

Effects of Nutrient Enrichment and Flood Frequency on Periphyton Biomass in Northern Ozark Streams¹

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Ambient nutrient concentrations (TN and TP) and periphyton biomass (Chl a) were measured every 2 wk during March–November in 1985 and 1986 at 22 sites on 12 streams in the northern Ozarks, Missouri. Benthic Chl a was positively correlated in both years with log TN ($R^2 = 0.58, 0.60$) and with log TP ($R^2 = 0.47, 0.60$). When sites were grouped by the degree of enrichment and plotted over time, benthic Chl a decreased at all sites after flood events, but rebounded more rapidly at highly enriched sites. Differences in recovery following flooding were most obvious in fall 1986, when both high and moderately enriched sites exhibited similar biomass accrual patterns, reaching mean benthic Chl a of 397.4 and 321.1 $\text{mg}\cdot\text{m}^{-2}$, respectively, within 42 d after a catastrophic flood. In contrast, average benthic Chl a at nutrient-poor sites reached a maximum level of 76.8 $\text{mg}\cdot\text{m}^{-2}$ within 28 d after flooding, suggesting that maximum standing crops are influenced by both nutrient supply and the length of the flood-free period.

Les concentrations ambiantes en matières nutritives (NT et PT) et la biomasse de périphyton (Chl a) ont été mesurées toutes les deux semaines en 1985 et 1986, de mars à novembre, en 22 endroits situés dans 12 cours d'eau du nord des Ozark, au Missouri. On a établi une corrélation positive, au cours de ces deux années, entre la Chl a benthique et le log NT ($R^2 = 0,58, 0,60$) et le log PT ($R^2 = 0,47, 0,60$). Après avoir regroupé les données en fonction de l'enrichissement en matières nutritives et tracé les courbes correspondant aux résultats en fonction du temps, on a noté une diminution de la Chl a benthique dans tous les sites à la suite d'inondations, mais ce taux a augmenté plus rapidement aux endroits très riches en matières nutritives. Les différences de récupération à la suite d'inondations ont été plus évidentes à l'automne de 1986, où les sites fortement et modérément enrichis ont présenté des profils similaires d'accroissement de la biomasse, pour atteindre respectivement la concentration moyenne de Chl a benthique, soit 397,4 et 321,1 $\text{mg}\cdot\text{m}^{-2}$, dans les 42 jours suivant une inondation catastrophique. Par contraste, la Chl a benthique dans des sites pauvres en matières nutritives a atteint un niveau maximal de 76,8 $\text{mg}\cdot\text{m}^{-2}$ dans les 28 jours suivant une inondation, ce qui laisse à penser que les populations exploitables sont tributaires de la disponibilité en matières nutritives ainsi que de la durée des périodes exemptes d'inondation.

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Nutrient enrichment experiments have demonstrated that nitrogen or phosphorus additions can stimulate periphyton growth in streams (Stockner and Shortreed 1978; Peterson et al. 1983; Grimm and Fisher 1986; Lohman et al. 1991). In regional studies, however, attempts to explain differences in periphyton biomass among streams by differences in nutrient concentrations have not shown clear relationships. Correlations between periphyton biomass and ambient nutrient concentrations have been noted among streams within regions in Japan (Aizaki and Sakamoto 1988) and New Zealand (Biggs and Close 1989), but no such relationship was found in two studies in the United States (Jones et al. 1984; Welch et al. 1988). Thus, whereas models relating phytoplankton biomass and nutrients have been highly successful lake management tools (e.g. Dillon and Rigler 1974; Jones and Bachmann 1976; Canfield 1983), empirical correlation may not be a reliable method for establishing nutrient guidelines in streams (Welch et al. 1988, 1989).

The importance of disturbance in stream ecosystems may explain why strong nutrient–biomass relationships have not been found in stream studies. Disturbance, most often by flooding, has been described as the dominant organizing factor in streams (Resh et al. 1988), and the dramatic effect of severe floods on periphyton biomass has been well documented (Douglas 1958; Tominaga and Ichimura 1966; Sumner and Fisher 1979; Rounick and Gregory 1981; Freeman 1986; Power and Stewart 1986; Fisher and Grimm 1988; Biggs and Close 1989; Grimm and Fisher 1989). In regions where streams are subject to large and frequent flood events, the effects of nutrient enrichment on periphyton growth may be obscured by resetting floods that prevent biomass accrual. If so, the length of flood-free periods may be the single most important factor in determining levels of periphyton biomass (Tett et al. 1978; Fisher and Grimm 1988; Biggs and Close 1989; Grimm and Fisher 1989).

Grimm and Fisher (1986) have hypothesized that nutrients regulate periphyton accrual in streams but that maximum standing crops are primarily a function of flood frequency. They predicted that, in the absence of other limiting factors, rates of biomass accrual should be greater in nutrient-rich than in nutrient-poor streams but that given sufficient time without a resetting flood, periphyton biomass in all streams should be

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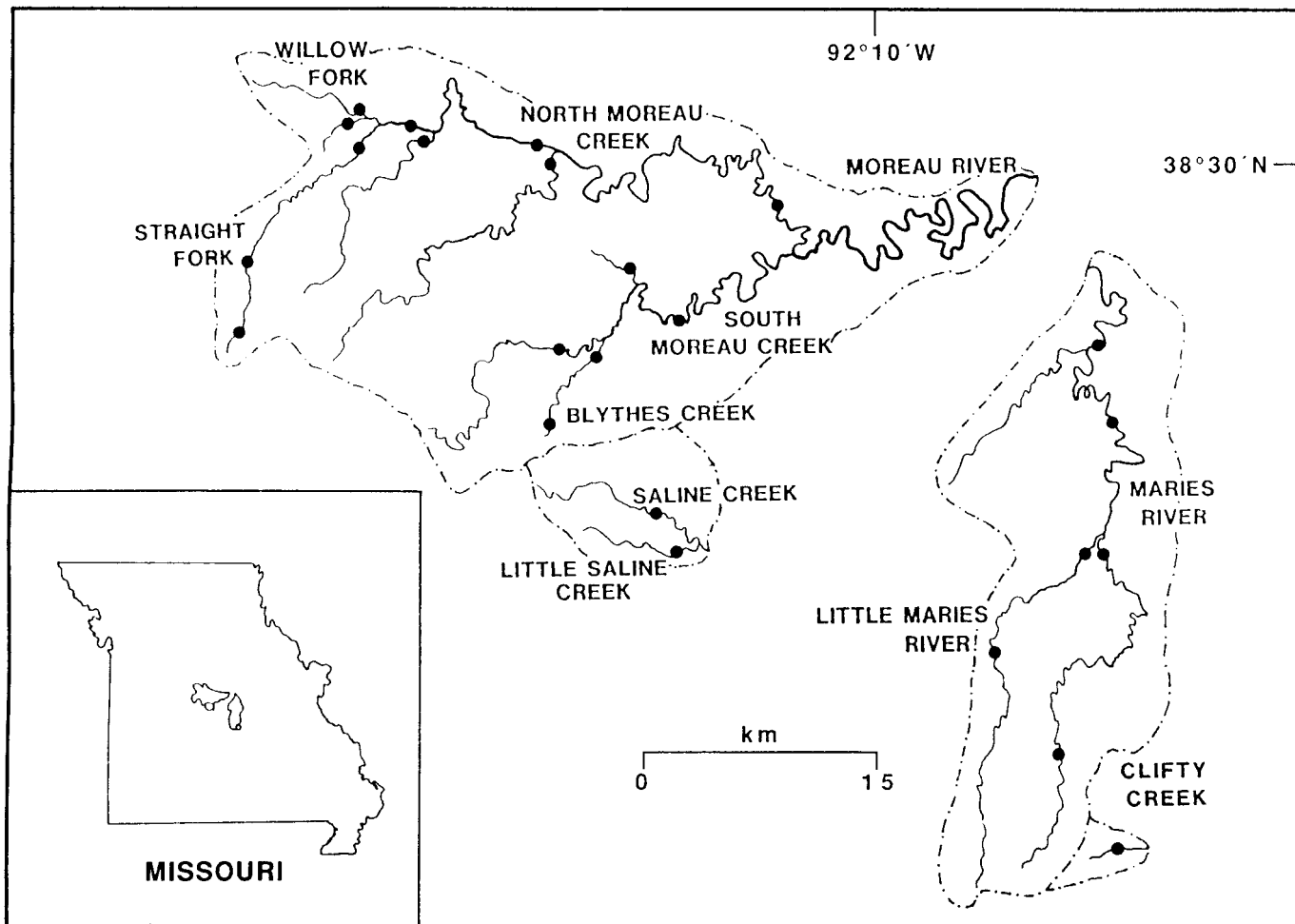


FIG. 1. Twenty-two stream sites in the northern Ozark Plateau sampled during 1985–86.

similar. This hypothesis suggests that whether differences in biomass among streams can be explained by differences in nutrients may well depend on both the interval between floods and the ambient nutrient concentrations. Detecting a nutrient effect on periphyton growth would seem most likely in a region where streams have a broad range of nutrient regimes and where flood-free periods are sufficient for substantial biomass accrual, but not so long that factors other than nutrients limit biomass.

In this study, we investigated the relation of nutrients to periphyton biomass in streams of the northern Ozarks. Our objectives were to determine whether differences in periphyton biomass among streams could be explained by differences in ambient nutrient concentrations and to relate temporal changes in periphyton biomass to nutrients and flood frequency. A catastrophic flood, followed by a prolonged flood-free period, also allowed us to conduct a fortuitous natural experiment comparing rates of periphyton accrual among streams with varying nutrient concentrations and to test the predictions of Grimm and Fisher's (1986) model of biomass accrual.

Description of Study Sites

Nutrient and periphyton data were collected over a 2-yr period at 22 sites on 12 streams in the northern Ozarks, Missouri (Fig. 1). Nineteen sites were located within the drainage basins of the Maries and Moreau rivers, two of the larger streams draining the region. The Maries River is a fourth-order

tributary of the Osage River and the Moreau River is a fifth-order tributary of the Missouri River. Three other sites were located within two watersheds (Saline and Clifty creeks) adjacent to the Maries and Moreau river drainage basins.

Drainages of the Maries and Moreau rivers reflect the transitional nature of the northern Ozark region. The area drained by the Maries River is characterized by deeply dissected topography, similar to the Ozark Plateau, whereas the Moreau River watershed more closely resembles the till plains of northern and western Missouri. Bedrock geology in both watersheds is predominantly Jefferson City limestone and dolomite of lower Ordovician age (Collier 1953; Missouri Department of Natural Resources 1984). Forest covers greater than 50% of the Maries River watershed; row crop and pasture predominate in the Moreau River watershed. Urban area makes up less than 5% of both watersheds. Presettlement vegetational cover was forest in the Maries River watershed and a mosaic of forest and prairie in the Moreau River watershed (Schroeder 1981).

Methods

Sample Collection, Water Chemistry, and Chlorophyll *a* Analysis

Sites were visited over three consecutive days every 2 wk during March–November in 1985 and 1986. A composite water sample, from middepth at three intervals across the stream, was collected at each site. Thirty-eight samples were collected at

TABLE 1. Mean annual TP, TN, and benthic Chl *a* at 22 sites on 12 streams in the northern Ozarks. Sites were classified as high, moderate, or unenriched based on TP concentrations, with the exception of Maries River, site 1, which was classified as moderately enriched based on known point-source additions not reflected in the ambient nutrient concentrations.

	TP ($\mu\text{g}\cdot\text{L}^{-1}$)		TN ($\mu\text{g}\cdot\text{L}^{-1}$)		Benthic Chl <i>a</i> ($\text{mg}\cdot\text{m}^{-2}$)	
	1985	1986	1985	1986	1985	1986
High enrichment						
Blythes Creek						
Site 1	3264	2923	9188	7682	216.7	182.2
Site 2	288	411	947	1024	100.6	146.9
Straight Fork						
Site 1	2447	1825	4509	3758	67.6	113.9
Site 2	554	395	1484	999	123.9	107.7
Willow Fork	1073	713	2080	2116	56.4	83.4
North Moreau Creek						
Site 2	212	240	872	974	46.8	70.0
Moderate enrichment						
South Moreau Creek						
Site 1	52	47	450	467	29.2	61.0
Site 2	79	93	515	436	59.9	85.9
Straight Fork						
Site 3	104	62	574	521	76.8	81.6
Smiths Creek	81	44	643	414	35.9	54.1
Burris Fork	70	70	428	614	28.4	77.3
North Moreau Creek						
Site 1	101	82	603	498	30.6	41.5
Site 3	98	125	621	773	37.7	30.1
Little Saline Creek	30	28	516	550	50.8	86.6
Maries River						
Site 1	17	14	276	186	37.0	78.6
Site 4	32	34	319	306	39.9	71.6
Low enrichment						
Maries River						
Site 2	16	19	304	284	39.9	44.4
Site 3	15	19	329	269	59.8	50.9
Little Maries River						
Site 1	14	13	229	210	54.9	45.0
Site 2	15	15	283	259	33.2	39.9
Saline Creek	19	19	199	166	31.3	39.4
Clifty Creek	6	6	148	159	10.3	20.1

each of the 22 sites over the 2-yr period. For convenience, values averaged across the March–November period are referred to as mean annual values.

Nutrient concentrations were measured as total phosphorus (TP) and total nitrogen (TN). TP was determined using the ascorbic acid method after persulfate oxidation (Prepas and Rigler 1982). TN was analyzed by cadmium reduction after persulfate oxidation (D'Elia et al. 1977). Periphyton samples were collected on each sampling date for analysis of chlorophyll *a* (Chl *a*). Periphyton within a 5.3-cm² area was scraped from five rocks collected along a transect across a riffle at each site. Each scraping was washed into a scintillation vial with distilled water and later rinsed onto a Gelman type A/E glass fiber filter. Chl *a* was extracted by placing filters in a 50:50 mixture of dimethyl sulfoxide (DMSO) and 90% acetone in the dark for 24 h (Shoaf and Lium 1976). After extraction, Chl *a* was determined fluorometrically and corrected for phaeopigments by acidification (Knowlton 1984). Samples analyzed before July 1985 were not acidified; however, a good correlation was found between Chl *a*, corrected for phaeopigments, and unacidified samples analyzed between July 1985 and November 1986 ($\text{Chl } a_{\text{acidified}} = 0.41 + 0.86 \text{ Chl } a_{\text{unacidified}}$, $R^2 = 0.98$,

$p \leq 0.0001$, $n = 2820$). This equation was used to estimate Chl *a*, corrected for phaeopigments, from unacidified samples analyzed before July 1985.

Regression Analysis

Mean annual density of benthic Chl *a* and mean annual concentrations of TN and TP were calculated for each site. Chl *a* values $< 2.0 \text{ mg}\cdot\text{m}^{-2}$ were considered the result of recent flooding and were not included in calculating means. To normalize nutrient concentrations, log-transformed values of mean TP and TN were used in linear regressions of each nutrient against Chl *a*. Separate models were constructed for each year and covariance analysis used to test for differences between years.

Temporal Patterns in Benthic Chl *a*

Based on mean annual TP concentrations (Table 1), sites were classified as high enrichment (six sites affected by secondarily treated sewage effluent), moderate enrichment (10 sites, most receiving some enrichment from agricultural land use activities), and low enrichment (six sites draining primarily

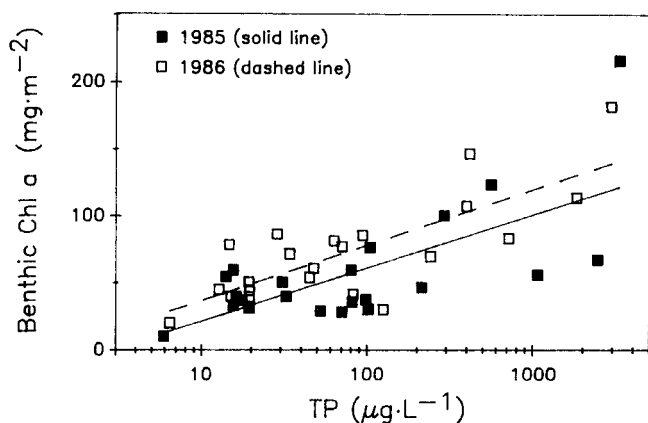
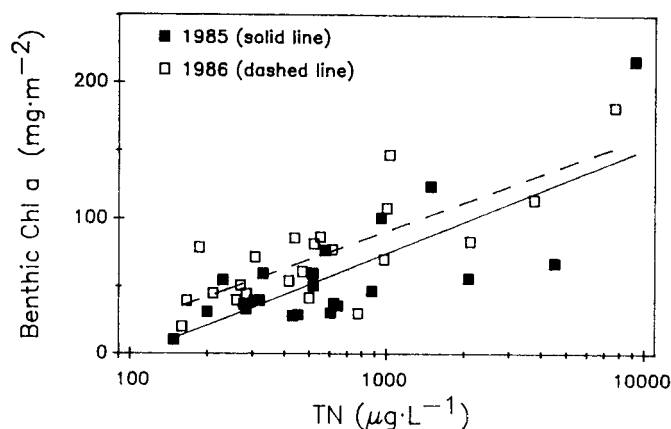


FIG. 2. Regressions of log TN and log TP against benthic Chl *a* using annual means (March–November) for 1985 and 1986 from 22 stream sites in the northern Ozark Plateau.

forested watersheds). One site (Maries River, site 1), which would have been characterized as low enrichment based solely on TP concentration, was placed in the moderately enriched category. Chloride and sulfate concentrations 1.5–3 times higher than at downstream sites on the Maries River indicated that chemical conditions at this site were influenced by a wastewater discharge located 20 km upstream and that TN and TP supply were likely higher than that suggested by ambient concentrations. Mean annual TP was 212–3264 $\mu\text{g}\cdot\text{L}^{-1}$ in enriched sites, 14–125 $\mu\text{g}\cdot\text{L}^{-1}$ in moderately enriched sites, and 6–19 $\mu\text{g}\cdot\text{L}^{-1}$ in sites of low enrichment. Mean benthic Chl *a* on each sampling date was calculated for each level of enrichment and plotted over time. Because bimonthly sampling was conducted over 3-d periods, not all sampling reflected similar flood histories. To illustrate the effects of nutrient enrichment on periphyton biomass in the context of flood frequency, benthic Chl *a* over time was compared from sites on three streams (Blythes, Little Saline, and Saline creeks) considered representative of the high-, moderate-, and low-nutrient classifications. These streams were sampled on the same dates. Their watersheds are adjacent, receive similar rainfall, and are subject to similar flood frequencies. Weekly rainfall, based on data from a recording station located near the source of all three streams (NOAA 1985, 1986), was used as a measure of flood frequency.

Postflood Recovery of Periphyton

Decimation of periphyton standing crops following a catastrophic flood allowed us to compare postflood recovery of

periphyton among stream sites of high, moderate, and low nutrient enrichment. Rainfall of 30–40 cm within a 2-wk period in September–October 1986 occurred throughout the northern Ozarks (NOAA 1986), and streams at all study sites were bank-full or out of their banks during the first week in October. Benthic Chl *a* at 20 of 22 sites, measured within 2–3 d after flood waters receded, was $<0.1 \text{ mg}\cdot\text{m}^{-2}$. We continued to measure Chl *a* at 2-wk intervals for 6 wk following the flood, during which time no substantial increase in discharge occurred. Growth curves for groups of high-, moderate-, and low-nutrient sites were fitted by polynomial regression in which the intercept term was omitted.

Results

Regression Analysis

Benthic Chl *a* was positively correlated with log-transformed concentrations of TN in both 1985 and 1986 (Fig. 2):

- (1) $\text{Chl } a = 76.9 \log \text{ TN} - 155.8$
 $R^2 = 0.58, p \leq 0.001, n = 22$ (1985)
- (2) $\text{Chl } a = 69.3 \log \text{ TN} - 116.7$
 $R^2 = 0.60, p \leq 0.001, n = 22$ (1986).

Covariance analysis indicated that the slopes were not significantly different between years ($F = 0.15, p = 0.70$) but that intercepts were significantly different ($F = 4.93, p = 0.03$). Similar relationships were present between Chl *a* and log TP (Fig. 2):

- (3) $\text{Chl } a = 39.9 \log \text{ TP} - 18.1$
 $R^2 = 0.47, p \leq 0.001, n = 22$ (1985)
- (4) $\text{Chl } a = 41.1 \log \text{ TP} - 4.1$
 $R^2 = 0.60, p \leq 0.001, n = 22$ (1986).

Slopes of these equations did not differ significantly ($F = 0.22, p = 0.90$) but intercepts were different between years ($F = 3.73, p = 0.06$). Higher intercepts in both Chl *a*–log TN and Chl *a*–log TP regressions reflect higher overall levels of benthic Chl *a* in 1986 than in 1985.

Temporal Patterns in Benthic Chl *a*

Benthic Chl *a* was consistently greater at sites classified as highly enriched than at sites of low and moderate enrichment throughout most of 1985–86 (Fig. 3). Greatest benthic Chl *a* was seen during spring and fall in both years at all three types of sites. During spring and fall, average benthic Chl *a* commonly exceeded $150 \text{ mg}\cdot\text{m}^{-2}$ at highly enriched sites. Maximum Chl *a* measured at individual sites over 1985–86 was $41.5\text{--}678.1 \text{ mg}\cdot\text{m}^{-2}$ and the frequency of benthic Chl *a* $>150 \text{ mg}\cdot\text{m}^{-2}$ ranged from 0 to 42.1% (Table 2).

Temporal patterns in benthic Chl *a* among the three streams with similar flood histories were also characterized by peaks in spring and fall (Fig. 4). High rainfall caused intense flooding in November 1985 and late September–October 1986, resulting in benthic Chl *a* $<1.0 \text{ mg}\cdot\text{m}^{-2}$ at all three streams. Lesser rainfall events in June 1985 and April, May, and July 1986 also coincided with large reductions in benthic Chl *a*. Postflood recovery of benthic Chl *a* was always most rapid in the highly enriched stream (Blythes Creek) and slowest in nutrient-poor Saline Creek. Over the 2-yr sampling period, benthic Chl *a* $>150 \text{ mg}\cdot\text{m}^{-2}$ occurred on nine of 38 sampling dates at Blythes Creek and on four dates at moderately enriched Little

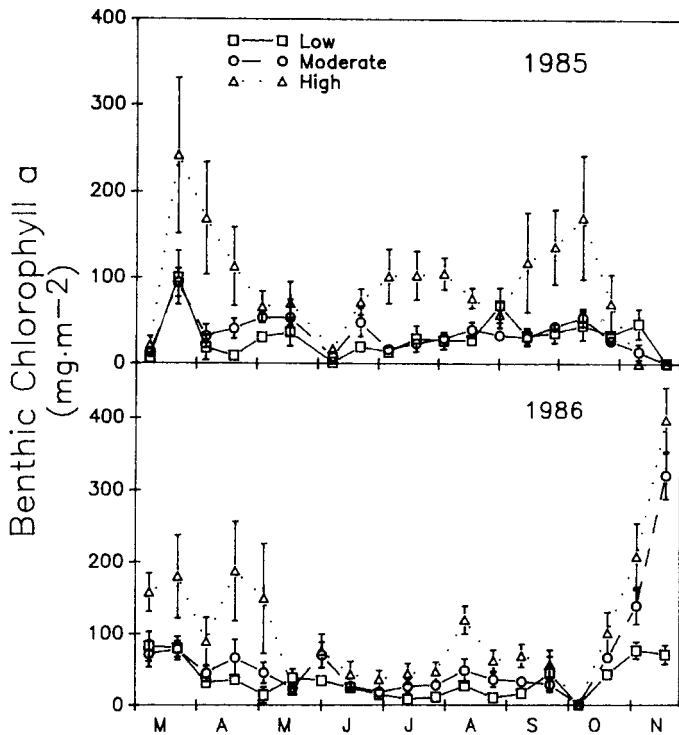


FIG. 3. Temporal changes in benthic Chl *a* in stream sites of high, moderate, and low nutrient enrichment in the northern Ozark Plateau. Values are means \pm SE; $n = 6$ for high- and low-enrichment sites and $n = 10$ for moderate-enrichment sites.

Saline Creek. The maximum level of benthic Chl *a* recorded at Saline Creek was $109.0 \text{ mg}\cdot\text{m}^{-2}$.

Periphyton Accrual after a Catastrophic Flood

Patterns of periphyton accrual after a catastrophic flood in fall 1986 were similar at high- and moderately enriched sites (Fig. 5). Recovery of benthic Chl *a* at these sites was well described by second-order polynomial regressions:

High enrichment:

$$(5) \text{ Chl } a = 4.88t + 0.11t^2 \\ R^2 = 0.89, F = 89.9, p \leq 0.0001$$

Moderate enrichment:

$$(6) \text{ Chl } a = 1.75t + 0.14t^2 \\ R^2 = 0.89, F = 144.5, p \leq 0.0001$$

where t = days after flooding. Regressions for high- and moderately enriched sites differed from that for low-nutrient sites which included a negative quadratic term:

Low enrichment:

$$(7) \text{ Chl } a = 4.26t - 0.06t^2 \\ R^2 = 0.87, F = 71.8, p \geq 0.0001.$$

Covariance analysis indicated that all three curves were significantly different from one another (high versus moderate, $F = 4.98, p = 0.03$; high versus low, $F = 18.08, p < 0.0001$; moderate versus low, $F = 16.27, p = 0.0002$).

Discussion

Periphyton biomass was highly correlated with ambient concentrations of both TN and TP in northern Ozark streams. Our results contrast with Welch et al. (1988), where no relationship

TABLE 2. Percent of benthic Chl *a* samples exceeding $75 \text{ mg}\cdot\text{m}^{-2}$ and $150 \text{ mg}\cdot\text{m}^{-2}$ and maximum benthic Chl *a* observed at 22 sites on 12 streams in the northern Ozarks during March–November 1985 and 1986 ($n = 38$ for each site).

	Percent of samples		Maximum benthic Chl <i>a</i> ($\text{mg}\cdot\text{m}^{-2}$)
	$>75 \text{ mg}\cdot\text{m}^{-2}$	$>150 \text{ mg}\cdot\text{m}^{-2}$	
High enrichment			
Blythes Creek			
Site 1	65.8	42.1	678.1
Site 2	57.9	23.7	525.9
Straight Fork			
Site 1	42.1	15.8	393.8
Site 2	60.5	8.4	437.2
Willow Fork	28.9	5.3	341.4
North Moreau Creek			
Site 2	18.4	7.9	321.4
Moderate enrichment			
South Moreau Creek			
Site 1	13.2	2.6	367.2
Site 2	28.9	7.9	285.0
Straight Fork			
Site 3	36.8	7.9	440.6
Smiths Creek	10.5	2.6	220.0
Burris Fork	13.2	7.9	332.2
North Moreau Creek			
Site 1	10.5	2.6	235.8
Site 3	10.5	0.0	149.0
Little Saline Creek	31.2	10.5	335.7
Maries River			
Site 1	23.7	5.3	348.1
Site 4	13.2	5.3	498.7
Low enrichment			
Maries River			
Site 2	15.8	0.0	142.5
Site 3	23.7	2.6	272.1
Little Maries River			
Site 1	15.8	0.0	144.0
Site 2	15.8	0.0	122.5
Saline Creek	7.9	0.0	109.0
Clifty Creek	0.0	0.0	41.5

was found between mean summer Chl *a* and ambient soluble reactive phosphorus in six western Washington streams, and with Jones et al. (1984), where neither N nor P could account for variation in benthic Chl *a* among streams in the Ozark Plateau. Our findings are consistent, however, with Aizaki and Sakamoto (1988) who found that periphyton biomass was highly correlated with TN and TP in 12 Japanese streams.

Biggs and Close (1989) found a strong correlation ($r = 0.74$) between geometric annual means of Chl *a* and TP in nine New Zealand streams. For comparison with our data, we log-transformed their TP data and regressed them against Chl *a*:

$$(8) \text{ Chl } a = 47.6 \log \text{ TP} - 31.9 \\ R^2 = 0.57, p = 0.02, n = 9.$$

An analysis of covariance, including data from Biggs and Close (1989) with both years of our data in one model, indicated that neither the slope nor the intercept of the regression equation for New Zealand streams was significantly different from the equations derived for Chl *a* – log TP in northern Ozark streams. The similarity of these regressions, as well as the highly significant correlations, suggests that empirical models may prove useful in assessing stream periphyton–nutrient dynamics under some circumstances.

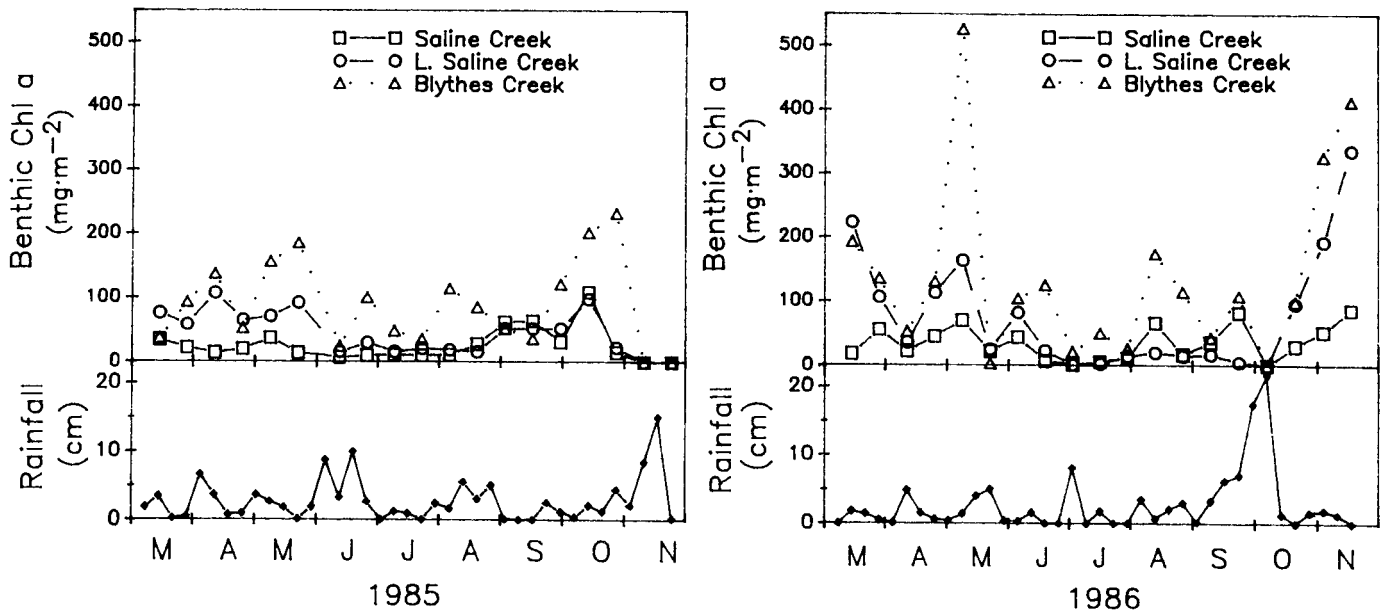


FIG. 4. Temporal changes in benthic Chl *a* in three streams representative of high (Blythes Creek), moderate (Little Saline Creek), and low nutrient enrichment (Saline Creek). Rainfall is the amount occurring during the preceding 7 d.

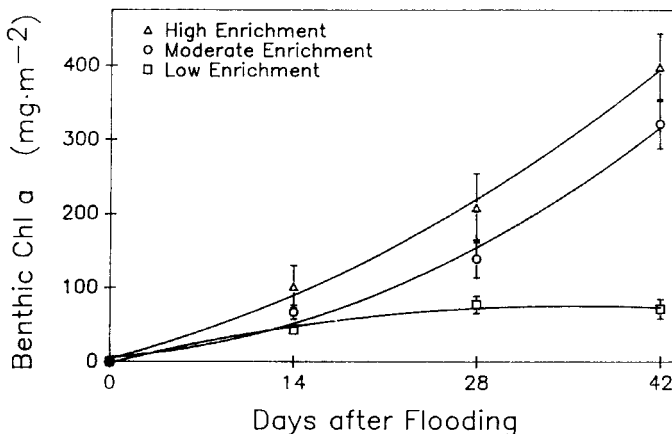


FIG. 5. Growth curves fitted for stream sites classified as high-, moderate-, and low-nutrient sites following a catastrophic flood in fall 1986. Points are means \pm SE; $n = 6$ for high- and low-enrichment sites and $n = 10$ for moderate-enrichment sites. See text for the regression equations.

The strength of biomass–nutrient regressions in the northern Ozarks can be partially explained by the broad range of nutrient conditions in the streams we sampled (Table 1). TN and TP concentrations ranged over 1–3 orders of magnitude and regressions were strongly influenced by high biomass in sites classified as highly enriched. A similar nutrient range was present in the streams sampled by Aizaki and Sakamoto (1988). Another factor adding to the strength of our regressions is the use of long-term averages of TN and TP, which likely provide a more accurate measure of nutrient loading than single point or seasonal mean estimates (Biggs and Close 1989).

Intercorrelation between TN and TP ($r = 0.97$) prevented a determination of the relative influence of each nutrient. Nitrogen, however, is likely the more important of the two in northern Ozark streams. Except in highly enriched sites, mean annual TN was $<750 \mu\text{g}\cdot\text{L}^{-1}$, considerably lower than the range of summer means ($1110\text{--}2560 \mu\text{g}\cdot\text{L}^{-1}$) typical of streams in the

Ozark Plateau (Jones et al. 1984; Smart et al. 1985). TN and $\text{NO}_3\text{-N}$ concentrations in northern Ozark streams are particularly depressed during low-flow periods, and experimental enrichments conducted in one stream in the region have demonstrated that periphyton is N-limited (Lohman et al. 1991).

While floods were most common in spring and fall in northern Ozark streams, benthic Chl *a* maxima also occurred during these seasons. Sumner and Fisher (1979) noted that benthic Chl *a* maxima in Fort River, Massachusetts, coincided with the period before full canopy development in May and again in November after leaf fall, suggesting that shading may limit periphyton growth during summer. More intense grazing pressure may also suppress periphyton biomass during summer months in northern Ozark streams. Snail grazing is conspicuous in some streams in the region during summer (Lohman et al. 1991). Stoneroller minnows (*Camptostoma anomalum*), shown to be important grazers in prairie-margin streams (Power and Matthews 1983), are also ubiquitous throughout the northern Ozarks (Pflieger 1975), but we do not know if they ever limit periphyton biomass in these streams or if their impact is greater in summer than in other seasons.

Although floods periodically reduced periphyton biomass in all northern Ozark streams, recolonization was always most rapid at sites with high levels of nutrient enrichment. These temporal patterns indicate that while flood frequency and intensity are dominant factors, nutrients are influential in determining periphyton biomass during flood-free periods. Horner et al. (1983) have suggested that nuisance algal conditions occur when levels of periphytic Chl *a* exceed $100\text{--}150 \text{ mg}\cdot\text{m}^{-2}$. Chl *a* was greater than $150 \text{ mg}\cdot\text{m}^{-2}$ on 18.9% of the dates sampled in highly enriched streams, 5.3% of the time in moderately enriched streams, and only 0.4% at low-nutrient sites (Table 2). Notwithstanding floods, nutrient enrichment is a strong indication of potential nuisance algal conditions in northern Ozark streams.

Postflood recovery rates during fall 1986 were clearly influenced by ambient nutrient concentrations, and patterns of recolonization differed between sites of low enrichment and those

of high and moderate enrichment. Based on the growth curves fitted for each nutrient group, periphyton biomass would reach nuisance densities ($>150 \text{ mg}\cdot\text{m}^{-2}$) within 21 d after catastrophic flooding in highly enriched sites and within 28 d in moderately enriched sites, but average benthic Chl *a* would never exceed roughly $75 \text{ mg}\cdot\text{m}^{-2}$ in low-nutrient sites. Our analysis provides an approximation of maximum biomass that might be expected in northern Ozark streams during prolonged flood-free periods. Actual measurements of maximum biomass over 1985–86 at low-enrichment sites were greater than predicted but at five of six sites were $<150 \text{ mg}\cdot\text{m}^{-2}$ and were generally far below maximum levels measured at high- and moderately enriched sites (Table 2). These differences in periphyton accrual patterns suggest that nuisance conditions are unlikely to develop in northern Ozark streams with TN and TP concentrations less than those that occur in the sites classified as low nutrient. In contrast, nuisance algal conditions could be expected in nutrient-rich streams when flood-free periods exceed 3–4 wk, especially if such periods occur during spring or fall.

Our results support the hypothesis of Grimm and Fisher (1986) that nutrient availability strongly influences rates of periphyton accrual. Their model would also predict that, regardless of nutrient conditions, all sites should arrive at a similar maximum standing crop unless preempted by some other limiting factor. Patterns of periphyton growth in northern Ozark streams, however, do not support this conclusion. Differences in biomass among high-, moderate-, and low-nutrient groups during fall 1986 persisted after 42 d of colonization. Whereas biomass in low-nutrient sites reached a steady state after 28 d, periphyton continued to accrue for 42 d after disturbance in high- and moderately enriched sites.

Differences in maximum standing crops may reflect differences in algal community structure. Welch et al. (1988) found that diatom-dominated assemblages were not associated with high biomass whereas assemblages dominated by filamentous species could be expected when benthic Chl *a* exceeded $100 \text{ mg}\cdot\text{m}^{-2}$. Although we did no taxonomic analysis of algal communities in fall 1986, Baysinger-Daniel (1989) identified predominant taxa in the same study sites during fall 1984 and found that filamentous species (*Cladophora*, *Stigeoclonium*) were more common in sites that we have designated as high and moderately enriched whereas low-nutrient sites were dominated by diatom–blue-green assemblages. Thus, differences in community composition may help to explain differences in both the shape and magnitude of periphytic growth patterns among streams with various nutrient regimes.

Our results demonstrate that periphyton biomass and the development of nuisance algal mats are strongly associated with nutrient enrichment in northern Ozark streams. Establishing nutrient guidelines to control periphyton biomass in streams, however, is complicated by the interacting effect of flood disturbance. As pointed out by Welch et al. (1989), the use of empirical correlation to determine the critical nutrient concentrations that will limit algal biomass in streams may not always be reliable. Nevertheless, patterns of periphyton biomass in northern Ozark streams indicate that it is possible to determine which streams are most likely to develop high periphyton biomass when hydrologic conditions are favorable for growth.

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