

Grazers and Nutrients Simultaneously Limit Lotic Primary Productivity¹

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Nitrate and phosphate were added to two of four flow through channels in a second-order stream in eastern Tennessee to raise nutrient concentrations to 3–4 times background, while two of four sets of colonized ceramic tiles in each channel were raised above the substratum to exclude grazing snails (*Elimia clavaeformis*). Snail grazing maintained a thin layer of periphyton dominated by *Stigeoclonium* basal cells, regardless of nutrient regime. Although nutrient effects on periphyton ash-free dry mass were statistically insignificant, nutrient additions significantly increased chlorophyll *a*, especially where snails were excluded. Snail densities were 89% higher in nutrient-enriched channels. Photosynthesis–irradiance data suggested that nutrient enrichment increased self-shading in the periphyton. Areal-specific productivity was simultaneously limited by grazing and low nutrient concentrations: snail exclusion and nutrient enrichment both increased productivity >2 times. The negative effect of snails on areal-specific productivity was due to (1) reduction in biomass by cropping and (2) depression of chlorophyll-specific productivity. The means by which *Elimia* depresses chlorophyll-specific productivity is unclear, but the depression is clearly disadvantageous to food-limited grazers. Because *Elimia* was the dominant invertebrate, our results indicate that low nutrient concentrations limit secondary as well as primary production in autumn.

Du nitrate et du phosphate ont été ajoutés à deux des quatre chenaux d'un cours d'eau de second ordre de l'est du Tennessee afin d'élever les concentrations de bioéléments par un facteur de 3 à 4 fois la concentration ambiante, tandis que deux des quatre séries de carreaux céramiques colonisés placés dans chaque chenal ont été élevés au-dessus du substrat pour en exclure l'escargot brouteur *Elimia clavaeformis*. Indépendamment du régime nutritif, le broutage n'a pas éliminé la mince couche de périphyton où dominait des cellules basales de *Stigeoclonium*. Même si les incidences de bioéléments sur la masse sèche sans cendre du périphyton n'étaient pas statistiquement significatives, l'ajout de bioéléments a entraîné une augmentation significative de la chlorophylle *a*, surtout en l'absence d'escargots. Par contre, la densité des escargots étaient de 89% plus élevée dans les chenaux enrichis. Les données sur la photosynthèse et le niveau d'éclairement portent à croire que l'ajout de bioéléments a mené à une augmentation de l'auto-ombrage du périphyton. Par contre, la productivité spatiale était simultanément limitée par le broutage et de faibles concentrations de bioéléments; l'élimination des escargots et l'ajout de bioéléments ont tous deux mené à une augmentation de la productivité par un facteur supérieur à 2. L'incidence négative des escargots sur la productivité spatiale résultait des deux facteurs suivants : 1) la réduction de la biomasse par le broutage et 2) la baisse de la productivité liée à la chlorophylle. On ne sait pas de quelle manière *Elimia* diminue cette productivité, mais il est évident que cette diminution désavantage nettement ces brouteurs. Comme *Elimia* était le principal invertébré, les résultats portent à croire que de faibles concentrations de bioéléments limitent la production primaire et secondaire en automne.

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Biomass accrual by periphyton is the integration of gains and losses. Biomass is gained primarily from in-place biosynthesis, although immigration can be important in early stages of lotic periphyton development (Bothwell and Jasper 1983; Stevenson 1986). Factors that influence biosynthesis in lotic periphyton have been moderately well studied, with much of the emphasis on nutrient limitation (e.g. Stockner and Shortreed 1978; Peterson et al. 1983; Bothwell 1985; Grimm and Fisher 1986; Pringle 1987). Losses of periphyton biomass occur due to consumption by grazers, dislodgement and export of cells by current, and mortality due to pathogens or senescence. Factors influencing biomass loss have generally received less attention than those that affect biomass gain, but grazing

studies have recently become prominent (e.g. Lamberti and Resh 1983; Hill and Knight 1987; Stewart 1987; Feminella et al. 1989).

Nutrient limitation of lotic periphyton is a complex interaction of nutrient concentration, water velocity, competition, and diffusion. It was initially thought that nutrients did not limit algal growth in streams because flowing water provided a constant supply of new nutrients to attached algae (Wuhrmann 1974). Furthermore, Bothwell (1988) demonstrated that cellular growth rates of lotic periphyton saturated at nutrient concentrations much lower than found in most streams. To accommodate the abundant empirical evidence of nutrient limitation at concentrations above cellular saturation levels, it is necessary to invoke the effect of periphyton biomass on its own metabolism (Bothwell 1989). Even thin periphyton is a three-dimensional matrix of algae and microscopic heterotrophs sur-

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rounded by biogenic mucilage (Lock et al. 1984). Diffusion of nutrients through the overlying boundary layer and into this matrix is slow compared with stream flow, and the closely packed microorganisms within the matrix create a relatively high demand for metabolic substrates (e.g. Carlton and Wetzel 1987). Bothwell (1989) identified two types of growth versus nutrient curves for periphyton: (1) a rapidly saturating, Monod type evident in phytoplankton and early periphyton stages and (2) a more linear, slowly saturating type found in older periphyton. The latter diffusion-limited curve reflects the effect of biomass on periphyton productivity.

The consumption of algal cells by grazers obviously diminishes productive periphyton biomass. However, positive effects of grazing on the periphyton left uneaten have been observed or implicated in a number of studies (Gregory 1983; Lamberti and Resh 1983; Hill and Knight 1987; Stewart 1987; Power et al. 1988; McCormick and Stevenson 1989, 1991; Hill and Harvey 1990). Grazers are thought to increase biomass-specific production of periphyton by recycling limiting nutrients, cropping senescent cells, selecting for the establishment of rapidly dividing algal taxa, or mitigating the self-shading and diffusion limitation associated with vertical biomass accrual. Some investigators have reported that positive indirect effects of grazing can outweigh negative direct effects, so that net production in grazed communities exceeds that in ungrazed communities (Cooper 1973; Flint and Goldman 1975; Kesler 1981).

In this experiment, we examined the effects of nutrient limitation, grazing, and the potential interaction of nutrients and grazing on periphyton productivity in a headwater stream in eastern Tennessee. Many streams in this area have dense populations of grazing snails and low nutrient concentrations (e.g. Elwood et al. 1981), suggesting that primary production may be closely constrained by high loss rates and low photosynthetic rates. We experimentally excluded grazers and amended nutrient levels to determine if these factors alone or together limited periphyton biomass and production.

Materials and Methods

Study Site

White Oak Creek is a tributary of the Clinch River that flows through the Oak Ridge National Laboratory (35°55'N, 84°19'W), Tennessee, USA. This experiment was conducted in upper White Oak Creek ("WOC 6.8" in Loar et al. 1991), a relatively undisturbed second-order stream with an adjacent deciduous forest. Shading by streamside trees is extensive during summer, but light reaching the stream increases substantially after autumn leaf-fall. Like many headwater streams in eastern Tennessee, upper White Oak Creek has moderately alkaline water (approximately 120 mg CaCO₃·L⁻¹) and relatively low nutrient concentrations (Loar et al. 1991). Densities of the prosobranch snail *Elimia clavaeformis*, the predominant grazer, are quite high. Snail biomass is 10 times periphyton biomass (W. Hill, unpubl. data). Average water temperature in upper White Oak Creek during October is approximately 12°C (Loar et al. 1991).

Experimental Design

Nutrient additions and snail exclusions were performed in four Plexiglas channels (each 122 cm long, 30 cm wide, and 41 cm high) that were open at each end and on top. The channels were placed side by side on the stream bed in White Oak

Creek with their longitudinal axes parallel to the current. Plastic mesh (6.4-mm openings) was attached to the upstream end of each channel to prevent drifting leaves from fouling experimental substrata. Surface velocity, measured by timing the transit of a leaf of watercress down each channel, averaged 7.6 cm·s⁻¹.

Experimental substrata consisted of unglazed ceramic tiles (4.8 cm per side) that were conditioned in White Oak Creek for >1 yr before the experiment. The tiles were attached to bricks (seven tiles per brick) with silicon glue before conditioning. At the beginning of the experiment, tiles from half of the bricks were removed and secured with rubber bands to Plexiglas plates (seven tiles per plate) that were suspended approximately 5 cm above the channel bottoms with wires clamped to the channel sides. The seven tiles on each suspended Plexiglas plate were essentially inaccessible to grazing snails; each channel contained two suspended plates. Each channel also contained two bricks (with attached tiles) that were set on the bottom of the channel and were accessible to snails. The four sets of tiles in each channel were placed in a line parallel to the current, approximately 10 cm apart. Tiles suspended on the Plexiglas plates were kept at the same distance above the channel bottom as the tiles attached to bricks. Cobbles from the stream bed were added to the channels around the tiles to provide additional natural substratum for snails that entered the channels from the open downstream ends.

Nutrients were added to the upstream ends of two of the channels by dripping a stock solution of 50 g KNO₃·L⁻¹ and 7.6 g K₂HPO₄·L⁻¹ from a carboy placed nearby on the stream bank. Several bricks placed crosswise in the channels just downstream from the nutrient drip lines provided turbulence to mix the stock solution with water flowing into the two channels. Nutrient stock was added at a rate to increase nitrate and phosphate concentrations in the two channels 3–4 times background levels. Because nutrients were applied to whole channels that contained two types of tiles (grazed and ungrazed), the resulting design was a 2 × 2 split-plot factorial. Experimental units for nutrient effects were the channels whereas sets of tiles (four per channel, 16 total) served as experimental units for determining grazing effects and nutrient × grazing interactions.

Tiles were placed into the channels and nutrient amendments were begun on 6 October 1989. Beginning a week later, the snails on each set of tiles in each channel were counted daily until the end of the experiment. The few snails found on the suspended tiles were removed after counts were made. The positions of the four sets of tiles in each channel were changed every 2 d to minimize the potential effect of position within the channel. Nutrient concentrations in the channels were checked once during the experiment, and nutrient concentrations in White Oak Creek (immediately upstream from the channel location) were analyzed just before the experiment began and near its end 3 wk later. Nutrient concentrations were analyzed on a Lachat autoanalyzer using standard methods (Loar et al. 1991). Photosynthetically active radiation (PAR) was measured at midday on the day before the experiment ended with a LiCor quantum sensor held over the channels.

Periphyton Analyses

Tiles were collected from the channels on the morning of 27 October 1989, removed from the Plexiglas plates and bricks, and taken to the laboratory in water-filled containers. Periphyton was firmly attached to the tiles, and there was no visual evidence that it detached during the transfer to the laboratory or during subsequent photosynthetic measurements. Photosyn-

TABLE 1. Nutrient concentrations ($\mu\text{g}\cdot\text{L}^{-1}$) in upper White Oak Creek, autumn 1989. TN = total nitrogen, TP = total phosphorus, $\text{NO}_3\text{-N}$ = nitrogen in the form of nitrate, SRP = soluble reactive phosphorus, N:P = molar ratio of $\text{NO}_3\text{-N}$ /SRP.

Date	Sampling location	TN	TP	$\text{NO}_3\text{-N}$	SRP	N:P
26 Sept.	Stream	80	13	46	11	9.3
17 Oct.	Channel 1 (nutrients)	263	28	—	—	—
	Channel 2 (control)	60	8	—	—	—
	Channel 3 (control)	70	9	—	—	—
	Channel 4 (nutrients)	296	31	—	—	—
23 Oct.	Stream	119	14	32	5	14.2

thesis was measured at six irradiances: 44, 130, 250, 420, 590, and $1300 \mu\text{mol quanta}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. To make these measurements, tiles were placed in circular glass chambers (19 cm diameter, 10 cm height) containing 900 mL of water from the appropriate channel. Individual pumps connected to the chambers provided recirculating flow at a velocity of approximately $30 \text{ cm}\cdot\text{s}^{-1}$ inside the chambers. The chambers were kept at 13°C in a water bath. A 100-W metal halide lamp with a phosphor-coated bulb provided light; the various irradiances were achieved by placing different numbers of neutral-density screens over individual chambers. One tile from each set of seven was exposed to one irradiance, so that each set received the entire range of irradiances.

Following a 15-min exposure to the experimental irradiance, 740 kBq of $\text{NaH}^{14}\text{CO}_3$ was injected into each chamber. Tiles were removed from the chambers 2 h after the ^{14}C was added, rinsed twice in stream water to remove unincorporated ^{14}C , and placed in jars containing 20 mL of dimethyl sulfoxide (DMSO). DMSO simultaneously extracts chlorophyll *a* and ^{14}C -labeled photosynthate (Palumbo et al. 1987). Extracted chlorophyll *a* was analyzed spectrophotometrically, and the concentration of chlorophyll *a* was calculated with the equations of Jeffrey and Humphrey (1975) and corrected for pheopigments. The validity of the Jeffrey and Humphrey (1975) extinction coefficients for chlorophyll *a* in DMSO was checked with pure chlorophyll *a* (Sigma). Extracted ^{14}C was counted in a Packard Tri-Carb 2000CA liquid scintillation analyzer, with quenching corrected by external standards. Nonphotosynthetic carbon uptake was determined in darkened chambers and subtracted from photosynthetic uptake.

Periphyton was brushed from the tiles with a toothbrush for the analysis of ash-free dry mass (AFDM) and algal biovolume. Except for four of the sets in which one tile was used as a dark control in the photosynthesis measurements, one tile from each set was brushed. Half of the brushed periphyton was dried on aluminum pans at 60°C , weighed, ashed at 480°C , and reweighed for AFDM determination. The other half was preserved in Lugol's solution and examined later with an inverted microscope. At least 500 individual cells or filaments in each sample were counted at $400\times$ magnification. The average cell volume of each algal taxon was estimated by using average cell dimensions in appropriate geometric formulae.

Data Analysis

Photosynthesis-irradiance (P-I) data were fitted to the three-parameter photoinhibition model of Platt et al. (1980) with least-squares, nonlinear regression (SAS, PROC NLIN) (SAS 1985). In this model, $P = P_s (1 - e^{-a}) e^{-b}$, where P is carbon uptake at a given irradiance (I), P_s is the theoretical maximum value of P in the absence of photoinhibition, $a = \alpha I/P_s$, $b = \beta I/P_s$, α is the slope of the initial linear portion of the curve,

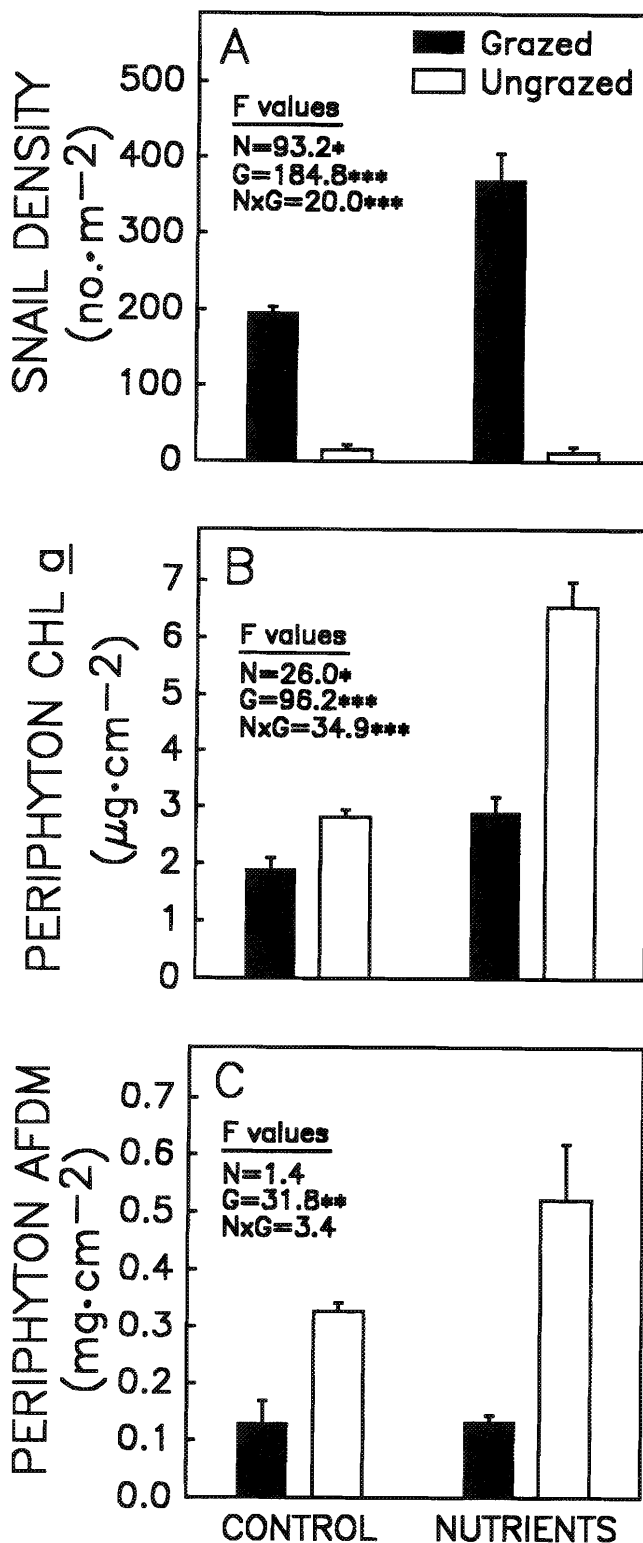


FIG. 1. Effects of experimental manipulations on (A) Snail density, (B) periphyton chlorophyll *a*, and (C) periphyton AFDM. N = nutrients; G = grazing. Bars represent means \pm 1 SE. F degrees of freedom from ANOVA of snail density and chlorophyll *a*: N = 1, 2; G = 1, 10; N \times G = 1, 10. F degrees of freedom for AFDM: N = 1, 2; G = 1, 6; N \times G = 1, 6. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

and β is a photoinhibition parameter. Four other P-I parameters, P_{\max} , I_{\max} , I_k , and T_b were calculated from the estimated model parameters as per Platt et al. (1980). P_{\max} represents the maximum rate of carbon uptake, I_{\max} is the irradiance at which P_{\max} occurs, I_k estimates the onset of photosaturation, and I_b is the irradiance at which photoinhibition reduces P to 37% of P_s . Individual P-I models were generated for each set of tiles. P-I parameters from these models, as well as periphyton biomass and snail density parameters, were analyzed with a nested (split-plot) model (SAS, PROC GLM) (SAS 1985). Parameters were log transformed when variances were correlated with means.

Results

Approximately 95% of the leaves on streamside trees had fallen by the end of this experiment, allowing high irradiances on the stream bed. PAR measured over the channels on 26 October was $1400 \mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ at midday. Nitrate and soluble reactive phosphorus (SRP) concentrations in upper White Oak Creek were moderately low both before and near the end of the experiment (Table 1). Nutrient addition raised total nitrogen and phosphate concentrations 3–4 times that measured in control channels.

Average snail density on the experimental tiles was significantly affected by both treatment factors (Fig. 1A). Snails were abundant on tiles that were contiguous with the stream bed ("grazed" tiles) whereas very few snails were found on the suspended tiles ("ungrazed" tiles), confirming the efficacy of the grazer exclusion method. No grazers other than snails were observed on the tiles during the experiment. Grazed tiles in nutrient-enriched channels had 89% more snails than grazed tiles in control channels (Fig. 1A).

Snail grazing decreased periphyton chlorophyll a , particularly in the nutrient-enriched channels (Fig. 1B). Grazed periphyton in nutrient-enriched channels showed a modest, but statistically significant, increase over grazed periphyton in control channels. Tiles that were both ungrazed and enriched with nutrients accrued 2–3 times more chlorophyll a than the other treatment combinations, indicating a strong interaction between nutrients and grazing on periphyton biomass.

Grazing decreased periphyton AFDM regardless of nutrient regime (Fig. 1C). Overall nutrient effects were not significant ($P = 0.36$), and although ungrazed tiles in nutrient-enriched channels had the largest mean AFDM, the nutrient \times grazing interaction was not significant ($P = 0.11$). Less statistical power was available for testing grazing and nutrient \times grazing effects on AFDM than on chlorophyll a (6 error degrees of

freedom versus 10) because four tiles were sacrificed for use in ^{14}C dark uptake controls.

Algal assemblages on the tiles were relatively simple. Five taxa comprised 84% of total algal biovolume (Table 2). *Stigeoclonium* sp. was the largest single contributor in all treatments. Several replicates of periphyton samples from the grazed tiles dried during storage, so statistical power was even more limited (only 4 error degrees of freedom for grazing and nutrient \times grazing effects) than in the AFDM analysis. This limited power, and the great variability between replicates, explains why neither the grazing term nor the grazing \times nutrient term in the ANOVA was significant, even though the mean *Stigeoclonium* biovolume on ungrazed tiles from enriched channels was 4–9 times greater than that on the grazed tiles. The biovolume of two diatoms, *Gomphonema dichotomum* and *Achnanthes minutissima*, was statistically greater on ungrazed tiles, however. Total algal biovolume was also significantly greater on ungrazed tiles than on grazed tiles. Neither nutrient nor nutrient \times grazing effects on algal biovolume were statistically significant.

Substantial grazing and nutrient effects on areal-specific production were evident at all irradiances (Fig. 2A, 2B). Maximal photosynthetic rates increased >2 times when snails were excluded and increased >2 times when nutrients were added; P_{\max} for ungrazed periphyton in enriched channels was approximately 5 times greater than grazed periphyton in control channels (Table 3). The slope (α) of the linear phase of the P-I relationship was affected by grazing and nutrient treatments in the same manner as P_{\max} , so that α was >4 times larger for ungrazed, enriched periphyton than it was for grazed periphyton in control channels. The inhibition constant β was significantly larger for ungrazed periphyton, but was unaltered by nutrients. Grazing did not significantly affect either the irradiance at which saturation began (I_k) or the irradiance at which P_{\max} occurred (I_{\max}). The effect of nutrients in increasing I_{\max} was nearly significant ($P = 0.07$), however. Nutrient addition caused approximately 2 times increase in I_b , the inhibition parameter independent of P_{\max} (Platt et al. 1980), suggesting that periphyton from enriched channels experienced less photoinhibition than periphyton from control channels.

Grazing significantly depressed chlorophyll-specific productivity (Fig. 2C, 2D). Chlorophyll-specific P_{\max} was 37 and 20% lower in control channels and nutrient-enriched channels, respectively (Table 3). Nutrient effects on chlorophyll-specific P_{\max} were not significant, and although the mean P_{\max} for grazed periphyton in nutrient-enriched channels was greater than the mean P_{\max} for grazed periphyton in control channels, the grazing \times nutrient interaction was not significant.

TABLE 2. Biovolumes ($10^6 \times \mu\text{m}^3 \cdot \text{cm}^{-2}$) of major alga taxa on experimental substrates. Biovolume values are means \pm 1 SE. Biovolumes (μm^3) per cell were: *Stigeoclonium* = 221, *Phormidium tenue* = 3, unidentified cyanophyte = 8, *Gomphonema dichotomum* = 1060, *Achnanthes minutissima* = 64. N = nutrients, G = grazing. * $P < 0.05$, ** $P < 0.01$.

	Control		Nutrients		ANOVA F values		
	Grazed ($n = 1$)	Ungrazed ($n = 3$)	Grazed ($n = 3$)	Ungrazed ($n = 3$)	N ^a	G ^b	N \times G ^b
<i>Stigeoclonium</i> sp.	11.6	24.9 \pm 8.8	6.9 \pm 2.4	104.9 \pm 75.6	0.23	3.00	1.44
<i>Phormidium tenue</i>	1.2	7.0 \pm 3.0	1.5 \pm 0.7	7.3 \pm 3.9	0.39	3.80	0.69
Unidentified cyanophyte	0.9	0.5 \pm 0.1	0.9 \pm 0.3	0.9 \pm 0.6	0.10	1.44	0.42
<i>Gomphonema dichotomum</i>	0.4	17.3 \pm 6.2	0.3 \pm 0.3	21.1 \pm 14.1	2.08	8.02*	1.12
<i>Achnanthes minutissima</i>	0.2	1.6 \pm 0.5	0.2 \pm 0.1	3.2 \pm 1.5	0.65	27.73**	1.82
Total biovolume	20.0	60.5 \pm 21.8	10.7 \pm 4.1	155.9 \pm 97.1	0.37	10.14*	2.75

^a $F_{1,2}$.

^b $F_{1,4}$.

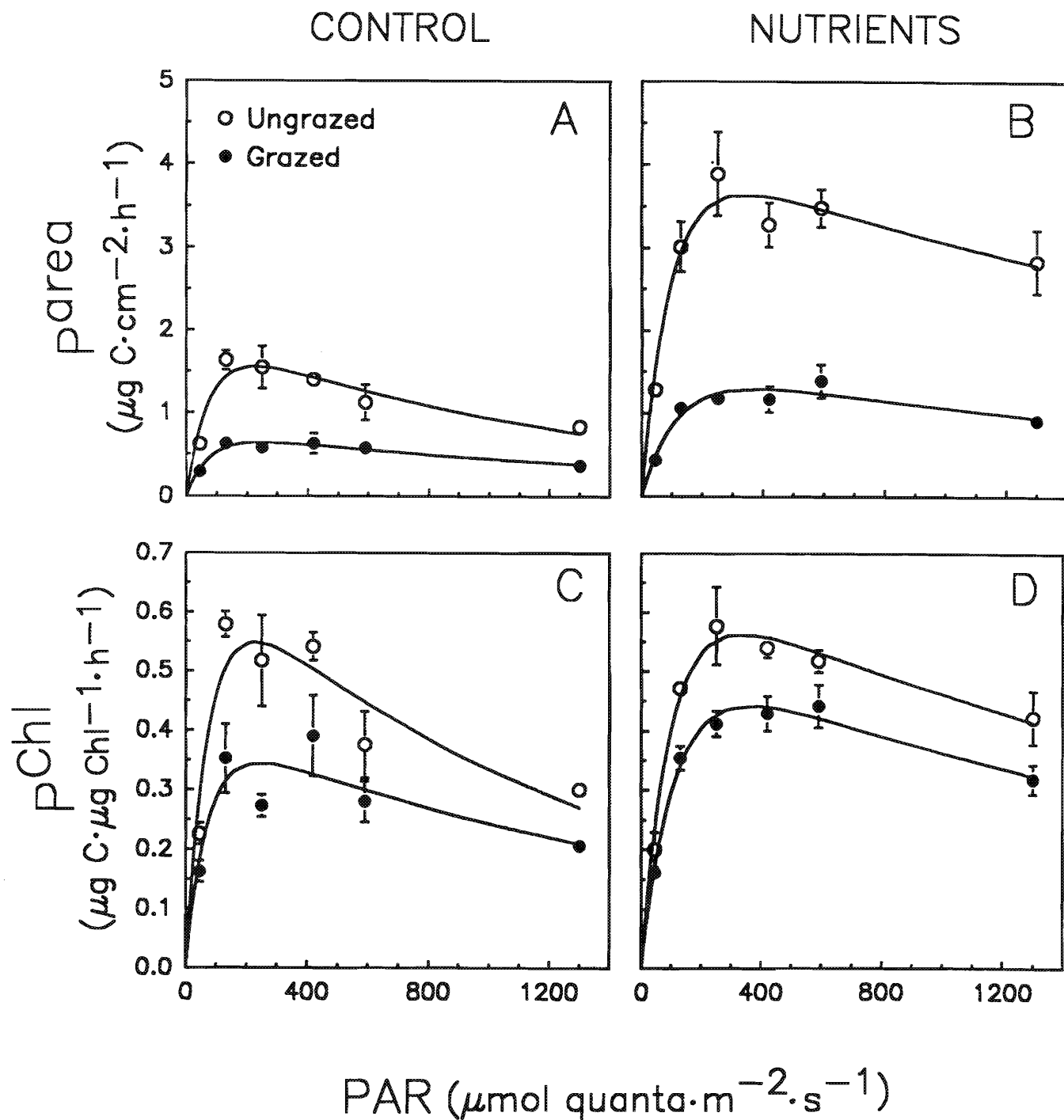


FIG. 2. Periphyton carbon uptake. P_{area} = areal-specific uptake; P^{chl} = chlorophyll *a* specific uptake; PAR = photosynthetically active radiation. Values are means \pm 1 SE ($n = 4$). Photosynthesis-irradiance curves were fit using the three-parameter photoinhibition model to Platt et al. (1980).

Discussion

Biomass Response

The results of this experiment demonstrate that snail grazing can limit periphyton accrual in White Oak Creek. All three biomass parameters (chlorophyll *a*, AFDM, and biovolume) increased when snails were excluded from experimental substrata, especially in nutrient-enriched channels. Grazing has been shown to limit periphyton accrual in many other in situ experiments (e.g. Lamberti and Resh 1983; McAuliffe 1984;

Hill and Knight 1987, 1988a; Feminella et al. 1989; Feminella and Resh 1990), and in this experiment, snails limited periphyton biomass to low levels even in nutrient-enriched channels. The added production provided by nutrient enrichment appeared to be channeled into increased grazer production. Our results are similar to those of Stewart (1987), who found that the grazing minnow *Campostoma* kept pace with nutrient-stimulated algal growth and maintained steady periphyton biomass despite increased productivity.

TABLE 3. Photosynthesis-irradiance parameters calculated for tiles from individual bricks; $n = 4$ for each treatment combination. Values are means ± 1 SE. N = nutrients, G = grazing. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

	Control		Nutrients		ANOVA F values		
	Grazed	Ungrazed	Grazed	Ungrazed	N ^a	G ^b	N \times G ^b
P_{\max} (area) ^c	0.68 \pm 0.09	1.67 \pm 0.23	1.31 \pm 0.13	3.75 \pm 0.35	40.13*	67.02**	0.43
α (area) ^d	10 \pm 2	25 \pm 1	14 \pm 8	44 \pm 3	37.62*	117.05***	0.56
β (area) ^d	0.5 \pm 0.1	1.6 \pm 0.5	0.6 \pm 0.1	1.2 \pm 0.1	0.58	14.50**	0.37
P_{\max} (Chl) ^e	0.37 \pm 0.05	0.59 \pm 0.06	0.47 \pm 0.03	0.59 \pm 0.02	1.51	15.52**	1.36
α (Chl) ^f	5.5 \pm 0.8	9.0 \pm 0.5	4.7 \pm 0.4	6.8 \pm 0.7	1.59	42.95***	2.65
β (Chl) ^f	0.2 \pm 0.1	0.5 \pm 0.2	0.2 \pm 0.02	0.2 \pm 0.1	5.41	2.95	1.86
I_{\max}^g	255 \pm 25	222 \pm 14	349 \pm 36	339 \pm 15	13.04	0.77	0.49
I_k^g	72 \pm 11	66 \pm 9	95 \pm 15	86 \pm 5	4.96	0.36	0.00
I_b^g	1650 \pm 30	1240 \pm 170	2600 \pm 530	3060 \pm 360	416.10***	0.05	1.84

^a1, 2 degrees of freedom.

^b1, 10 degrees of freedom.

^c $\mu\text{g C}\cdot\text{cm}^{-2}\cdot\text{h}^{-1}$.

^d $(\text{ng C}\cdot\text{cm}^{-2}\cdot\text{h}^{-1})\cdot(\mu\text{mol quanta}\cdot\text{m}^{-2}\cdot\text{s}^{-1})^{-1}$.

^e $\mu\text{g C}\cdot\mu\text{g Chl a}^{-1}\cdot\text{h}^{-1}$.

^f $(\text{ng C}\cdot\mu\text{g Chl a}^{-1}\cdot\text{h}^{-1})\cdot(\mu\text{mol quanta}\cdot\text{m}^{-2}\cdot\text{s}^{-1})^{-1}$.

^g $\mu\text{mol quanta}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

Snails maintained low levels of periphyton biomass in nutrient-enriched channels at least partly because of a numerical response. Snails were 89% more abundant on tiles in nutrient-enriched channels, presumably exerting a grazing pressure proportional to their density. The similarity between the increase in snail density (89%) and the increase in productivity (92% higher areal-specific P_{\max}) in nutrient-enriched channels suggests that snail density closely tracked local variations in primary productivity. Snail response to increased periphyton productivity was apparently mediated by a subtle cue, as periphyton biomass and taxonomic composition were very similar on grazed tiles in control and nutrient-enriched channels. Differences in snail reproduction within control and nutrient-enriched channels could not have caused the different snail densities because all snails counted on the tiles were orders of magnitude larger than 3-wk-old snails.

Taxonomic Response

Periphyton communities experiencing heavy grazing pressure by invertebrates are characteristically dominated by adnate algae that have a refuge close to the substratum (Sumner and McIntire 1982; Hill and Knight 1987; Steinman et al. 1987; Lowe and Hunter 1988; DeNicola et al. 1990). In streams like White Oak Creek where grazing snails are very abundant, basal cells of *Stigeoclonium* often dominate the periphyton (Stock and Ward 1989). These prostrate cells appear to be grazer resistant (Steinman et al. 1987; Steinman 1991) and may depend on grazers to remove overgrowing taxa that could diminish their access to light and nutrients (McCormick and Stevenson 1989). In this experiment, however, *Stigeoclonium* did not suffer in the absence of grazing. Potential competitors (especially the diatoms *Gomphonema dichotomum* and *Achnanthes minutissima*) were considerably more abundant in ungrazed periphyton, yet mean biovolume densities of *Stigeoclonium* were also several times larger on ungrazed tiles. The high variability of this alga in nutrient-enriched channels and the limited statistical power in the ANOVA (1, 4 degrees of freedom) resulted in grazing effects that were not statistically significant ($F = 3.00$, $P < 0.16$), but *Stigeoclonium* was the major contributor to the statistically significant increase in total algal biovolume when snails were excluded (Table 2). We

therefore cannot confirm the deleterious effect of grazer removal on *Stigeoclonium* abundance reported by McCormick and Stevenson (1989, 1991). In habitats like White Oak Creek, where algal biomass is very low, it may require more than 3 wk for other algae to accumulate and replace *Stigeoclonium* when snails are excluded.

Productivity Responses

In contrast with biomass, primary productivity was significantly affected by both grazing and nutrients. These two factors appeared to operate simultaneously, for areal-specific productivity was significantly increased by relaxing the constraint of either factor. The simultaneous, rather than hierarchical, effect of grazing and nutrients may be the result of these factors acting on different parts of the periphyton carbon budget. Grazers increase loss rates by consuming and dislodging productive algal cells, while nutrients operate to increase rates of biosynthesis. Although the removal of algal biomass was probably the largest effect of snails, they also reduced areal-specific productivity by lowering biomass-specific productivity.

The prevailing view in stream ecology is that positive indirect effects mitigate at least some of the negative effects of biomass loss caused by grazing. This view is supported by numerous reports of grazing-induced increases in chlorophyll-specific or AFDM-specific productivity (Gregory 1983; Lamberti and Resh 1983; Lamberti et al. 1987; Stewart 1987; Hill and Harvey 1990) and even a few reports of grazing-increased areal-specific productivity (Cooper 1973; Kesler 1981; Flint and Goldman 1975). The decreased chlorophyll-specific productivity caused by *Elimia* in this experiment was therefore unexpected, especially since snails markedly reduced periphyton biomass. Due to self-limitation within periphyton communities, biomass-specific primary production is highest when biomass is low (Pfeifer and McDiffett 1975; Marker 1976; Hudon et al. 1987). At low biomass, individual cells within the periphyton matrix are less likely to suffer from shading and nutrient depletion by overlying cells and consequently exhibit high biomass-specific productivity (Hill and Boston 1991).

The mechanism behind *Elimia*'s depression of biomass-specific productivity is unclear. One possible explanation is that *Stigeoclonium* basal cells are particularly inefficient photosyn-

thetically. They may funnel energy and resources into protective mechanisms or features that allow persistence under intense grazing pressure and are consequently unable to invest those resources in photosynthetic enzymes and pigments. Prostrate forms of marine algae that persist under intense grazing have lower growth rates than upright forms (Lubchenco and Cubitt 1980). However, grazing by *Elimia* also depresses biomass-specific productivity in periphyton dominated by diatoms (Mulholland et al. 1983) and cyanophytes (W. R. Hill, unpubl. data), indicating that *Stigeoclonium* does not have a unique response to grazing by *Elimia*. A second possibility is that mucus deposited by grazing *Elimia* may contain substances that inhibit periphyton metabolism, but gastropod mucus is usually regarded as a source of nitrogen and other stimulatory nutrients (e.g. Calow 1979; Connor and Quinn 1984; Herndl and Peduzzi 1989). A third possibility is that intense grazing by snails removes most algal cells except those that are in cracks and crevices in the substratum. These recessed cells may have reduced access to light or metabolic substrates (carbon, nutrients) and consequently exhibit low photosynthetic rates.

The direct experimental evidence for nutrient limitation was very strong. Although we did not perform indirect analyses (e.g. assays of alkaline phosphatase activity or periphyton elemental composition) that could corroborate nutrient limitation, nutrient enrichment significantly increased (1) snail density, (2) periphyton biomass where snails were excluded, and (3) areal-specific productivity of both grazed and ungrazed periphyton. These effects were statistically significant despite low statistical power available to detect nutrient effects (only 2 error degrees of freedom in the split-plot ANOVA). The absence of statistically significant nutrient effects on chlorophyll-specific productivity is inconsistent with the other strong indicators of nutrient limitation, but may be explained by low statistical power or increased chlorophyll *a* per cell in nutrient-enriched periphyton. Increases in cellular-specific chlorophyll *a* concentration commonly occur in nitrogen-efficient algae when nitrogen is added (Thomas and Dodson 1972; Osborne and Geider 1986; Cleveland and Perry 1987), and increases in cellular concentrations of chlorophyll *a* can obscure biomass-specific photosynthetic rates when chlorophyll *a* is used to normalize photosynthetic rates (Prezelin 1981). Increased chlorophyll *a* per cell could also explain why nutrient enrichment increased total chlorophyll *a* (micrograms per square centimetre of substrate) in grazed periphyton, but not AFDM or biovolume. There was no direct evidence, however, that the periphyton was nitrogen deficient.

We could not specify whether nitrogen or phosphorus limited productivity in White Oak Creek because our enrichments contained both nutrients. The N:P ratio in unamended White Oak Creek water at the end of the experiment was very close to the Redfield (1958) ratio of 15 that has been used to delimit the boundary between nitrogen and phosphorus limitation. Periphyton productivity in White Oak Creek may be alternately limited by either nutrient, depending on the temporal and spatial variability of the N:P ratio. Algal cells in any one location could be simultaneously limited by nitrogen and phosphorus, and the strong productivity response we observed in this experiment may have required both nutrients.

Despite the strength of the experimental evidence, it is somewhat surprising that periphyton as sparse as that in White Oak Creek could be nutrient limited. Flowing water provides constant renewal of nutrients (Wuhrmann 1974), so supply rates of nitrogen and phosphorus to attached cells should be adequate unless biomass develops to the point that a nutrient diffusion

gradient exists within the periphyton (Bothwell 1989). Periphyton on both grazed and ungrazed substrates exhibited little vertical development (<1 mm), and concentrations of nitrogen and phosphorus in White Oak Creek were only moderately low. Inherently high requirements for nutrients by the dominant taxa, *Stigeoclonium*, may be the reason why nutrient addition increased productivity of our thin periphyton. Filamentous green algae generally have relatively high extracellular requirements for nitrogen and phosphorus (Francke and Den Oude 1983; Horner et al. 1983; Bothwell 1989), and Rosmarin (1983) reported that the growth rate of *Stigeoclonium tenue* saturated at approximately $30 \mu\text{g P}\cdot\text{L}^{-1}$, a concentration several times greater than SRP in White Oak Creek. Thus, nutrient limitation in this experiment may have occurred because of Monod type kinetics at the cellular level instead of diffusion kinetics at the community level (Bothwell 1989).

We would like to emphasize that this experiment was performed just after leaf fall, a time when nutrients are most likely to be limiting. Nutrient demand by heterotrophic microbes on leaves is maximum within 20–30 d after leaf fall and presumably reduces the supply of nutrients to periphyton (Mulholland et al. 1984, 1985). More importantly, PAR reaching the stream bed had risen from <50 to >1300 $\mu\text{mol quanta}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ with the loss of canopy leaves. Nutrients are not likely to limit productivity when canopy leaves are present, as periphyton photosynthesis in shaded eastern Tennessee streams saturates above 100 $\mu\text{mol quanta}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Boston and Hill 1991). Summer-time experiments in White Oak Creek (W. R. Hill, unpubl. data), nearby Ish Creek (Hill and Harvey 1990), and Walker Branch (A. D. Steinman, unpubl. data) have demonstrated that periphyton productivity is very strongly light dependent. Several studies in shaded oligotrophic streams have shown that light must first be augmented before nutrient amendments have any effect on periphyton biomass or productivity (Gregory 1980; Triska et al. 1983; Hill and Knight 1988b). The relatively warm water temperature in early autumn probably accentuates nutrient demand by both autotrophic and heterotrophic microbes in White Oak Creek.

Photosynthesis-irradiance responses were not strongly affected by grazing or nutrients. We hypothesized that photosynthesis would saturate at higher light intensities as biomass accrual was released from grazing (Paul and Duthie 1989), but neither the onset of saturation (I_k) nor the irradiance of maximum photosynthesis (I_{max}) was significantly influenced by grazing. This lack of grazing effect is not altogether surprising, as even the biomass of the ungrazed, enriched periphyton was low compared with that found in other habitats. There was some evidence of moderate self-shading induced by nutrient enrichment: periphyton in nutrient-enriched channels had higher I_{max} values that were nearly significant (with only 2 error degrees of freedom) and appeared less susceptible to photoinhibition (significantly greater I_b values). Nutrient-induced self-shading may have been caused by increased cellular pigment levels (Osborne and Geider 1986; Cleveland and Perry 1987; Herzig and Falkowski 1989). The slope of the light-limited portion of the P-I curve (α) and the photoinhibition constant (β) were strongly affected by grazing and nutrients, but the interpretation of these effects is confounded by the dependence of these parameters on P_{max} (Platt et al. 1980; Hill and Boston 1991).

Despite considerable research on nutrient spiralling at the Oak Ridge National Laboratory, sustained increases in periphyton biomass as a result of in situ nutrient amendments have not been reported for eastern Tennessee streams. Elwood et al. (1981) suggested that the immigration of additional grazers

(*Elimia*) was responsible for the failure of their unreplicated phosphorus addition to maintain higher levels of periphyton biomass in Walker Branch. Our results in nearby White Oak Creek support both the potential of nutrient limitation and the ability of *Elimia* to respond numerically to localized increases in productivity. Increases in primary productivity on larger scales (e.g. the entire stream), however, would require significant functional responses by grazers to control periphyton biomass over the short term. *Elimia* is food limited and appears to have submaximal ingestion rates in White Oak Creek (W. Hill, unpubl. data), so a functional response of some magnitude to increased productivity is probable. Over the long term, *Elimia* would probably respond to increased primary production with increased reproduction. Long term diminishment of physico-chemical constraints on primary production should be manifest in increased grazer biomass rather than increased periphyton biomass when grazers are food limited.

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