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rticle: Matlock, MD | Storm, DE | Smolen, MD | Matlock, ME: Determining the lotic ecosystem nutrient and trophic status of three streams in eastern Oklahoma over two seasons

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Aquatic Ecosystem Health & Management

Determining the lotic ecosystem nutrient and trophic status of three streams in eastern Oklahoma over two seasons

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Abstract

Nutrient limitations in three streams in the Upper Illinois River Basin in eastern Oklahoma (Peacheater, Tyner and Battle Creek) were measured using the Matlock periphytometer in April and September, 1995. The Matlock periphytometer was also used to measure baseline primary productivity and maximum primary productivity of the three streams over two seasons. The measured maximum primary productivity was interpreted to represent the rate of periphytic growth when the nutrients are not limiting. We calculated a lotic ecosystem trophic status index using the ratio of baseline and nutrient enriched growth to MPP. This index is by definition a functional index and may provide a classification tool for lotic ecosystem trophic status. We observed fluctuations in nutrient limitations in the streams over time and detected co-limitations of nitrogen and phosphorus in two of the three streams.

Keywords: Periphyton; Co-limitation; Nitrogen; Phosphorus; Enrichment

1. Introduction

The relationships between physical and chemical stress of lotic ecosystems and characteristics of the submerged attached micro-community, or periphytic community, have been investigated for many years (Patrick, 1949; Kolkwitz and Marsson, 1967). The periphytic community has an architectural continuity from substrate to open water composed of a productive base (brown, red, green, blue-green and gold algae), a layer of macrofauna (pereitrichous ciliates, hydrozoans and bryozoans), and a secondary productive layer of diatoms (Calow and Petts, 1992). Within this community, bacteria, fungi and viruses interact as parasites, detritivores, and pathogens (Roos, 1983). In general, however, the periphytic community is characterized by some measure of the primary producers (algae) within the community. The algal component of the periphytic community is often referred to as periphyton (Roos, 1983).

The complexity of this community, the diversity of environments within the ecosystem, the logistic problems with sampling rivers, the intricacy of the interactions of the component assemblages, and the diversity of organisms within the lotic biota make the lotic ecosystem functional processes that are very difficult to investigate. Growth of the periphytic community is a function of loading and transport of nutrients in the upper reaches of the lotic ecosystems, as well as physical and hydrologic characteristics of the stream. The factors that regulate the spatial and temporal distributions of the periphytic community are poorly understood (Calow and Petts, 1992).

The objectives of this project were to quantify the response of periphytic communities in three similar

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1463-4988/99/$20.00
PII: S1463-4988(99)00022-6

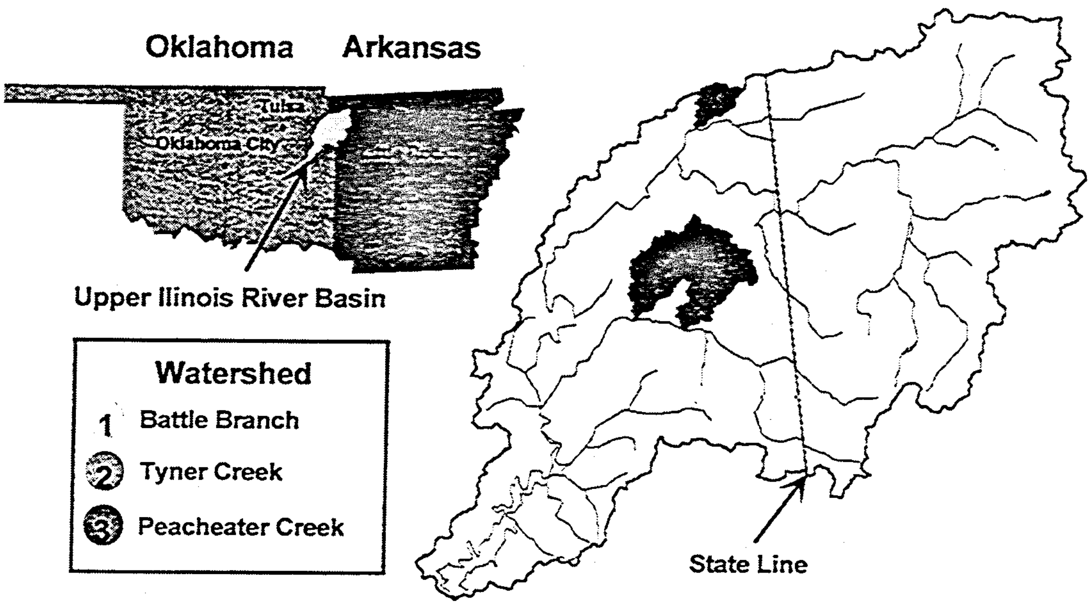

Fig. 1. Location of sample sites in eastern Oklahoma.

streams to nutrient enrichment, and to develop a lotic ecosystem trophic status index for comparing these responses. We attempted to develop a tool for characterizing the degree of impact of streams from nutrient enrichment. The lotic ecosystem trophic status index (LETSI) uses the ratio of baseline periphyton primary production (BP) to maximum potential primary production (MPP) in characterizing the stream ecosystem status. Three second-order streams in the Illinois River Basin in eastern Oklahoma were selected for investigation. The study streams were sampled using the Matlock periphytometer in April and October 1995, to determine their limiting nutrient(s) and trophic status.

2. Methods

2.1. Site description

The Upper Illinois River Basin covers approximately 400 000 ha in northwest Arkansas and northeast Oklahoma (Fig. 1). The Illinois River is a designated scenic river in Oklahoma and is a significant recreational resource for the state. Water quality in the Illinois River has been degrading at an accelerated rate for more than 20 years (Gakstatter and Katko, 1986). The primary source of degradation is nutrient enrichment; 95% of nutrient loading to the Illinois River is from non-point sources (Gakstatter and Katko, 1986).

Table 1

Historical water quality data from Battle, Tyner and Peacheater Creeks in the Illinois River Basin in eastern Oklahoma, expressed as means, minimums (Min), and maximums (Max) (mg l^{-1}) (United States Geological Services, 1991–1994; Oklahoma Conservation Commission, 1995)

Water quality	Battle Creek (1991–1994)			Peacheater Creek (1993)			Tyner Creek (1991)		
Parameter	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min
Nitrate–nitrite nitrogen	2.16	3.90	0.81	2.27	3.10	1.50	1.98	3.60	0.00
Ammonia nitrogen	0.02	0.03	0.01	0.02	0.03	0.01	–	–	–
Total phosphorus	0.13	0.46	0.08	0.07	0.28	0.02	0.04	0.01	0.11
Ortho-phosphorus	0.11	0.34	0.06	0.05	0.20	0.02	–	–	–

Table 2
Summary of land use by area (ha) for Battle, Tyner and Peacheater Creek watersheds in the Illinois River Basin in eastern Oklahoma

Land use description	Battle Creek		Peacheater Creek		Tyner Creek	
	Ha	%	Ha	%	Ha	%
Pasture and range	1414	63	4172	64	4328	68
Forest	752	34	2337	35	2054	32
Crop	8	–	1	–	6	–
Urban, homestead and transportation	64	3	43	1	8	–
Total	2238	100	6553	100	6396	100

The poultry industry represents a potential source of increased nutrient loading to the Illinois River; more than 200 million broiler chickens are reared in the Upper Illinois River Basin annually (Soil Conservation Service, 1990). The litter produced by poultry production is often applied to permanent pasture at rates based on crop nitrogen demand, which may result in excess phosphorus application and soil phosphorus build-up.

Based on the limited information available, three of the most impacted streams in the Upper Illinois River Basin (Battle, Peacheater and Tyner Creeks) were selected for study (Fig. 1). Historical water quality data from these streams are presented in Table 1. These data were compiled from the US Geological Survey Water Resources Data from water years 1991–1994 (United States Geological Services, 1991–1994), and from the unpublished data provided by the Oklahoma Conservation Commission (Oklahoma Conservation Commission, 1995). The study stream watersheds are in the Boston Mountains Ecoregion of Oklahoma, characterized by relatively high rainfall (122–127 cm annually), hilly terrain, expansive forests and savannas (Omernik, 1987). All three watersheds are similar in their physical characteristics, with a mean annual rainfall of 110 cm. The streams are fourth order, with roughly the same number of dairies, poultry houses and residences. The predominant land uses are pasture and woodland, with increasing numbers of concentrated animal feeding operations (predominantly poultry). The watershed land uses are summarized in Table 2.

Battle Creek is a tributary of the Illinois River; its watershed covers 2236 ha in the northern portion of the Illinois River Basin (Fig. 1). The predominant land uses are pasture and woodland. There are over fifty farms, with an average farm size of less than 65 ha in the watershed. The sample site is located at 94°41′30″ latitude, 36°12′45″ longitude. Peacheater Creek watershed covers about 6560 ha and is located in the central portion of the basin. The sample site is located at 94°41′15″ latitude, 35°57′15″ longitude. Tyner Creek watershed covers about 6475 ha and is adjacent to the Peacheater Creek watershed on the eastern side (Fig. 1). The sample site is located at 94°43′30″ latitude, 36°1′45″ longitude. The average temperatures in these watersheds in July range from 25 to 27°C.

2.2. Limiting nutrient determination

Limiting nutrients for the streams were determined using Matlock periphytometers (Matlock et al., 1998). Six nutrient enrichment treatments were used:

1. Nitrate, consisting of a 4.9 mM solution of $NaNO_3$ (300 ppm as NO_3) in deionized water;
2. Phosphate, consisting of a 2.6 mM solution of Na_2HPO_4 (240 ppm as PO_4^{2-}) in deionized water;
3. Nitrate and Phosphate, consisting of treatments 1 and 2 (same concentrations) combined;
4. Micro-nutrients (B, Mn, Mg, Fe, Ca, Cl, Cu, Zn, Mo, Se) from Weber et al. (1989) at 200 times the concentration cited;
5. Total nutrients, consisting of treatments 3 and 4 (same concentrations) combined; and
6. Control, consisting of deionized water, with a nominal conductivity of 30 μS cm^{-2}.

Each site was sampled using a randomized block design consisting of a treatment array of six treatments per block, and six replicates of each block per site. Each treatment block of six Matlock periphytometers was supported in a rigid aluminum frame so

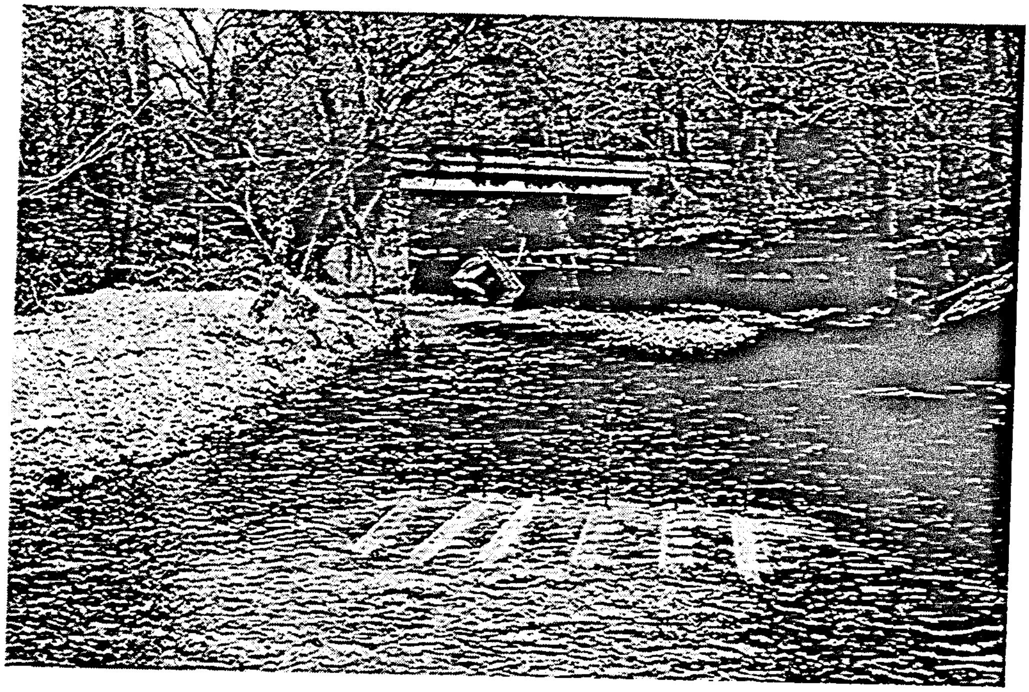

Fig. 2. Matlock periphytometer treatment arrays as deployed.

that the growth surfaces were oriented perpendicular to the channel bottom and parallel to the stream flow. The treatment arrays were secured to the stream substrate in a run 0.3 m deep in the stream above a riffle for 14 d (Fig. 2). The algal growth surfaces were protected from fish and macro-invertebrate grazing by placing an aluminum screen (8 mesh, or approximately 3 wires per cm (diameter of wire: 0.7 mm) over the face of the racks, approximately 5 cm from the glass fiber filter growth surfaces.

At the end of the growth period, the colonized filters were removed from the bottles, placed in 3 ml of 90% acetone solution, saturated with magnesium carbonate at 5°C, wrapped in aluminum foil, and transported to the laboratory for analysis. The chlorophyll was extracted from the filters for direct measurement in the laboratory using EPA Standard Method 10200H.3 (American Public Health Association, 1989). The chlorophyll *a* data from each sample site were expressed as mass (μg) per unit of exposed surface area of the filter (6.6 cm^2) for comparison. The mean chlorophyll *a* concentrations for each treatment were compared using the Waller–Duncan *K*-ratio *t* test ($\alpha = 0.20$) using SAS/STAT© (SAS Institute Inc., Cary, NC). The upper and lower 80% confidence intervals ($\alpha = 0.20$) were calculated for direct comparison of treatment mean chlorophyll *a* concentration at each site.

2.3. Lotic ecosystem trophic status index

The LETSI is the ratio of the BP (Matlock periphytometer control treatment) to the MPP (Matlock periphytometer total nutrient treatment). This value represents the proportion of MPP currently manifested in the stream. The Matlock periphytometer total nutrient treatment provides a measurement of the MPP of a stream at a given site over a given time period. The MPP, therefore, represents the level of periphytic primary productivity (measured as chlorophyll *a* production) that occurs when the nutrients are not limiting.

Reason suggests that if a single nutrient is limiting primary productivity in a stream, the ratio of an enriched treatment of that nutrient to the total nutrient treatment should approach 1.0. We evaluated the P, N, and P + N enrichment responses using the LETSI concept. The phosphorus LETSI (P-LETSI), nitrogen

Table 3
Summary of annual dairy, poultry and human populations in Battle, Tyner and Peacheater Creek watersheds in the Illinois River Basin in eastern Oklahoma (Oklahoma Conservation Commission, 1995)

Watershed	Poultry houses	Broilers (thousand)	Layers (thousand)	Others[a] (thousand)	Dairy cows	Homes
Battle Creek	29	412	0	28	415	124
Peacheater Creek	59	745	257	135	804	176
Tyner Creek	96	1692	155	60	400	194
Total	184	2849	412	223	1619	494

[a] Includes cornish hens, turkeys and pullets.

LETSI (N-LETSI), and nitrogen plus phosphorus LETSI (NP-LETSI) are the ratios of the N enriched treatment and N + P enriched treatments to the MPP, respectively.

3. Results

3.1. Watershed land use comparison

The Battle, Peacheater and Tyner Creek watersheds were similar in size and primary land-use distribution (Table 2). The predominant land use in the watersheds was pasture and range (63–68%), with substantial forest cover (32–36%). The principal difference in land uses between the three watersheds was the impact from anthropogenic activity. Tyner Creek had two to three times the number of poultry houses as Battle and Peacheater Creeks, while Peacheater Creek had twice the number of dairy cows as the other two watersheds (Table 3). Tyner Creek was the most populated by humans, followed by Peacheater and Battle Creeks.

3.2. Limiting nutrient of a lotic ecosystem

The mean chlorophyll *a* concentrations, with variances, from nutrient enrichment treatments using the Matlock periphytometer in April and September 1995 for Battle, Peacheater and Tyner Creeks are presented in Tables 4 and 5, respectively. Sample replicate numbers less than six indicate loss of samples. High flow events occurred in Battle Creek during both the sampling periods, resulting in the loss of replicates due to scouring of the filter papers. Comparisons of the treatment chlorophyll *a* means using the Waller–Duncan *K*-ratio *t* test ($\alpha = 0.20$) for Battle, Tyner, and Peacheater Creeks for April and October, 1995, are presented in Tables 6 and 7.

3.2.1. Spring sampling results

The April 1995 Battle Creek results showed a significant increase ($\alpha = 0.20$) in the chlorophyll *a* production for the nutrient enriched treatments (Waller group A, Table 6(a)). The P and N + P enriched treatments were not significantly different from the total nutrient treatment, yet they were significantly different from the control. The N treatment was neither significantly different ($\alpha = 0.20$) from the total nutrient treatment, nor was it significantly different from the control. Therefore, at $\alpha = 0.20$ it is not possible to say whether the N was truly the result of N enrichment. Based on these results, the periphytic community in Battle Creek was probably P limited in the spring.

The April 1995 Peacheater Creek results suggested a potentially co-limited system (Table 6(b)). The total, N + P and P nutrient treatment chlorophyll *a* concentrations at this site (Waller group A) were significantly higher ($\alpha = 0.20$) than the micro-nutrient and control treatments (Waller group C). However, the N-enriched treatment was also significantly higher than the control and micro-nutrient treatments (Waller group B). Adding N and/or P to this system increased the periphytic community's production of chlorophyll *a*. As with Battle Creek, the data indicate that P was principally responsible for limiting primary production, as the P treatment was the same as the total nutrient treatment. Nitrogen, however, was secondarily limiting primary production, as N enrichment increased the chlorophyll *a* production relative to the control.

The Tyner Creek data for the spring sampling period showed no significant difference ($\alpha = 0.20$)

Table 4
Chlorophyll *a* concentrations for nitrogen (N), phosphorus (P), nitrogen plus phosphorus (N and P), micro-nutrients, total nutrients, and control treatments using the Matlock periphytometer in Battle, Peacheater and Tyner Creeks, Oklahoma during the period of 8–21 April 1995

Site	Treatment	Replicate number	Mean Chl. *a* ($\mu g\ cm^{-2}$)	Standard deviation ($\mu g\ cm^{-2}$)	Coefficient of variation (%)
Battle Creek	N	5	1.16	0.64	60
	P	1	1.61	–	–
	N and P	5	1.67	0.60	36
	Micro-nutrients	5	0.48	0.76	160
	Total nutrients	2	1.98	0.39	19
	Control	6	1.05	0.30	28
Peacheater Creek	N	6	1.05	0.42	40
	P	6	1.38	0.44	32
	N and P	6	1.61	0.72	45
	Micro-nutrients	6	0.35	0.10	28
	Total nutrients	6	1.66	0.69	20
	Control	6	0.51	0.23	46
Tyner Creek	N	6	0.31	0.17	57
	P	6	0.20	0.08	42
	N and P	5	0.28	0.11	40
	Micro-nutrients	6	0.20	0.15	77
	Total nutrients	6	0.33	0.10	29
	Control	6	0.21	0.14	65

Table 5

Chlorophyll *a* concentrations for nitrogen (N), phosphorus (P), nitrogen plus phosphorus (N and P), micro-nutrients, total nutrients, and control treatments using the Matlock periphytometer in Battle, Peacheater and Tyner Creeks, Oklahoma during the period of 20 September–3 October 1995

Site	Treatment	Replicate number	Mean Chl. *a* ($\mu g\ cm^{-2}$)	Standard deviation ($\mu g\ cm^{-2}$)	Coefficient of variation (%)
Battle Creek	N	4	0.33	0.05	17
	P	2	0.24	0.26	109
	N and P	4	0.63	0.36	56
	Micro-nutrients	2	0.21	0.09	42
	Total nutrients	4	0.57	0.14	25
	Control	4	0.28	0.17	62
Peacheater Creek	N	6	0.55	0.18	33
	P	6	0.35	0.06	16
	N and P	6	0.55	0.55	49
	Micro-nutrients	6	0.23	0.23	24
	Total nutrients	6	0.69	0.69	50
	Control	6	0.28	0.04	11
Tyner Creek	N	6	1.09	0.43	40
	P	6	1.06	0.20	19
	N and P	5	1.01	0.24	24
	Micro-nutrients	5	0.45	0.21	46
	Total nutrients	6	0.98	0.40	41
	Control	6	0.55	0.19	35

Table 6
Waller–Duncan *K*-ratio *t* test ($\alpha = 0.20$) for chlorophyll *a* collected using the Matlock periphytometer from 8–21 April 1995. Means with the same letter are not significantly different: (a) Battle Creek, (b) Peacheater Creek, and (c) Tyner Creek

Waller grouping		Treatment	Mean (μg cm^{-2} Chl. *a*)	Number of replicates
(a) Battle Creek				
	A	Total	1.98	2
	A	N and P	1.67	5
	A	P	1.61	1
B	A	N	1.16	5
B		Control	1.05	6
B		Micro	0.48	5
(b) Peacheater Creek				
	A	Total	1.66	6
	A	N and P	1.61	6
B	A	P	1.38	6
B		N	1.05	6
	C	Control	0.51	6
	C	Micro	0.35	6
(c) Tyner Creek[a]				
	A	N	0.31	6
	A	P	0.20	6
	A	N and P	0.28	6
	A	Total	0.33	6
	A	Control	0.21	6
	A	Micro	0.20	6

[a] The Waller–Duncan *K*-ratio *t* test could not be performed on the Tyner Creek data collected in the spring due to a very low value of *F* (less

Table 7
Waller–Duncan *K*-ratio *t* test ($\alpha = 0.20$) for chlorophyll *a* collected using the Matlock periphytometer from September 20–October 3, 1995. Means with the same letter are not significantly different: (a) Battle Creek, (b) Peacheater Creek, and (c) Tyner Creek

Waller grouping		Treatment	Mean (μg cm^{-2} Chl. *a*)	Number of replicates
(a) Battle Creek				
	A	N and P	0.63	4
B	A	Total	0.57	4
B	A	N	0.33	4
B	A	Control	0.28	4
B	A	P	0.24	2
B		Micro	0.21	2
(b) Peacheater Creek				
	A	Total	0.69	6
	A	N and P	0.55	6
B	A	N	0.55	6
B		P	0.35	6
	C	Control	0.28	6
	C	Micro	0.23	6
(c) Tyner Creek				
	A	N	1.09	6
	A	P	1.06	6
	A	N and P	1.01	5
	A	Total	0.98	6
B		Control	0.55	6
B		Micro	0.45	5

Table 8
Lotic ecosystem trophic status indices (LETSI's) reflecting the ratios of the control, nitrogen and phosphorus enriched treatment chlorophyll *a* concentrations (μg cm^{-2}) with the total nutrient concentrations for Matlock periphytometer samples collected from Battle, Peacheater and Tyner Creeks, Oklahoma, in spring (8–21 April) and fall (20 September–3 October 1995)

Season	Sample site	Mean productivity[a]	LETSI	P-LETSI	N-LETSI	N and P-LETSI
Spring	Battle Creek	1.054	0.60	0.92	0.66	0.84
	Peacheater Creek	0.506	0.30	0.83	0.63	0.97
	Tyner Creek	0.211	0.64	0.60	0.92	0.83
Fall	Battle Creek	0.281	0.49	0.42	0.57	1.10
	Peacheater Creek	0.284	0.41	0.51	0.81	0.81
	Tyner Creek	0.548	0.56	1.08	1.12	1.04

[a] Measured as chlorophyll *a* production (μg cm^{-2}) over 13 d on a control surface.

in the response of the periphytic community to nutrient enrichment (Table 6(c)). The implication is that some factor other than nutrients was limiting the periphytic primary production in the stream. The most probable limiting factor is light, as the canopy at this site was relatively closed, although the possibility exists that some micro-nutrient or vitamin not present in the total or micro-nutrient treatments was limiting the growth.

3.2.2. Fall sampling results

The October 1995 Battle Creek results showed no significant difference ($\alpha = 0.20$) in the response of the periphytic community to nutrient enrichment (Table 7(a)). While there were two Waller groups (A and B), the only difference in the groups was the inclusion of micro-nutrients or N + P treatments. The implication is that some factor other than nutrients was limiting the periphytic primary production in the stream. However, the loss of replicates in all treatments due to high flow compromised the statistical inferences of these data. While it is possible that light is the limiting factor, it is more likely that repeated sampling will detect a nutrient limitation.

The October 1995 Peacheater Creek results were similar to the April results, with the exception that N was the primary limiting nutrient and P the secondary limiting nutrient (Table 7(b)). The N treatment response was not significantly different ($\alpha = 0.20$) from that of the total or N + P treatments, though the phosphorus treatment was significantly different. However, the phosphorus-enriched treatment was also significantly higher than the control and micro-nutrient treatments (Waller group B). Adding N and/or P to this system increased the periphytic community production of chlorophyll *a*, suggesting a co-limited system.

The October Tyner Creek data showed significant increases in chlorophyll *a* concentration resulting from nutrient enrichment (Table 7(c)). There was no detectable increase in the primary production resulting from micro-nutrient enrichment (Waller group B). Nitrogen and/or P limited the primary production in Tyner Creek during the sample period in apparently equal proportions.

With the exception of Tyner Creek in April 1995, it is apparent that nutrient enrichment with N and/or P increased the chlorophyll *a* production in all the streams in April and October 1995. However, given this data set alone, it is difficult to assess which nutrient (N or P) is exerting the most influence on primary productivity. The data suggest that micro-nutrients are not limiting in these lotic ecosystems.

3.3. Lotic ecosystem trophic status indices

3.3.1. Spring lotic ecosystem trophic status index results

In the spring (8–21 April 1995), Battle and Tyner Creeks were at approximately 60% of MPP, while Peacheater Creek was at 30% MPP (Table 8). However, Battle and Peacheater Creeks had similar MPP values (1.98 and 1.66 mg cm^{-2} chlorophyll *a*, respectively), while Tyner Creek MPP was much lower (0.33 mg cm^{-2}). Comparison of the nutrient treatment LETSIs for both Battle and Peacheater Creeks suggested that P was the nutrient primarily responsible for limiting the growth of the periphytic

Table 9
Summary of limiting nutrient status of Battle, Peacheater and Tyner Creeks in the Spring and Fall of 1995, based on LETSI analysis (Pr: primary; S: secondary)

Season	Site	Limiting nutrient(s)		
		P	N	N and P
Spring	Battle Creek	Pr		
	Peacheater Creek	Pr	S	
	Tyner Creek		Pr	
Fall	Battle Creek			Pr
	Peacheater Creek	S	Pr	
	Tyner Creek	Pr	Pr	

community during the sample period. The LETSI analysis suggests that N was secondarily limiting chlorophyll *a* production in Peacheater Creek (Table 9); this analysis is supported by the Waller–Duncan mean comparison test (Table 6). Based on the LETSI analysis, the periphytic community in Tyner Creek was N limited, though the results of the Waller–Duncan comparison (Table 6(c)) demonstrated that the means of all six treatments were not significantly different from each other.

3.3.2. Fall lotic ecosystem trophic status index results

In the Fall (20 September–3 October 1995), Peacheater Creek was at 41% MPP, while Battle and Tyner Creeks were at 49 and 56% MPP, respectively. Battle and Peacheater Creeks had similar BP and MPP, while Tyner Creek BP and MPP were considerably higher (Table 8). Primary productivity in Peacheater Creek was primarily N limited in the fall, with secondary P limitation. In Battle and Tyner Creeks, periphyton appeared to be co-limited (Table 8). These results are consistent with the Waller–Duncan comparison of the means (Table 7). In the fall, periphyton in the Battle Creek responded to both N and P enrichment, but not to N or P individually. While this phenomenon might be an artifact, it might also be the result of low-level community co-limitation by N and P. When the periphytic community was enriched with N or P alone, a limitation in the alternate nutrient may have been induced. Enrichment with both N and P resulted in increased chlorophyll *a* production, suggesting that both nutrients were limiting growth. Nutrient enrichment of Tyner Creek in the Fall elicited a significant response, though the differences between individual nutrient enrichment treatments were not significant. Tyner Creek periphyton responded similarly to nutrient enrichment with N, P, N + P and total nutrients.

4. Discussion

The LETSI represents the proportion of maximum potential productivity manifested in the stream during the sample period. The theoretical LETSI ranges from 0 to 1, from the lowest to highest degree of impact from nutrient loading. A stream with a LETSI of 0.50 can be said to be at 50% of its MPP, or at half the potential growth based on nutrient availability. A LETSI of 1.0 suggests that the stream is approaching its maximum potential productivity, and adding nutrients will not increase the chlorophyll *a* production in the periphytic community. The LETSI is a relatively imprecise measure of assimilative capacity, and should not be over-interpreted; the variability of the components of the LETSI is relatively high, yet it is difficult to express this variability in a ratio.

Analyzing the limiting nutrients using the LETSI differs from previous methods by comparing responses to nutrient enrichment to maximum potential responses, providing a perspective for comparison (Table 9). The ratio of a nutrient enrichment response to the total provides a comparative analysis of the role of that nutrient in limiting the primary productivity. For example, N-LETSI of 1.0 suggests that the N-enriched treatment response was the same as the total nutrient enrichment response. In this case, N would be the limiting nutrient.

The LETSI was designed as a tool for comparing watersheds with respect to the impact of nutrient enrichment on periphytic productivity. While considerably more data must be collected before generalizations may be made regarding the significance of the LETSIs in a basin, some speculation is possible and perhaps useful. In the spring sampling period, Battle and Tyner Creeks had the same LETSIs (60% of MPP), yet Tyner Creek baseline productivity (0.21 mg cm^{-2}) was 20% of Battle Creek's baseline productivity (1.05 mg cm^{-2}) and Tyner Creek's MPP (0.33 mg cm^{-2}) was less than 17% of Battle Creek's MPP (1.98 mg cm^{-2}). It would be inaccurate to assert that these two streams were equally affected by nutrient loading. A speculative interpretation of these data would be that Tyner Creek was less productive than Battle Creek due to variables other than nutrient loading, and was proportionally affected by nutrients. An alternative hypothesis is that the periphytic community in Battle Creek evolved with a higher resource availability, resulting in a higher primary productivity, while Tyner Creek periphyton are less efficient in utilizing episodic increases in nutrient availability. It is possible to conclude, however, that for the spring sample period, Battle Creek was more productive and generally more enriched by nutrients than Peacheater and Tyner Creeks.

During the Fall sampling period, Battle and Peacheater Creeks were equally productive and nutrient enriched. Tyner Creek was twice as productive, yet the degree of impact was proportionally similar to the other two streams. However, caution must be used in comparing these data. If nothing else, these data illustrates temporal variability in nutrient loading and stream responses to environmental conditions. Many other factors such as light, temperature, flow rate and suspended sediment concentration may exert more influence on periphyton growth than nutrients. This work does suggest that the LETSI might be useful in assessing the most sensitive season for nutrient loading to the stream. However, additional confirmation is appropriate before direct conclusions may be drawn from the comparison of watershed data.

Classic nutrient limitation theory is based on the response of individual organisms or monocultures of plants to nutrient limitations, and states that only one nutrient limits the growth of a plant at a time (Lawes and Gilbert, 1880). The periphytic community is not a monoculture, however, and responds to nutrient enrichment in a more complex manner. The periphytic community in an episodically nutrient enriched stream may have populations of algae that sequester nutrients during times of excess, via luxury consumption, releasing these nutrients to the community during times of nutrient stress.

The co-limitation of nutrients observed in Battle Creek during the fall sampling period suggested that both N and P were simultaneously limiting. When phosphorus was added in excess, N limitation was immediately induced and vice versa for N. However, when N and P were added in excess simultaneously, neither was limiting, and primary productivity increased. These conclusions must be tempered by considering that nutrient limitations can be induced by providing another nutrient in excess; the response of the periphytic community to nutrient stimulation may be considerably different than to the absence of a nutrient.

The response of Tyner Creek to nutrient enrichment in the Fall suggests that the Tyner Creek periphyton community reacted facultatively to the nutrients that were enriched. It is possible that some components of the periphytic community stored molecular N and others stored molecular P (presumably during luxury consumption), hence when one or the other nutrient was present the respective periphytic community component could respond accordingly. The response suggests that components of the periphytic community interact in order to collectively increase the primary production through population-level selective uptake and sequestering of nutrients.

The proposed LETSI index is analogous to the algal growth potential test (AGPT) using the *Selenastrum capricornutum* bottle assay in lakes (Raschke and Schultz, 1987), except the LETSI uses indigenous algae rather than a standard test organism. This assay measures the growth of *S. capricornutum* in bottles filled with lake water (control) and nutrient-enriched media to determine the ratio of the baseline growth to MPP. As with the index we propose, Raschke and Schultz's assay is based on the premise that the maximum yield is proportional to the amount of nutrient which is present and biologically available in minimal quantity with respect to the growth requirement of algae (American Public Health Association, 1989). A trophic status index for lentic ecosystems was developed based on the AGPT, and was applied to lakes and reservoirs in the south-eastern US for over a decade (Raschke and Schultz, 1987).

As with any broadly applied measure of community productivity, there are many sources of variability that must be recognized and addressed when using the LETSI method. These sources include grazing, turbulent or laminar scouring, light limitation, siltation and temporal fluctuations in stream velocities. The growth surfaces were protected from fish and macroinvertebrate grazing by placing an aluminum screen over the surface of the treatment blocks. The screen reduced the direct light by approximately 12% for all treatments (Matlock et al., 1998). Sites were selected to avoid scouring under normal (base) flow. Siltation was minimized by orienting the growth surface perpendicular to the stream surface. High flow events were avoided as much as possible by sampling during low rainfall seasons. The aluminum screen reduced the flow across the growth surfaces, and also reduced scouring. All treatment blocks were placed in similar light environments to reduce the variability associated with direct and indirect light exposure.

Growth on each treatment replicate is a function of colonization composition and rate, light intensity and duration, temperature, and limiting resource competition. Light and temperature were standardized across experimental blocks. Virtually all periphytic growth in a stream reach is the result of immigration and colonization of periphytic propagules which emigrated from upstream (Allan, 1995). Composition and rate of colonization, and to a lesser degree competition for limiting resources, are stochastic processes; they were assumed to be responsible for the major part of treatment variability. The number of replicates was selected to provide an acceptable degree of confidence in the treatment response. The control treatment response for a sample station is a measure of ambient primary productivity at a site, while nutrient enriched treatment response reflects the potential level of periphyton growth in the stream when N and/or P is elevated.

Morin and Cattaneo (1992) reported field studies "will only detect differences in periphyton abundance or productivity where the means differ by a factor of 2 or more." In our study, the periphytic chlorophyll *a* concentration resulting from P-enrichment was twice the N-enriched and control chlorophyll *a* concentrations, consistent with Morin and Cattaneo's (1992) analyses of the variability inherent to periphytic sampling methods. The sensitivity of this method could likely be enhanced significantly by increasing the replicate number to 20 or more (Morin and Cattaneo, 1992). Periodic deployments of the Matlock periphytometer throughout the year and over multiple years could be used to detect seasonal and inter-annual changes in resource limitation.

Acknowledgements

Research reported in this investigation was supported in part by the US Environmental Protection Agency, the Oklahoma Conservation Commission, the United States Department of Agriculture—National Needs Fellowship Program, the Oklahoma Agricultural Experiment Station and Oklahoma Cooperative Extension Service. This research is a contribution to United States Department of Agriculture—Cooperative State Research Service Regional Project S-249. The authors would like to give a special note of appreciation to the United States Department of Agriculture—Hydrology Research Laboratory in Stillwater, Oklahoma, for their generous assistance and use of facilities.

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