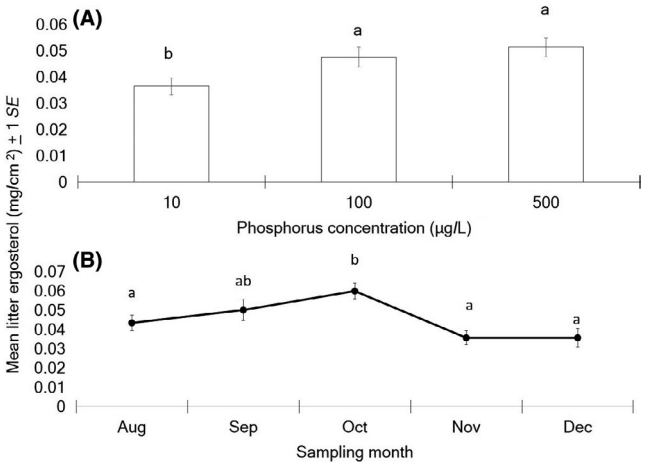

FIGURE 5 (A) Mean ± 1 *SE* detritus-associated (litter) fungal biomass estimated as ergosterol (mg/cm^2) across low, moderate, and high (10, 100, and 500 µg/L) phosphorus (P) treatments. (B) Mean ± 1 *SE* litter detritus fungal biomass estimated as ergosterol (mg/cm^2) across repeated measures increments in months abbreviated as follows: Aug, August; Sep, September; Oct, October; Nov, November; Dec, December. Data were log-transformed for statistical analyses. Significant differences due to P main effects (A) and time main effects (B) as per repeated measures two-way analysis of variance (α = 0.05) and Tukey's HSD post hoc analyses are indicated by letters

TABLE 2 Two-way analysis of variance (α = 0.05) output for litter mass remaining (g) and *k*-rates (day^{-1}) for total dry mass (TDM) and fibre (cellulose + lignin)

Response variable	Factors	Df	F	*p*
Litter mass (g) remaining				
TDM	L	1	0.001	0.980
	P	2	1.004	0.374
	L × P	2	1.310	0.279
Fibre	L	1	5.598	**0.022**
	P	2	1.066	0.352
	L × P	2	3.750	**0.030**
Litter *k*-rates (day^{-1})				
TDM	L	1	0.017	0.895
	P	2	0.985	0.381
	L × P	2	1.268	0.290
Fibre	L	1	5.369	**0.025**
	P	2	1.207	0.308
	L × P	2	3.921	**0.026**

Note: Laboratory analysis results for litter components were provided as percentages (%) and converted to g for statistical analyses. Significant *p* values are shown in bold. Tukey's HSD was conducted post hoc as necessary to discern significant comparisons. Factor abbreviations are as follows: L, light treatment; P, phosphorus treatment. Column header key: *df*, degrees freedom; *F*, ANOVA test statistic; *p*, probability value.

Total dry mass decomposition *k*-rates did not differ, and variation was similar across treatments, but there was a significant interaction between light and P for fibre mass decomposition *k*-rates (Table 2 and Figure 7A,B). For fibre *k*-rates, low, moderate, and high P/shade light treatments and low and moderate P/ambient light treatments were similar (Figure 7B). High P/ambient light had significantly faster fibre decomposition than other treatments (Figure 7B). In general, fibre decomposition slowed with increasing P/shaded conditions and fibre decomposition sped up with increasing P/ambient light (Figure 7B). There tended to be faster fibre decomposition with increased light, except in the low P where the opposite was true (Figure 7B). Variation was similar across treatments for litter dry mass *k*-rates (Figure 7A) and litter fibre mass *k*-rates (Figure 7B). Plot data are given in Table S8.

The light effect sizes within a given P concentration, which were calculated as LRR (Eq2), serve as quantitative values for PEs where positive LRR = positive PE and negative LRR = negative PE. The magnitude and direction of LRRs/PEs for litter TDM and fibre mass and are visualised in Figure 8 along with the 95% CI around each point. Litter TDM LRRs/PEs were negative under the low and moderate P conditions and became positive in the high P concentration (Figure 8). Litter fibre mass LRRs/PEs were negative under low P conditions and became increasingly positive in moderate to high P concentrations (Figure 8). The 95% CI widened with increasing P concentrations for litter TDM and fibre mass and 95% CIs were generally wider for fibre mass as compared to TDM (Figure 8). Trends in litter fibre mass LRRs were more pronounced than in TDM LRRs, resulting in decreasing amounts of overlap and eventually distinct separation in 95% CIs with increasing P (Figure 8). Plot data are given in Table S9.

4 | DISCUSSION

By mediating heterotrophic activity, environmental factors such as nutrient and light availability may influence the magnitude and sign of priming (Evans-White & Halvorson, 2017; Guenet et al., 2010), and therefore determine the role of priming in C fluxes within freshwater systems (Benstead et al., 2009; Webster et al., 1999). Light and nutrient manipulations resulted in changes in aquatic microbial communities (algal and fungal biomass), the size of the water column LOM pool measured as DOC, and ultimately litter ROM decomposition *k*-rates. Light was shown to be a statistically important driver of suspended algal biomass and DOC over time. Light also interacted with P to significantly drive changes in litter algal biomass. This reinforces the importance of including light along with nutrients as factors in further PE model development such as in our *light-nutrient* PE model. Our study also illustrates the importance of separating out ROM decomposition *k*-rates for use as a response variable in PE model development, as PEs specific to ROM pools were clearly more pronounced than in TDM data in our work.

One noteworthy caveat is that our *light-nutrient* PE model may lead to the assumption that the PE patterns postulated are in response to changes in the concentration of only a single nutrient (as was our original perception) because the *x*-axis is non-specific regarding nutrient identity. However, the effects of increased nutrient levels may depend on the availability of other nutrients in the system (i.e. the ratio of nutrients such as N:P; Halvorson et al., 2019). It is important to note that our experimental nutrient manipulations, which included increasing concentrations of dissolved inorganic P together with a consistent concentration of dissolved inorganic N, led to decreasing N:P ratios across treatments. While our sub-hypotheses regarding our model parameters were met reasonably well, N:P ratios could explain some of the patterns seen in our data and why our calculated PEs were counter to our predictions.

We predicted an increase in algal biomass with increasing light due to relief of light-related limitation, but that there would be little to no difference between light treatments regarding algal biomass at lower P concentrations due to nutrient limitations. Our data for algal biomass support this hypothesis. We also predicted an increase in algal biomass with increasing P concentrations within a given light level due to relief of P constraints. Our detrital algal biomass data for higher light levels support our hypothesis, but algal biomass at lower light levels remained statistically similar across P treatments. Algal cellular nutrient content was probably altered by interactions of changing light and nutrient availability in our study and therefore could have altered, which nutrient would limit algal growth (Sterner & Elser, 2002; Verhoeven, Koerselman, & Meuleman, 1996). The demand for P could have become greater under higher light levels, but lower light

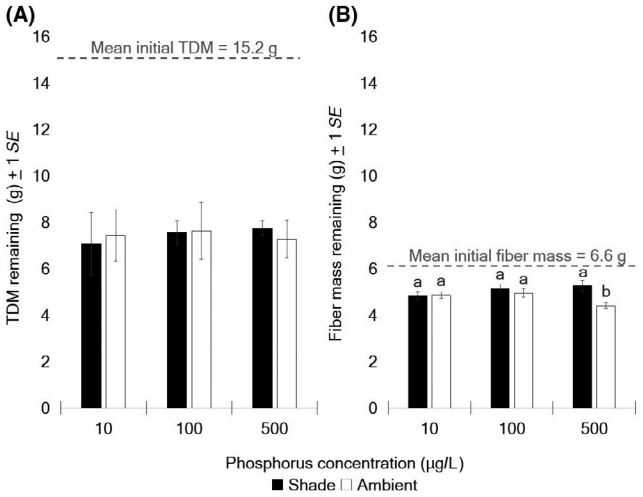

FIGURE 6 Mean ± 1 *SE* total dry mass (TDM, g) remaining (A) and fibre (cellulose + lignin) mass (g) remaining across low, moderate, and high (10, 100, and 500 µg/L) phosphorus (P) treatments. Shaded treatments = black bars and ambient light treatments = white bars. Significant differences in fibre mass remaining (B) due to a light × P interaction as per repeated measures two-way analysis of variance (α = 0.05) and Tukey's HSD post hoc analyses are indicated by letters. Horizontal dashed lines are provided for comparison and indicate initial TDM (A) and fibre mass (B) values (g)

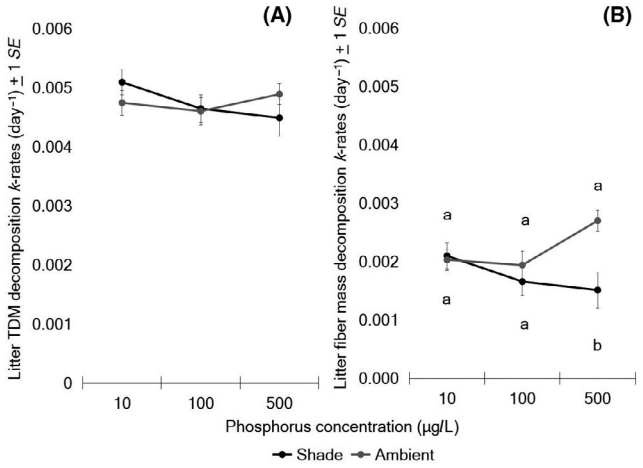

FIGURE 7 Mean ± 1 *SE* total dry mass (TDM) and fibre (cellulose + lignin) decomposition *k*-rates (day^{-1}) across low, moderate, and high (10, 100, and 500 µg/L) phosphorus (P) treatments (A and B, respectively). Shaded treatments = black lines and ambient light treatments = grey lines. Significant differences in fibre decomposition *k*-rates (B) due to a light × P interaction as per repeated measures two-way analysis of variance (α = 0.05) and Tukey's HSD post hoc analyses are indicated by letters

levels could result in a higher N demand for algae to produce N-rich pigments such as chlorophyll (Elliott & White, 1994; Healey, 1985; Sterner & Elser, 2002). This may explain why litter algal biomass did not respond as expected with increasing P (decreasing N:P)/shade conditions; N was becoming increasingly limiting to algal growth in the shade.

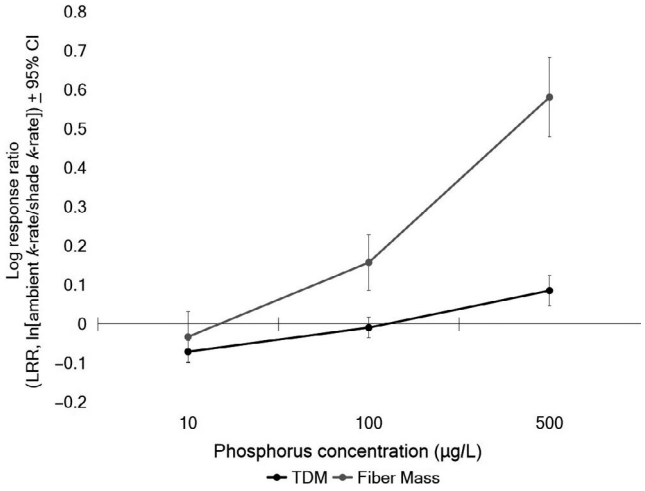

FIGURE 8 Log response ratio (LRR, calculated as *ln*[ambient *k*-rate day^{-1}/shade *k*-rate day^{-1}]) ± 95% confident interval (CI) as quantification of priming effect (PE) within a given phosphorus (P) concentration across low, moderate, and high (10, 100, and 500 µg/L) P treatments. Positive LRR = positive PE and negative LRR = negative PE. Total dry mass (TDM) LRR/PE = black line and fibre (cellulose + lignin) mass LRR/PE = grey line

We predicted and then observed that fungal biomass increased with increasing P concentrations as found in many previous studies, but we also saw shaded ROM *k*-rates were significantly slower than ambient light ROM *k*-rates in the highest P concentration (opposite of our model prediction). The ROM *k*-rates data resulted in the greatest positive PE where P concentrations were highest, which was counter to our predictions. This could have been due to decreasing N:P ratios, competition between algae and fungi for nutrients in the water column, and insufficient DOC to stimulate fungi towards mining ROM for limiting nutrients under shaded conditions. Fungal acquisition of N from the water column may have further constrained algal productivity due to increased N demand by algae as N:P ratios decreased under shaded conditions. These constraints on algae may also have been partially responsible for decreased DOC exudation which therefore became energetically limiting to fungi. Limitation of algal-derived carbon energy (DOC) would have reduced the ability of fungi to mine ROM for N in shaded conditions as N:P ratios decreased. Under ambient light conditions, the switch in algal demand for more P instead of N may have provided competitive relief for algae and, along with relieved light constraints, algae may have exuded more DOC that could then be used by fungi as an energy source for mining ROM.

Our PE predictions assumed that additions of DOC to the water column (presumably from algal exudates) provide energy for priming heterotrophic microbes, especially fungi. Evidence that fungi take up algal-derived DOC in aqueous environments has recently been provided by a study showing mutual exchange of C and nutrients between algae and fungi clearly showing that fungi do receive C derived specifically from living algae (Du et al., 2019). Our data show water column concentrations of DOC increase as algal biomass increase. DOC levels did not differ as strongly as algal biomass between the two light treatments, probably indicating high efficiency of heterotrophic turnover of

algal-derived DOC within the water column in ambient light. Moreover, our data are not entirely conclusive as to the origins of the additional DOC, only that DOC did increase under ambient light conditions over time and, therefore, could be a potential source of energy for heterotrophic microbes. Firstly, suspended algae might have had an advantage over detrital algae in intercepting more light for photosynthetic activity leading to more exudation of DOC. Detrital algae may have become crowded and slightly more shaded within the detrital biofilm, reducing photosynthesis and exuding less DOC. Secondly, trends in DOC mimicked trends in suspended algae over time across both light treatments. However, amounts of additional DOC were relatively large so it is reasonable to suggest that algal exudates were not the only source of DOC. Photodegradation of litter detritus could have been another potential source of additional water column DOC (Wetzel, Hatcher, & Bianchi, 1995) since litter decomposition increased with increasing light. Increasing DOC could have also been due to increased fungal processing of litter in ambient light conditions, which would result in increased leaching of the litter.

Radioisotopes could be used to trace proportional usage of DOC from different sources by heterotrophic microbes to confirm whether fungi are using a substantial amount of algal-derived DOC as an energy source for mining litter ROM in low-nutrient environments. Additionally, radioisotope tracers could further our understanding of the part played by heterotrophic bacteria in the cycling of algal- versus detrital-derived DOC in stream systems. We did not measure bacterial responses, but studies have shown that heterotrophic bacteria can assimilate algal-derived DOC to enhance growth rates (Kuehn, Francoeur, Findlay, & Neely, 2014). However, many recent priming studies that quantified bacterial activity or biomass found relatively weak or negligible responses for bacterial growth/production (Halvorson et al., 2019; Soares, Kritzberg, & Rousk, 2017). Heterotrophic bacteria can preferentially use DOC from different sources and the preference is probably specific to the type of bacteria present. Terrestrial literature indicates that Gram-negative bacteria have the most affinity for DOC originating from autotrophic exudation (Hotchkiss, Hall, Baker, Rosi-Marshall, & Tank, 2014). Using radioisotopes to link DOC (and its origin) to fungi and heterotrophic bacteria (especially according to species), could assist our understanding of the level of competition and perhaps mutualism that may occur between biofilm microbes as it relates to PEs and may reveal mechanisms of PEs.

We chose the LRR as a measure of effect size based on ROM *k*-rates, which is common in ecological studies (Halvorson et al., 2019; Rosenberg et al., 2013), to quantify PEs as suggested by our *light-nutrient* PE model. We saw weak PEs within our litter TDM data, and this could be because algae in our study did not differ enough between light regimes to provide sufficient contrast for testing PEs, which may be a problem in other studies as well. However, we saw a strong positive PE in the highest P treatment (lowest N:P) specific to litter ROM, which may have been obscured had we not separated out litter OM pools. As discussed previously, we presume that our PE results are due to a change in which nutrient, N or P, was a limiting factor for microbial productivity and the different ways in which microbes handled nutrient availability depending on light. The trend in ROM decomposition in ambient light is still indicative of positive PEs occurring in low-nutrient environments, but in this case, it is due to increasing N limitation as indicated by the decreasing N:P ratio. This suggests that predicting PEs reliably will require consideration of changing nutrient ratios rather than changing concentrations of a single nutrient.

Overall, our data provide further evidence that human activities affecting nutrient and light levels in headwaters can result in altered detrital decomposition and therefore C and nutrient cycling at the ecosystem level through the mediation of microbial priming. These results provide yet another reason why shading by the riparian canopy is an important part of managing human impacts on streams. Our modifications of the PE model, although imperfect, are a step in the right direction to improve our understanding of the occurrence of PEs in aquatic environments. The use of isotope tracers to link LOM to microbial biomass, photosynthetic efficiencies of algae, and competition for or exchange of resources between algae and heterotrophic microbes are all seemingly important parts of the PE puzzle that deserve further consideration in hypothetical model development. Additionally, improvements to the PE model could be made by incorporating a wider range of light levels and nutrient concentrations (with special consideration for nutrient ratios) as well as a variety of leaf litter species. More data points would help to discern the actual shape of the resulting PE curves and help to identify how positive/negative PE change points differ at varying light levels under similar nutrient concentrations.

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AUTHOR CONTRIBUTIONS

All authors conceived the design. Brooke Howard-Parker, Brendon White, and Halvor Halvorson conducted the experiment under mentorship of Michelle Evans-White. Brooke Howard-Parker led data analysis and was assisted by Brendon White. Brooke Howard-Parker interpreted data with insight from Halvor Halvorson and Michelle Evans-White. Brooke Howard-Parker led writing of the manuscript and revisions based on critical review and consideration by all co-authors. All authors gave approval of the final version of this manuscript to be published and agreed to be accountable for all aspects of the work.

DATA AVAILABILITY STATEMENT

Data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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