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Factors related to algal biomass in Missouri Ozark streams[1]

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With 1 figure and 3 tables in the text

Introduction

In this paper we examine factors related to benthic and suspended algal biomass in selected Missouri Ozark streams. Our purpose was to describe algal biomass values in these streams and test the hypothesis that physical conditions and nutrient concentrations account for differences in algal biomass among streams and over time. In this analysis we assumed that the suspended algae in these streams originate from periphyton attached to the streambed (Swanson & Bachmann 1976).

Methods and materials

Twelve sites on eight streams in the Missouri Ozark Plateau province in south-central Missouri were sampled every 7 to 10 days during June—December 1978 and March—September 1979. Characteristics of the streams and their watersheds were described by Smart et al. (1981). Urban, pasture, and forest areas made up 94 to 100 % of the watershed areas. All streams were greater than third order, the point at which autotrophic processes are considered to be the predominant energy source (Vannote et al. 1980). There were no known point-source inputs of wastewater within the sampled reaches of these streams.

All limnological analyses were conducted within the time limits specified with standard methodology (EPA 1974; APHA 1976). Algal biomass was estimated by measuring chlorophyll *a*. Extractions were performed according to the methods of Yentsch & Menzel (1963), and chlorophyll *a* concentrations were calculated using the monochromatic equation of Jeffrey & Humphrey (1975). Water samples for nutrient and suspended chlorophyll analyses were collected at mid-depth in the thalweg. Benthic algal samples were obtained from the cobble substrate by collecting a stone without conscious bias from several points (usually 3) across the width of the stream at each site. Attached periphyton was removed from a 4.5-cm^2 area of each stone using the methods of Douglas (1958). Collections were made in an area of open canopy to minimize the effects of shading by riparian vegetation. Coefficients of variation for triplicate samples of benthic chlorophyll *a* averaged 45 %, which is consistent with other studies (Tett et al. 1978; Wylie & Jones 1981). Daily values are represented by the arithmetic mean of the replicates.

To minimize the effect of temporal variation in our analyses, we divided the data from all sites for both years into seasons based on water temperatures; 4—12 °C in spring (3 March—14 May), 13—25 °C in summer (15 May—8 September), and 8—16 °C in autumn (9 September—19 December).

Results and discussion

Benthic algal biomass

Daily values of benthic chlorophyll *a* ranged from 1.8 to 392 mg · m^{-2}; mean and median values were 101 and 84 mg · m^{-2}, respectively. About 20 % of the values were greater than 150 mg · m^{-2}, a value associated with nusiance conditions in streams (Welch

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Table 1. Mean discharge, benthic chlorophyll *a*, suspended chlorophyll *a*, and export of chlorophyll *a* at the 12 sites by season.

Season	Mean discharge ($m^3 \cdot km^{-2} \times 10^{-4} \cdot s^{-1}$) of watershed area	Mean benthic chlorophyll *a* ($mg \cdot m^{-2}$)	Mean suspended chlorophyll *a* ($mg \cdot m^{-3}$)	Mean export of chlorophyll *a* ($mg \cdot m^{-2} \cdot day^{-1}$) of upstream bottom area
Summer 1978	44	82^{a}	5.0^{a}	0.5^{a}
Fall 1978	38	160^{b}	4.1^{a}	0.4^{a}
Spring 1979	205	72^{a}	3.6^{a}	2.1^{b}
Summer 1979	95	73^{a}	3.8^{a}	1.3^{c}

$^{a, b, c}$ Means with the same superscript within each column are not significantly different ($P < 0.05$).

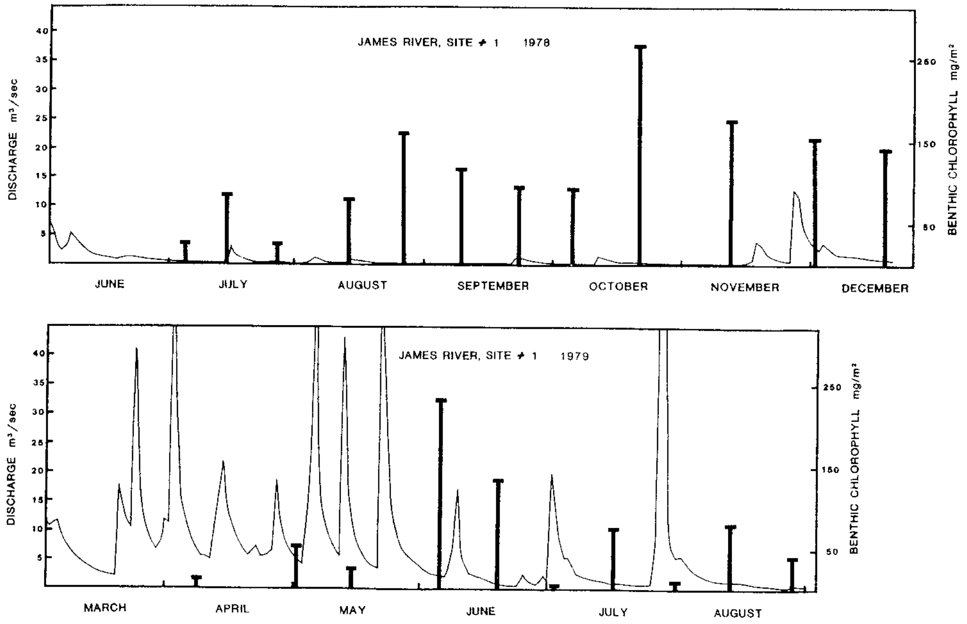

Fig. 1. Discharge ($m^3 \cdot s^{-1}$) and benthic chlorophyll *a* concentrations (bars, $mg \cdot m^{-2}$) for 1978 and 1979 at James River, site 1. Average discharge for period of record (6 years) is $4.9\ m^3 \cdot s^{-1}$.

et al. 1982). Most high values occurred during fall 1978, when stream discharge was low (Table 1). At that time, filamentous algae (e.g. *Oscillatoria* and *Cladophora*) were predominate in the periphyton. Chlorophyll *a* values were significantly greater in fall 1978 than during the other seasons when diatoms were the major component of the periphyton (Table 1, Kruskal-Wallis test, $P < 0.01$). About 10% of the values were less than $17\ mg \cdot m^{-2}$; most of these data were collected during spring 1979, a period of high stream discharge (Table 1), or during the other seasons concurrent with spates when the scouring action of currents and suspended materials seemed to reduce attached algal biomass (see also Gale et al. 1979; Horner & Welch 1981). There was generally an inverse relation between high stream discharge and benthic chlorophyll (Fig. 1); throughout the

Table 2. Mean (± standard error) benthic ($mg \cdot m^{-2}$) and suspended ($mg \cdot m^{-3}$) chlorophyll *a* values at the sites by season.

	Summer 1978	Fall 1978	Spring 1979	Summer 1979
	Benthic chlorophyll *a*			
James River, site 1	81±21	154±26	30±11	81±30
James River, site 2	50± 8	105±12	–[a]	–[a]
Finley Creek, site 1	107±48	141±32	67±27	38±10
Finley Creek, site 2	126±47	308±22	91±43	74±15
Bryant Creek	79±14	193±21	41± 3	141±23
Spring Creek	87±23	161±20	120±49	68±10
Potters Creek	116±33	102±11	48±17	70±25
North Fork, White River	69±12	181±23	67±25	86±22
Big Piney River, site 2	78±16	183±42	127±73	74±15
Big Piney River, site 3	65±14	147±24	85±44	36± 8
Big Piney River, site 4	77±26	93± 6	41±20	49±16
Gasconade River	48±22	140±39	69±53	85±26
	Suspended chlorophyll *a*			
James River, site 1	6.6±1	4.7±1	3.7±1	4.4±1
James River, site 2	14.4±3	11.4±3	3.8±0.3	8.8±1
Finley Creek, site 1	3.8±1	2.1±0.3	2.7±0.3	2.3±0.3
Finley Creek, site 2	8.4±3	4.2±1	5.0±1	4.0±1
Bryant Creek	4.7±1	2.6±0.3	4.4±0.3	3.8±1
Spring Creek	1.8±0.2	3.4±1	2.9±0.5	2.0±1
Potters Creek	1.8±0.4	3.4±1	2.5±0.5	1.7±0.3
North Fork, White River	2.4±0.2	3.4±1	2.7±0.4	1.9±0.2
Big Piney River, site 2	3.5±0.3	2.2±1	3.0±0.4	5.0±2
Big Piney River, site 3	3.8±1	2.2±0.4	3.7±1	2.9±1
Big Piney River, site 4	4.8±1	4.1±1	4.4±1	3.7±1
Gasconade River	3.8±0.5	4.9±1	4.4±1	4.5±1

[a] No data for this site.

study benthic algal chlorophyll at all sites was significantly lower during high flow (definded as greater than three times average discharge for period of record, USGS 1978, 1979) than for other sampling dates (MANN-WHITNEY test, $P < 0.01$). We also found rapid recovery of benthic chlorophyll following periods of high-flow (Fig. 1), which is consistent with the findings of KAUFMAN (1980).

Some differences in mean benthic chlorophyll *a* values among the 12 sites were significant during fall and summer 1979, but none were significant during summer 1978 or spring 1979 (Table 2, KRUSKAL-WALLIS test, $P < 0.05$). The cause of these differences, or lack of them, among sites within a season is not known. During each season, simple correlations between mean benthic chlorophyll by site and mean nutrient concentration, current velocity, discharge, nutrient supply (concentration x flow), gradient of the streambed, and watershed area were not significant ($P > 0.05$). Nor were multiple regression analyses of these data significant. Such analyses are not particularly informative, however, because at any given time a number of factors (i. e. light intensity, substrate type, water quality and movement and grazing by invertebrates and fishes) may regulate the growth and biomass of periphyton, and the factor of prime importance can change over time (WEITZEL 1979; HORNER & WELCH 1981). In addition, natural variability in biomass measurements can be sufficient to mask ecological interactions in streams (KAUF-

MAN 1980; WYLIE & JONES 1981). We also found that distinguishing differences in algal biomass among streams is further complicated by the relation between attached algae and nutrient concentrations within individual streams over time. Within each season, at each site, benthic chlorophyll *a* values generally showed no correlation, or a strong negative correlation ($P < 0.05$), with nutrient concentrations (nitrogen forms, phosphorus forms and SiO_2). A negative relation would be expected during periods of high stream flow when benthic algal biomass is low as a result of scour, such as occurred during 1979 (Fig. 1). Negative correlations with nutrient concentrations, however, also occurred in certain streams during low-flow conditions in 1978, suggesting that attached algae can lower nutrient concentrations in streams over time by uptake and incorporation. The relations between benthic algal biomass and nutrients were thus similar in the streams during low and high-flow periods; these relations, however, are likely the result of different processes and are not consistent over time. Based on these data, nutrient concentration values alone are likely to be poor predictors of benthic algal biomass in streams.

Suspended algal biomass

Suspended chlorophyll at the various sites ranged from 0.1 to 27.7 $mg \cdot m^{-3}$; mean and median values were 4.2 and 3.0 $mg \cdot m^{-3}$, respectively. Only 10 % of the values were greater than 8.0 $mg \cdot m^{-3}$, and most of these values occurred during low-flow periods. About 10 % of the values were less than 1.6 $mg \cdot m^{-3}$, but the low values did not follow a consistent pattern; most were collected during spates and presumably indicate dilution of algal biomass by high streamflow. However, several low values occurred during low-flow periods as well.

Mean suspended chlorophyll concentrations at the sites did not differ significantly among seasons (Table 1, KRUSKAL-WALLIS test, $P > 0.05$). These data indicate that averaged over time the concentration of algal cells in these streams is relatively constant. However, because of differences in stream discharge among seasons (Table 1), algal production was not constant over time. For example, if comparisons are made on the basis of mean daily export rate per unit of upstream bottom area (chlorophyll *a* concentrations x flow/upstream bottom area, after SWANSON & BACHMANN 1976), algal export was significantly higher during spring (Table 1) when high-flow and absence of shading by a leaf canopy on the riparian trees probably favored algal production, dislodgment from the periphyton, and export. During spring 1979, the average chlorophyll *a* export ($mg \cdot m^{-2} \cdot day^{-1}$) from the streams represented a daily loss of 2.9 % of the mean benthic standing crop at these sites. During summer 1979, summer 1978 and fall 1978, daily exports averaged 0.9 %, 0.6 % and 0.25 % of the mean benthic standing crop, respectively. The low percentage of export during fall 1978 may represent a low rate of cell dislodgment from the dominant filamentous algae and may similarly account for some of the low concentrations of suspended chlorophyll *a* during this period.

The export values and daily loss rates of suspended chlorophyll *a* in these Missouri Ozark streams are a small fraction of the average export (4.5 $mg \cdot m^{-2} \cdot day^{-1}$) and loss rates (2 to 9 % of the standing crop) observed in central-Iowa streams (SWANSON & BACHMANN 1976). This difference between Missouri and Iowa is likely the result of differences in stream morphology and nutrient content of the water. In central-Iowa, streams originate in agricultural lands with little gradient and riparian vegetation and have the highest nutrient concentrations in the midwest (OMERNICK 1977). This condition favors autotrophic processes. In contrast, most Ozark streams originate in the deciduous forests of a dissected plateau and have some of the lowest nutrient concentrations in the midwest. Benthic algal chlorophyll *a* averages 160 mg · m^{-2} and suspended algal chlorophyll *a* averages 55 mg · m^{-3} in Iowa streams. These values are two and ten times greater than, respectively, Ozark stream averages (Table 1).

If discharge per unit watershed area is assumed to be nearly constant from stream-to-stream within this region of the Ozarks when averaged over a season (supported by data from USGS 1978, 1979), we can use suspended chlorophyll *a* concentrations rather than export values to compare algal production. We elected this approach because suspended algal concentrations in streams are more easily interpreted than are export values and are not subject to the potential errors of discharge estimates. For testing purposes, we reasoned that if cell loss per unit area of streambed was constant among streams, flow would dilute or concentrate the cells accordingly. While on any given day there may be differences in dilution of the suspended cells, these differences should average out over the season. Given these assumptions we would expect suspended chlorophyll *a* values at the sites to be positively correlated with the area of streambed above the sampling point. This relation occurs because the area of streambed increases at a faster rate than the watershed area; consequently, there is proportionately more surface area for algal growth and cell loss to the overlying water per unit of flow in the larger streams (SWANSON & BACHMANN 1976). These arguments also tend to favor the dominance of autotrophic processes in larger streams (cf. VANNOTE et al. 1980).

This was probably the case during spring 1979, when mean suspended chlorophyll *a* values (Table 3) among sites were significantly correlated with area of the watershed above the sampling point (range 38 to 1679 km^2). These data suggest that, during spring, physical characteristics of the streams rather than nutrient limitation determined concentrations of suspended algal cells. They also suggest that, during spring 1979, algal production per unit area of streambed and export downstream was relatively constant among streams within this region of the Ozarks. We might expect this to occur during periods of high-flow and open canopy (characteristic of springtime conditions) when major factors controlling algal production and export (nutrients, water movements, light and others) would be relatively homogeneous among streams and along the length of an individual stream. In contrast, during low-flow periods of summer and fall, shading by riparian vegetation and pool-riffle differences in current velocity would cause relatively patchy conditions for algal growth, cell dislodgment and export. Examination of effect coefficients from a path analysis of log chlorophyll *a* on log phosphorus and log watershed area showed that for spring 1979 the effect of log watershed area on log chlorophyll *a* was almost twice that of the other seasons.

Suspended chlorophyll concentrations collected during spates in summer 1979 (Fig. 1) were significantly correlated with area of the streambed ($r = 0.85$, $P < 0.01$). This correlation may result from scour of the periphyton from the streambed above the sampling point, and further indicates that during high-flow, physical processes can determine suspended algal biomass in these streams. In this situation, the standing crop of periphyton present when the spate occurred was an important factor in determining the impact of physical processes on suspended algal concentrations.

In contrast, significant differences in mean suspended chlorophyll *a* concentrations among the 12 sites occurred within summer 1978 and 1979, and fall 1978 (Table 2, KRUSKAL-WALLIS test, $P < 0.05$); the chlorophyll concentrations were generally signif-

Table 3. Correlation coefficients and seasonal mean nutrient concentrations by season.

Statistical information	Season			
	Summer 1978	Fall 1978	Spring 1979	Summer 1979
Correlation with log suspended chlorophyll a (mg · m^{-3})				
Log total phosphorus (mg · m^{-3})	0.86	n.s.[b]	0.82[c]	0.73
Log total nitrogen (mg · m^{-3})	0.65[a]	0.69	n.s.	0.73
Log watershed area (km^2)	n.s.	n.s.	0.71	n.s.
Seasonal mean ± standard error and (range) at the 12 sites				
Total phosphorus (mg · m^{-3})	101.3 ± 15.3 (27.4 – 184.5)	28.3 ± 6.1 (6.8 – 75.1)	36.3 ± 8.6 (14.6 – 125.4)	50.0 ± 6.8 (21.2 – 111.6)
Total nitrogen (mg · m^{-3})	1077 ± 172 (575 – 2782)	2441 ± 594 (955 – 8112)	1023 ± 172 (478 – 2696)	1779 ± 126 (1278 – 2754)

[a] $P = 0.03$, all other r values $P < 0.01$.

[b] not significant.

[c] The strength of this correlation was in part due to the high degree of intercorrelation among total phosphorus, chlorophyll and watershed area (during spring, log phosphorus x log watershed area, $r = 0.76$, $P < 0.01$).

icantly correlated with differences in mean nutrient concentrations but not watershed area (Table 3). These analyses suggest that cell loss per unit area of streambed was not constant among the sites, and that algal production and export was stimulated by nutrient concentrations during these seasons.

Nutrient concentrations in Missouri Ozark streams are a function of land-use practices on the watershed (SMART et al. in press). Concentrations increase with the percentage of the watershed in urban and pasture area, and are negatively related to forest area. These increases are the result of non-point source anthropogenic inputs, agricultural practices, and differences the nutrient cycling processes that occur in urban areas, pastures and forests.

To describe the average relation between suspended chlorophyll *a* values and nutrient concentrations during summer 1978, 1979 and fall 1978, we carried out stepwise regression analyses by using the mean total phosphorus and total nitrogen concentrations at each site and classes for the seasons ($n = 36$ seasonal means) as independent variables. Logarithmic transformations (base 10) were used to be consistent with other nutrient-chlorophyll models used to describe algal biomass in lakes (e.g. CANFIELD 1983). Only the unique effects of P and N were significant:

$$\log(\mathrm{Chl}\,a) = -0.09 + 0.39\log(\mathrm{TP}),\ R^2 = 0.41 \tag{1}$$

$$\log(\mathrm{Chl}\,a) = 0.1 + 0.39\log(\mathrm{TP}) + 0.34\log(\mathrm{TN}),\ R^2 = 0.53 \tag{2}$$

where Chl*a* is the suspended chlorophyll *a* concentration ($mg \cdot m^{-3}$), TP is the total phosphorus concentration ($mg \cdot m^{-3}$), and TN is the total nitrogen concentration ($mg \cdot m^{-3}$).

These equations describe relations over a broad range of nutrient concentrations in Missouri Ozark streams (Table 3) and are similar to nutrient-chlorophyll *a* relations in lakes. Concentrations of P alone explain 41 % of the variance in suspended chlorophyll *a* among streams, while the addition of TN to the model explains 19.5 % of the remaining variability. These relations indicate that both nutrients stimulated algal production in Ozark streams during these 3 seasons. Although, we are uncertain of the functional mechanism involved, we hypothesize that higher nutrient concentrations stimulate growth and cell loss from the periphyton to the overlying water. Using artificial channels, WELCH et al. (1982) found biomass accrual of the periphyton to be directly related to P concentration. The role of N in our data is not surprising, because in 32 % of the samples the total nitrogen-total phosphorus ratio was < 17, which includes the range of N : P when N is considered limiting (< 10), and when dual N and P limitation (10 to 17) is thought to occur (CANFIELD 1983).

The major differences between these equations and those for lakes is that, in streams, nutrients explain a much lower percentage of the variance in algal biomass, and the slope coefficients are much lower than are slopes in similar models based on lake data. Using the median TP concentration in our data set ($30 \, mg \cdot m^{-3}$), the chlorophyll *a* value predicted by eq. (1) is one-fourth the value predicted by a similar equation for lakes (JONES & BACHMANN 1976; 3.1 vs $11.7 \, mg \cdot m^{-3}$, respectively). During our study about 60 % of the seasonal mean chlorophyll *a* values measured at the 12 sites were less than one-fourth the expected value in a lake (calculations based on mean TP concentration after JONES & BACHMANN 1976). This difference is in agreement with previous research demonstrating that algal biomass in streams is generally lower than might be expected in lakes on the basis of nutrient concentration (BURKHOLDER-CRECCO & BACHMANN 1979). Reasons for these differences between nutrient-algal biomass relations in lentic and lotic ecosystems are not well understood but are likely related to the complex interactions of physical, chemical and biological factors controlling nutrient assimilation by periphyton, algal growth, and subsequent export processes in stream ecosystems which vary over time (KAUFMAN 1980; VANNOTE et al. 1980).

Conclusions

The results of this study indicate that both physical characteristics and nutrient concentration determine suspended algal biomass in Missouri Ozark streams. While it is likely that both physical characteristics and nutrients have a continual effect on stream algal biomass, there is probably a shift in their relative importance over time. Flow is a major factor determining both benthic and suspended values. During periods of high flow, frictional shear stress removed periphyton from the streambed. These cells were subsequently concentrated during downstream transport so that the area of the watershed upstream from the sampling point explained a significant portion of the variance in suspended chlorophyll *a* concentrations among the 12 sites. Nutrients were not limiting during high-flow. In contrast, during the lower flows of summer and fall differences in suspended algal chlorophyll were significantly correlated with nutrient concentrations. Differences in benthic chlorophyll among sites did not show these nutrient relations. We hypothesize that, averaged over time, an increase in nutrient concentrations will stimulate growth and cell loss from the periphyton. Nutrient concentrations in Ozark streams are highly correlated with urban areas and agricultural practices. As these land-use practices expand in the region suspended chlorophyll *a* values will increase to a point where nutrients will become less important in limiting algal densities and physical characteristics will be the major factors determining algal chlorophyll in these streams.

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