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TOP-DOWN AND BOTTOM-UP CONTROL OF STREAM PERIPHYTON: EFFECTS OF NUTRIENTS AND HERBIVORES[1]

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Abstract. We conducted two experiments to determine the relative effects of herbivory and nutrients on an algal community in Walker Branch, a stream having effectively two trophic levels: primary producers and herbivorous snails. The first study (1989), performed in streamside channels, tested the effects of three factors: (1) stream water nitrogen (N), (2) phosphorus (P), and (3) snail grazing, on periphyton biomass, productivity, and community composition. The second study (1990), conducted in situ, tested the effects of snail grazing and nutrients (N + P). In the 1989 study, nutrients had positive effects, and herbivores had negative effects, on algal biomass (chlorophyll *a*, ash-free dry mass, total algal biovolume) and primary productivity (area- and chlorophyll-specific). Likewise, both nutrients and snail grazing exerted effects (+ and −, respectively) on biomass measured in the 1990 study (chlorophyll *a*, algal biovolume). Grazed communities were dominated by chlorophytes and cyanophytes, which were overgrown by diatoms when herbivores were removed. Algal species that were reduced most by herbivores were increased most by nutrient addition, and vice versa, suggesting a trade-off between resistance to herbivory and nutrient-saturated growth rates. Increases in algal biomass and productivity were slight with the addition of either N or P compared to responses observed when both nutrients were added together, suggesting that both nutrients were at growth-limiting levels. The greatest changes in periphyton structure or function were observed when both nutrients were added and simultaneously, grazers were removed, in contrast to lesser effects when nutrients were added under grazed conditions or grazers were removed at low nutrient levels, indicating dual control by both factors. Nutrient addition also positively affected snail growth in both experiments, indicating tight coupling between herbivore and algal growth (top-down effects) and that bottom-up factors that directly affected plant growth could also indirectly affect consumers belonging to higher trophic levels. Indices quantifying the direct effects of top-down factors relative to bottom-up factors (top-down index, TDI) and the importance of interactions between these factors (interaction coefficient, IC) were computed. These indices showed that the relative strength of top-down and bottom-up factors varied among biomass and productivity parameters and that top-down and bottom-up effects, alone, were less important than their combined effects.

Key words: algae; biomass; Elimia; *grazing; herbivory; nitrogen; nutrient limitation; periphyton; phosphorus; productivity; snails; stream.*

INTRODUCTION

Plant communities may be controlled from the bottom up (via growth limiting resources, e.g., nutrients) or from the top down (via consumption by herbivores). Using deductive reasoning, Hairston et al. (1960) suggested that terrestrial plant communities were primarily structured by competition for growth-limiting resources and not herbivory, because, they postulated, herbivores were controlled by their predators. However, Wiegert and Owen (1971) observed that plants in algal-based food webs, in contrast to terrestrial plants, are particularly vulnerable to consumption by herbivores. Others have suggested that top-down control can dominate depending on the number of trophic levels and the productivity of primary producers (Oksanen et al. 1981, Fretwell 1987, Oksanen 1990). Empirical work in lakes indicates that both factors are important in regulating phytoplankton populations (Carpenter et al. 1987, Leibold 1989, Hansson 1992). Models derived from lake systems further illustrate that plant populations can be under dual control by both resources and herbivores (McQueen et al. 1986).

Although the relative importance of top-down and bottom-up effects has been established in some lake communities (Lynch and Shapiro 1981, Vanni 1987, Vanni and Temte 1990), there has been less research

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in stream ecosystems (but see Stewart 1987, Power 1990). In this study, we focus on the relative importance of top-down (herbivore) and bottom-up (nutrient) effects on a stream periphyton community. Studies in many streams have shown that the growth of primary producers is nutrient limited (Stockner and Shortreed 1978, Elwood et al. 1981, Peterson et al. 1983, Bothwell 1985, Grimm and Fisher 1986, Pringle 1987, Hart and Robinson 1990), whereas others have demonstrated that herbivores largely control algal biomass and productivity (Lamberti and Resh 1983, Hart 1987, Hill and Knight 1987, Steinman et al. 1987, Power et al. 1988, Feminella et al. 1989). More recent studies have begun to address the effects of both nutrients and herbivory on stream algae (Stewart 1987, McCormick and Stevenson 1989, Winterbourn 1990, Mulholland et al. 1991, Hill et al. 1992), but have not been designed explicitly to test their relative importance in terms of top-down/bottom-up control.

This study was conducted in Walker Branch (WB), a woodland stream in eastern Tennessee. Primary producers in WB, like many forested, headwater streams, are potentially under limitation by both nutrients and herbivory; nutrient concentrations in water are low and densities of herbivores, high. Irradiance levels also potentially limit primary productivity in this stream (Steinman 1992, Rosemond 1993*a*); however, this study was conducted during the spring months, when irradiance levels were relatively high, and light should be least limiting. The most abundant herbivore in WB is the snail *Elimia clavaeformis* (Family: Pleuroceridae), which comprises >95% of invertebrate biomass (Newbold et al. 1983*a*) and occurs at densities >1000 individuals/m^2 year-round (A. D. Rosemond, *unpublished data*). Very low densities of crayfish, salamanders (Newbold et al. 1983*a*), darters, and minnows are present, but do not appear to regulate snail densities. In effect, the resulting trophic structure in WB appears to be quite simple, consisting primarily of only two levels: stream algae and grazing snails.

In an even-numbered trophic level system, such as the one studied here, Fretwell's (1987) model predicts that plants will be controlled from the top down by herbivores. That is, removal of herbivores should result in an increase in plant biomass. Additionally, in systems such as WB, in which there are simple direct links between plants and herbivores (in contrast to more complex, reticulate food webs), Strong (1992) predicts that plants will be under top-down control. In an earlier study based on a material balance of ^{32}P added to WB, Elwood and Nelson (1972) showed that grazing rates were equivalent to rates of net primary production, suggesting control of algal biomass by herbivores. However, an experimental phosphorus enrichment of WB resulted in increased algal biomass, suggesting nutrient limitation, although the increased growth was not sustained, presumably due to consumption by *E. clavaeformis* (Elwood et al. 1981). These results raise the question of whether algal growth in this stream is controlled more strongly by herbivory or nutrients.

We investigated the relative importance of herbivores and nutrients to periphyton in WB with two experiments, each lasting 7 wk. One experiment, conducted in streamside, flow-through channels, tested the separate and interactive effects of nitrogen (N), phosphorus (P), and snail grazing on algal biomass, productivity, and community composition. The channels offered experimental units in which nutrient levels and snail densities could be manipulated and replicated. A second experiment, conducted in situ, tested the effects of nutrients (N + P) and herbivory under natural stream conditions.

Methods

Study site

Walker Branch is a woodland stream (latitude 35°58′ N, longitude 84°17′ W) located on the Department of Energy's Oak Ridge Reservation in eastern Tennessee. WB flows over bedrock outcrops, gravel, and cobble. Pools in the stream are relatively shallow (typically <1 m in depth) and are underlain by gravel and organic sediments. Riparian vegetation consists largely of deciduous trees; however, these studies were conducted in the early spring months, before maximum leaf-out. More detailed descriptions of Walker Branch and its catchment are in Curlin and Nelson (1968) and Johnson and Van Hook (1989).

Streamside channel experiment (1989)

The first study was conducted from 15 March 1989 to 3 May 1989 in flow-through channels (102 cm long × 8 cm wide) constructed of Plexiglas, positioned in a small clearing next to the stream. We used a factorial design to investigate the effects of nitrogen (two levels), phosphorus (two levels), snail herbivory (two levels), and their interactive effects. Nutrient treatments consisted of (1) control, (2) addition of $NaNO_3$ and NH_4Cl to ≈210 μg/L NO_3^--N and 40 μg/L NH_4^+-N, (3) addition of P to ≈35 μg/L as K_2HPO_4, and (4) addition of both N and P. Nutrient concentrations were increased by continuously dripping (via metering pumps) concentrated nutrient solutions from carboys into mixing chambers upstream of individual channels to achieve roughly 10 times the yearly average concentrations in WB stream water. We wanted to increase nutrient concentrations above limiting levels, but at the same time, not above levels that would occur naturally in other streams (i.e., without anthropogenic influence). Grazing treatments consisted of (1) snails added at ambient stream densities (≈1300 snails/m^2 as determined from counts made with a 250-cm^2 underwater viewer) and (2) no snails. The eight different treatment combinations were duplicated and randomly assigned to 16 different channels. Unglazed ceramic

tiles (surface area = 5.3 cm^2), which had been placed in WB for colonization of periphyton several months prior to the study, were transferred to the channels ≈10 d prior to the start of the experiment and used as sampling units. Light levels at the stream surface were estimated using ozalid paper light meters (Friend 1961) to determine levels of photosynthetically active radiation (PAR) and to compare light levels across treatments. A layer of mosquito netting was placed over the channels to reduce incident light to levels that were typical of the stream at this time of year. Water velocity in the channels was maintained at ≈10–15 cm/s, which is characteristic of WB.

Carbon fixation rates of periphyton were determined in the laboratory at the beginning and at the end of the experiment using recirculating-flow chambers described in Boston and Hill (1991). Five tiles were randomly collected from each channel and placed with tiles from the same treatment in glass chambers containing 1 L of filtered (Gelman Type A/E filter) water from the treatment from which they were collected. All chambers (n = 8) were placed in a large tank in which water temperatures were maintained within 2°C of ambient. Light was provided by a metal halide lamp suspended over the tank and kept approximately at midday levels using screens. Water samples (25 mL) were taken from each chamber prior to the incubation for determination of total inorganic carbon (TIC) by infrared gas analysis (OI Model 700 Total Carbon Analyzer). Approximately 180–360 kBq of $NaH^{14}CO_3$ (specific activity 0.74 MBq/mmol) was added to the water in each chamber. After a 3-h incubation, tiles were removed from chambers, rinsed in stream water, and placed in jars containing 10 mL dimethyl sulfoxide (DMSO) for extraction of chlorophyll and ^{14}C-labelled photosynthate in the dark overnight at room temperature using the methods of Palumbo et al. (1987). Chlorophyll *a* was measured at other times during the experiment (weeks 1, 3, and 5) on five tiles that were collected from each channel and similarly extracted in 10 mL DMSO. Phaeopigment-corrected chlorophyll *a* level was determined on subsamples of the DMSO extract spectrophotometrically (Strickland and Parsons 1968) and ^{14}C was assayed by liquid scintillation counting. Periphyton ash-free dry mass (AFDM) was estimated at the beginning and end of the study by collecting five tiles from each channel, and determining differences between dry (at 60°C for 24 h) and ashed (at 500°C for 24 h) mass of each tile.

Five additional tiles were collected from each channel at the beginning of the experiment, during week 3, and at the end of the experiment to determine changes in algal community structure. Algae were brushed from the tiles with a toothbrush and the resultant slurry was preserved in 2% glutaraldehyde. Samples were processed with a tissue homogenizer, as required, to break up large aggregations, and then sonicated. Algal units with obvious cytoplasm (single cells or colonies) (>500/sample) were counted and identified at 400× using a Palmer–Maloney cell. All taxa were identified to the lowest possible taxonomic unit, with diatoms typically keyed to genus. To key diatom taxa to species at 1000×, permanent slides were made of an oxidized subsample using Hyrax medium. Biovolumes of all taxa were obtained by measuring individual cells (1–20 cells/taxon) with an ocular micrometer and using geometric formulae (modified from Kellar et al. 1980) to determine cell volume.

Periphyton nitrogen, phosphorus, and carbon contents were determined on the final sampling date. Approximately 20 tiles were collected from each channel, brushed with a toothbrush into a beaker, and the removal material dried at 60°C. A subsample of dried periphyton from each channel (5–10 mg) was weighed and analyzed for carbon and nitrogen content using a Carlo–Erba Model NA1500 CNS analyzer. An additional subsample of dried periphyton was weighed and ashed (at 500°C), and the ash was leached in 5 mL of hot 1 mol/L HCl for 30 min to extract P. The acid leachates were diluted to 100 mL with distilled water and phosphorus concentrations were determined using the ascorbic acid method as described for water samples.

Mass gain by snails during the experiment was estimated by changes in the mean width of 80 snails from each channel. Snail widths were initially measured with calipers to the nearest 0.01 mm and measured snails were marked with paint. Width of each marked snail was remeasured at the end of the experiment. Increases in mass were determined from measurements of snail width and a width : AFDM regression ($y = 1.2332 \times 10^{-5}x^{3.98363}$, $n = 50$, $R^2 = 0.96$) computed from snails previously taken from WB. Because we wanted to evaluate the effects of *Elimia* in this system without the confounding effects of changes in the densities of any other invertebrates, we removed other grazers that colonized the streamside channels at low densities when they were observed.

Water samples were taken weekly and filtered in the field through precombusted, washed glass fiber filters (Gelman type A/E, pore size = 1 μm). Concentrations of soluble reactive phosphorus (SRP), ammonium nitrogen (NH_4^+-N), and nitrate plus nitrite nitrogen ($[NO_3^- + NO_2^-]$-N) were measured in the filtrate. Concentrations of SRP were measured using the ascorbic acid method (American Public Health Association 1985), NH_4^+-N by phenate colorimetry using an autoanalyzer (Technicon TRAACS 800), and $[NO_3^- + NO_2^-]$-N by Cu–Cd reduction followed by automated colorimetric analysis (United States Environmental Protection Agency 1983).

In situ stream study (1990)

The second study was conducted from 5 March 1990 to 24 April 1990 in a second-order reach of Walker Branch about 150 m downstream from the streamside

TABLE 1. Nutrient concentrations, snail densities, and light levels during the 1989 and 1990 studies of a woodland stream community. Data are means* with ranges in parentheses.

Nutrient concentrations (μg/L)					
Control treatments = Stream			Enriched treatments		
$PO_4^{=}$-P	NO_3^--N	NH_4^+-N	$PO_4^{=}$-P	NO_3^--N	NH_4^+-N
21 March–1 May 1989					
1.94 (0.9–3.6)	18.3 (8.0–47.7)	6.0 (0–11.0)	36.6 (24.8–48.8)	207.8 (55.6–324.3)	33.8 (17.3–43.6)
8 March–23 April 1990					
2.4 (1.5–4.0)	10.1 (6.8–13.5)	2.0 (0–5.0)	44.1 (23.1–58.2)	223.3 (118.9–282.1)	44.1 (19.9–60.7)

Snail densities (no./m²)		
2 February–1 June 1989	15 March–3 May 1989	
Stream	"Grazed" channels	"Ungrazed" channels
1580 (1319–1736)	1368 (1352–1385)	0
26 January–30 May 1990	5 March–23 April 1990	
Stream	"Grazed" enclosures	"Ungrazed" enclosures
1199 (1074–1328)	1186 (1038–1483)	126 (0–198)

Light levels (photon flux density, $mmol \cdot m^{-2} \cdot d^{-1}$)			
5 March–27 April 1989		5 March–24 April 1990	
Stream	Channels	Stream	Enclosures
3394 (898–5438)	2872 (2195–3882)	3526 (2121–4235)	3134 (1929–4338)

* Means based on 7 weekly averages (from $n = 8$ samples in enriched treatments in 1989, $n = 6$ samples in enriched treatments in 1990, and $n = 1$ for control treatments during both studies from each week). Snail density means based on 3 averages from $n = 40$ samples taken from the stream bimonthly over the period indicated. "Grazed" and "ungrazed" channel means in 1989 based on 2 averages from $n = 8$ samples (channels) over the period indicated. "Grazed" and "ungrazed" enclosure means in 1990 based on 6 averages from $n = 6$ samples (enclosures) over the period indicated. Photon flux density means based on 3 averages from $n = 12$ stream readings over the period indicated. Channel means based on 3 averages (from $n = 2$ channels) in 1989. Enclosure means based on 2 averages (from $n = 12$ and $n = 4$ enclosures) in 1990.

channels used in the 1989 study. Twelve enclosures (1171 cm^2 each) were constructed on bedrock within a 15 m reach of the stream. Enclosures were constructed of 1 mm mesh stainless steel hardware cloth attached to a frame of bricks and surrounded by a single piece of black plastic mesh (2 mm). To ensure good contact with the bedrock, a hem of netting was attached to the bottom of the enclosures and filled with pea-sized gravel and sand. The twelve enclosures were divided into upstream ($n = 6$) and downstream ($n = 6$) groups separated by ≈5 m. Water velocity was reduced from ≈20–30 cm/s in this area of the stream to 8–10 cm/s within the enclosures; however, velocity was reduced to a similar extent in all enclosures and was similar to slower flowing areas of the stream. Nutrients were increased in all downstream enclosures by continuously dripping a concentrated nutrient solution ($NaNO_3$, NH_4Cl, and H_3PO_4) into the stream from a carboy (Mariotte bottle; Peterson et al. 1983) on the stream bank. Water samples were taken weekly and light levels were determined as for the 1989 study. Two grazing treatments (ambient densities [1200 snails/m^2] or no snails) were randomly assigned to enclosures within each nutrient treatment. We treated the design statistically as a factorial (nutrients × grazers), but we give a conservative interpretation of nutrient effects, as they were not true treatment replicates (sensu Hurlburt 1984), being confounded by distance downstream.

Chlorophyll *a* was measured at the beginning, during weeks 1, 3, 5, and at the end of the experiment. Algal community composition was determined initially, after 3 wk, and at the end of the experiment. Benthic algae were scraped directly off of the bedrock within an area circumscribed by a cylinder, with three samples taken per enclosure per date. Chlorophyll *a* was determined from subsamples that were filtered on to glass fiber filters (Whatman, pore size = 0.45 μm) and extracted and analyzed as described earlier. For determination of total algal biovolume and community composition, the three samples from each enclosure were combined before analyses, and processed as described for the 1989 study.

Snail growth was measured by individually marking snails with numbered bee tags (Chr. Graze, K.G., Weinstadt, Germany). Initially, 40 snails/enclosure (total = 240) were measured for width with calipers to the nearest 0.01 mm and tagged. After 10 d, ≈20 more tagged snails were added per enclosure to compensate

TABLE 2. ANOVA results of periphyton biomass and productivity from the midpoint (week 3) and end (week 7) of the 1989 experiment. Data given are F values from ANOVAs of chlorophyll a ($\mu g/cm^2$) from week 3 (CWK3) and week 7 (CWK7), ash-free dry mass ($\mu g/cm^2$) (AFDM), total algal biovolume ($\mu m^3/mm^2$) from week 3 (BVOL3) and from week 7 (BVOL7), area-specific productivity (as ^{14}C uptake, $\mu g \cdot cm^{-2} \cdot h^{-1}$) (ASP) and chlorophyll-specific productivity (as ^{14}C uptake, $\mu g \cdot \mu g^{-1} \cdot$

Treatment	df	CWK3	CWK7	AFDM	BVOL3
Overall	7	8.47**	16.23***	5.97*	140.58****
G	1	(−)30.88***	(−)10.46*	(−)13.88**	(−)956.74****
N	1	(+) 3.82†	(+)58.32****	(+)10.97*	(+) 5.86*
P	1	(+) 8.06*	(+)23.87**	(+) 4.28†	(+) 15.46**
N × P	1	2.28	10.46*	1.61	0.01
P × G	1	8.36*	0.63	1.44	5.85*
N × G	1	3.99†	6.10*	6.52*	0.06
N × P × G	1	1.88	3.74†	3.12	0.05

† $P < .10$, * $P < .05$, ** $P < .01$, *** $P < .001$, **** $P < .0001$.

for those that emigrated. During the rest of the experiment, snails were removed from ungrazed enclosures every 1–2 d and snails were added to grazed enclosures to compensate for immigration and emigration. Other invertebrates were also removed from enclosures when they were observed. We recovered an average of 25 tagged snails/enclosure at the end of the study from which growth estimates were determined as described for the 1989 experiment.

Statistical analyses

Data from the 1989 study were analyzed by a three-factor (nitrogen, phosphorus, grazing) analysis of variance (ANOVA) using the ANOVA procedure of Statistical Analysis Systems (SAS Institute 1985). Values used in the analyses of AFDM, chlorophyll *a*, area-specific and chlorophyll-specific productivity were means from five tiles from each replicate channel. The model we used tested for main effects of nitrogen addition (N), phosphorus addition (P), and grazing presence (G), and all possible interactive effects (P × G, N × G, P × N, P × N × G). Data from the 1990 study were analyzed by a two-factor [nutrients (N + P), grazing] ANOVA, which tested for main effects and interactions [(N + P) × G]. Algal biovolumes were log transformed and algal percentages were arcsine transformed (Zar 1984) before statistical analyses. Other percentage data (%C, %N, and %P of periphyton in 1989, and snail growth in 1989 and 1990) were also arcsine transformed. Snail growth data from the 1989 study were analyzed using a two-factor (N, P) ANOVA and from the 1990 study using a t test. Unless stated otherwise, ANOVAs on pretreatment values were not significant. Most data from these two studies are presented here. Additional data (results from weeks 1 and 5 from both experiments and more detailed taxonomic analyses) can be found in Rosemond (1993*b*).

RESULTS

Nutrient concentrations, snail densities, and light levels

During the 1989 and 1990 studies, mean nutrient ($PO_4^{\equiv}$-P, NO_3^--N, and NH_4^+-N) concentrations in the stream were low, and the enrichments resulted in a 15–20× increase in concentrations in the streamside channels and the downstream enclosures (Table 1).

Snail densities in grazed treatments in both experiments were generally similar to those in the stream (Table 1). Densities in the ungrazed treatments were maintained at 0 snails/m^2 in the 1989 study, but in the 1990 study, immigration of snails resulted in mean densities of 126 snails/m^2 in "ungrazed" enclosures. Other grazers were effectively excluded from the channels and enclosures, except for baetid mayflies, which colonized the streamside channels to a small degree. Counts of these mayflies, made on the last day of the experiment, indicated that densities of mayflies were not significantly different (one-way ANOVA among nutrient treatments), but were higher in N, P, and (N + P) channels than in controls (means ± 1 SE): control = 10.25 ± 2.27 mayflies/m^2, N = 20.5 ± 4.07, P = 19.5 ± 2.46, (N + P) = 35.0 ± 12.04.

Average light levels were similar between the stream and enclosures or channels during both experiments (Table 1).

Streamside channel experiment (1989)

Algal biomass.—Snails had a negative effect and P addition had a positive effect on chlorophyll *a* 3 wk after treatments were initiated; a significant P × G interaction reflected that differences between P and control treatments were observed in ungrazed, but not grazed, treatments (Table 2). At 3 wk, chlorophyll *a* was 10× greater in ungrazed treatments to which both N and P were added, compared to grazed treatments (Fig. 1a, b). By the end of the study (week 7), there was a negative effect of grazing on chlorophyll *a*, as well as positive effects of both N and P additions, and N × P and N × G interactions. The N × P effect was due to disproportionately higher chlorophyll *a* in (N + P) treatments than in treatments to which N and P were added singly. The N × G interaction indicated that N effects were more pronounced under ungrazed than grazed conditions.

All grazed treatments were lower in AFDM and algal biovolume than ungrazed treatments, with the greatest

h^{-1}) (CSP) from week 7. Treatment effects: G = grazing presence, N = nitrogen addition, P = phosphorus addition. (+) = positive treatment effects, (−) = negative treatment effects.

BVOL7	ASP	CSP
9.11**	73.81****	14.11***
(−)48.46****	(−)116.07****	(−)62.91****
0.20	(+)135.16****	0.73
(+)10.31**	(+)124.55****	(+)29.00***
2.69	60.17****	2.13
0.12	6.11*	0.55
0.13	47.22****	1.47
1.83	27.38***	1.97

values observed in ungrazed treatments to which both N and P had been added (Figs. 2 and 3). ANOVAs indicated that snails had negative effects and nutrients generally had positive effects on these biomass characteristics, with a significant N × G interaction for AFDM and a significant P × G interaction for biovolume after 3 wk (Table 2).

Productivity and periphyton N, P, and C content.—There were positive effects of N and P addition, negative effects of snail grazing, and significant interaction effects on periphyton area-specific productivity (ASP) at the end of the experiment (Table 2). The significant interaction effects indicated all three factors contributed to ASP; the greatest ASP was observed in ungrazed treatments to which both N and P had been added (Fig. 4a). Productivity per unit chlorophyll (CSP) was positively affected by P addition and negatively affected by grazing (Table 2, Fig. 4b).

Snail grazing and P addition both had positive effects on the N, P, and C content of periphyton and snail grazing a negative effect on the C:N ratio (Table 3a). The lowest values of %N, %P, and %C were in the ungrazed, control (low nutrient) treatment and the highest values in the grazed, (N + P) treatment; the lowest C:N was in the grazed, (N + P) treatment (Table 3b).

Algal community composition.—Changes in the composition of the algal community resulted from both nutrient and grazing manipulations, but were primarily driven by grazing effects. That is, communities changed much more when grazers were removed, with no addition of nutrients, than they did when nutrients were added under grazed conditions. Treatments were very similar in composition at the beginning of the study, being largely comprised of the diatoms *Cocconeis placentula* (Ehr.), *Peronia intermedium* (H.L. Sm.), and *Gomphonema olivaceoides* (Hust.) (each making up >10% total biovolume in most channels). After 3 wk, the proportion of diatoms declined in grazed treatments and increased in ungrazed treatments (Rosemond 1993*b*). Grazed communities were dominated by the diatoms *C. placentula* and *P. intermedium*, the

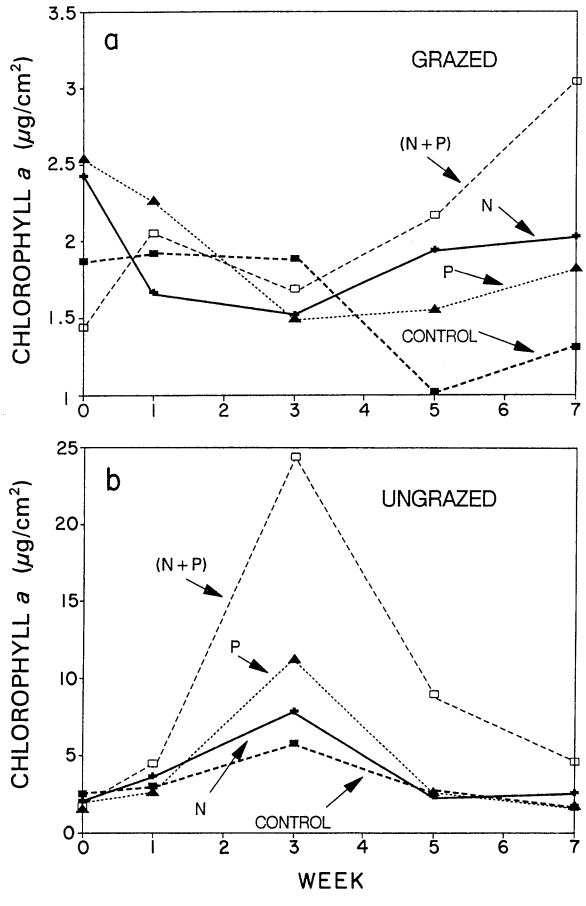

FIG. 1. (a) Chlorophyll *a* level during the 1989 study, grazed treatments. (b) Chlorophyll *a* during the 1989 study, ungrazed treatments. Abscissa label, week, = number of weeks since treatments were started; week 0 = initial sampling. Control = ambient stream water, N = addition of N, P = addition of P, (N + P) = addition of both N and P. Note that ordinates have different scales.

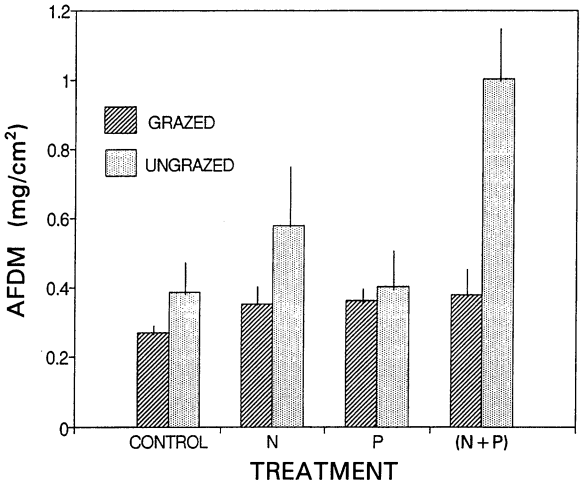

FIG. 2. Ash-free dry mass of periphyton on tiles from week 7 of the 1989 study. Control = ambient stream water, N = addition of N, P = addition of P, and (N + P) = addition of both N and P. Grazed = snails added at natural densities, ungrazed = snails not added. Error bars = 1 SE.

chlorophyte, *Stigeoclonium tenue* (Kuetz.) (basal cells) and cyanophytes (*Chamaesiphon investiens, Heteroleibleinia*), most of which had a prostrate growth form. Ungrazed communities were dominated by a filamentous diatom *Melosira varians* (Ag.) (most abundant), an erect diatom, *P. intermedium,* and a filamentous chlorophyte, *Draparnaldia* (Bory) sp. By the end of the study, diatoms (*M. varians, C. placentula,* and *P. intermedium*) continued to dominate ungrazed communities, with chlorophytes (*S. tenue* basal cells) and cyanophytes (*C. investiens*) being more important in grazed treatments (Fig. 3a, b).

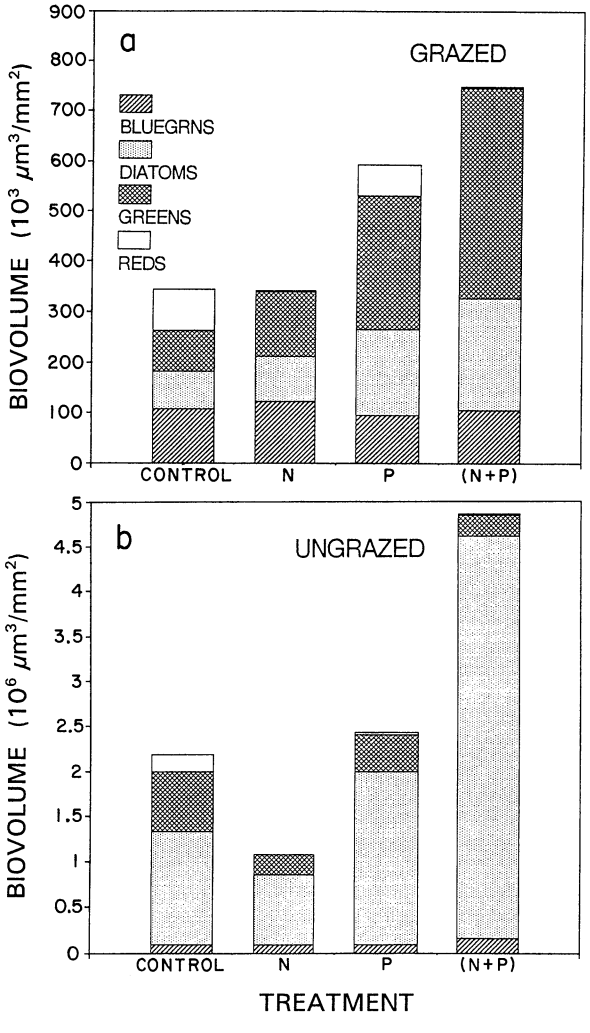

FIG. 3. Algal taxonomic composition and total algal biovolume from grazed (a), and ungrazed (b) treatments from week 7 of the 1989 study. Control = ambient stream water, N = addition of N, P = addition of P, and (N + P) = addition of both N and P. Bluegrns = biovolume of algae belonging to Division Cyanophyta; Diatoms = biovolume of algae belonging to Division Chrysophyta, Class Bacillariophyceae; Greens = biovolume of algae belonging to Division Chlorophyta; Reds = biovolume of algae belonging to Division Rhodophyta. Note that ordinates have different scales.

We tested for treatment effects on the 10 most abundant taxa and found that snail grazing had negative effects on the biovolume of several diatoms (*Achnanthes* (Bory) spp., *C. placentula, Gomphonema* (Ehr.) spp., *P. intermedium, M. varians*) and the chlorophyte *Draparnaldia* sp. (Table 4a). Snail grazing had positive effects on the biovolume of *Audouinella* sp., *C. investiens,* and *Heteroleibleinia,* presumably by removing competing taxa. Positive effects of nutrients were found only for species of diatoms. There were negative effects of nutrients on *Audouinella* sp., *C. investiens,* and *Heteroleibleinia.*

Grazing also reduced the proportion of diatom species and increased the proportion of chlorophytes, rhodophytes, and cyanophytes (Table 4b). Effects of nutrients on percentage composition were positive only for two diatom species; otherwise, effects of nutrients were negative.

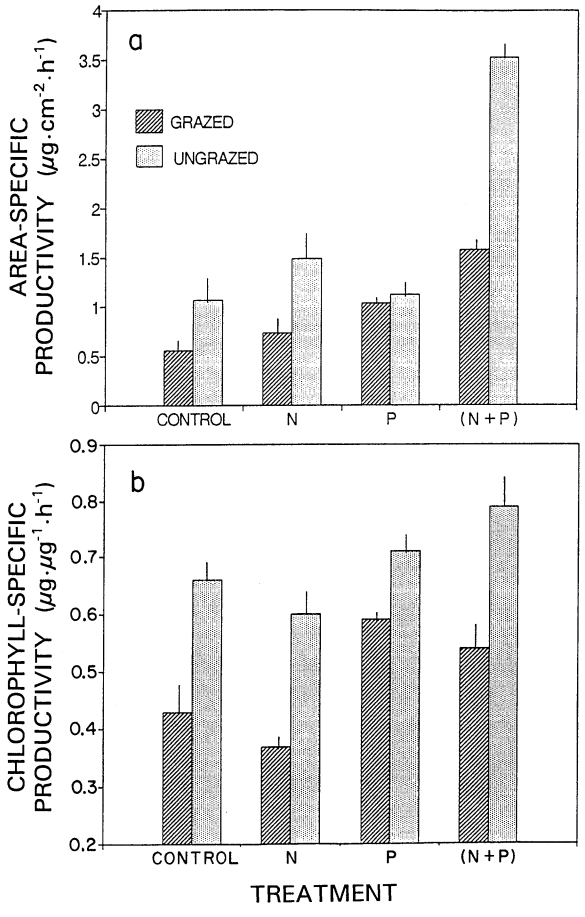

FIG. 4. Area-specific productivity (as ^{14}C uptake, $\mu g \cdot cm^{-2} \cdot h^{-1}$) (a) and chlorophyll-specific productivity (also as ^{14}C uptake, $\mu g \cdot \mu g^{-1} \cdot h^{-1}$) (b) of periphyton from the 1989 streamside channel study. Control = ambient stream water, N = addition of N, P = addition of P, and (N + P) = addition of both N and P. Grazed = snails added at natural densities, ungrazed = snails not added. Error bars = 1 SE.

TABLE 3. (a) ANOVA results of periphyton nutrient content and C:N ratios from the 1989 experiment. Data are from ANOVAs of %C, %N, %P, and C:N (mass ratios) from periphyton C, N, and P analysis. Treatment effects and degrees of freedom as in Table 2. (+) = positive treatment effects, (−) = negative treatment effects.

	%C		%N		%P		C:N	
Treatment	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
G	(+)31.54	.0005	(+)30.46	.0006	(+)28.99	.0007	(−)10.87	.01
N	NS		NS		NS		NS	
P	(+) 7.30	.03	(+) 5.52	.05	(+)16.27	.004	NS	
N × P	NS		NS		NS		NS	
P × G	3.42	.10	4.82	.06	NS		NS	
N × G	NS		NS		NS		NS	
N × P × G	NS		NS		NS		NS	

(b) Mean ± 1 SD of the parameters described in Table 3a. Cont = control (no nutrients added) treatments.

Treatment combination	%C	%N	%P	C:N
Grazed (N + P)	32.88 ± 5.38	3.91 ± 0.65	.22 ± 0.01	8.42 ± 0.02
Ungrazed (N + P)	15.89 ± 0.86	1.09 ± 0.07	.12 ± 0.006	16.64 ± 1.10
Grazed, N	21.38 ± 6.64	1.94 ± 0.84	.11 ± 0.025	11.32 ± 1.48
Ungrazed, N	16.45 ± 2.23	1.28 ± 0.65	.09 ± 0.010	14.24 ± 5.94
Grazed, P	25.11 ± 2.98	2.51 ± 0.48	.21 ± 0.008	10.08 ± 0.74
Ungrazed, P	16.15 ± 1.56	1.15 ± 0.24	.13 ± 0.032	14.50 ± 4.38
Grazed, Cont	20.26 ± 2.79	1.78 ± 0.42	.17 ± 0.056	11.52 ± 1.18
Ungrazed, Cont	13.12 ± 0.71	0.95 ± 0.21	.08 ± 0.027	14.08 ± 2.40

Snail growth.—We found marginally significant, positive effects of N ($F = 3.86$, $P = .1066$) and P ($F = 5.88$, $P = .0597$) additions on snail growth. When we compared growth of snails in N, P, and (N + P) treatments to growth in control treatments (Dunnett's test; Zar 1984), we found that the only difference was between controls and (N + P) treatments (and only at $P < .10$) (Fig. 5a).

Spring 1990 study

Algal biomass.—Effects of nutrients and grazers on chlorophyll *a* in the 1990 study were similar to those observed in 1989, insofar as there were positive effects of nutrient addition (N + P) and negative effects of grazing (Table 5). The (N + P) × G interaction was also significant after 7 wk, which was due to much larger differences in chlorophyll *a* in ungrazed vs. grazed high nutrient treatments compared to differences between grazed and ungrazed controls (Fig. 6).

Although we found no significant treatment effects on total algal biovolume at the beginning of the study (before treatments were started), large differences in biovolume were observed among treatment replicates and thus, the average differences between initial biovolume and biovolume on weeks 3 and 7 in each enclosure were used in ANOVAs (instead of absolute biovolume). After 3 wk, there was a positive effect of nutrient addition and a marginally significant negative effect of grazing on biovolume (Table 5). Both nutrient and grazing effects were significant after 7 wk.

Algal community composition.—Initially, communities in enclosures were dominated by chlorophytes (*Rhizoclonium hieroglyphicum* (Ag.)) and cyanophytes (*Heteroleibleinia* sp., *Chroococcus minutus* (Kuetz.)). After 3 wk, diatoms (*G. dichotomum* (Kuetz.), *Epithemia intermedia* (Fricke), *P. intermedium, C. placentula*) increased in importance in the ungrazed, high nutrient treatment (Rosemond 1993). After 7 wk, grazed communities continued to be dominated by chlorophytes and cyanophytes (which had primarily prostrate growth forms), whereas ungrazed communities had a greater proportion of diatoms (*Gomphonema* spp., *E. intermedia, C. placentula*), having both erect and prostrate growth forms (Fig. 7).

There were few significant effects of nutrients or grazing on the 10 most abundant species after 3 wk. However, by week 7, there were negative effects of grazing on the absolute and (for some species) percentage biovolume of all diatoms combined, and the diatoms *Gomphonema* spp., *C. placentula, P. intermedium,* and *M. varians,* when analyzed separately (Table 6a, b). The only positive effects of grazing were on the proportions of *C. minutus* and *R. hieroglyphicum.* Nutrient effects on the absolute or relative biovolume of individual species, when they occurred, were positive.

Snail growth.—Differences between average snail growth in control vs. (N + P) treatments were large (Fig. 5b), but were only marginally significant due to high variability within treatments ($t = 2.56$, $P = .06$).

Comparing top-down vs. bottom-up effects in both experiments

The relative strengths of top-down and bottom-up effects were compared by contrasting the effects of nu-

TABLE 4. (a) ANOVA results of log biovolume of different algal species from the 1989 experiment. Treatment effects: G = grazing presence, N = nitrogen addition; P = phosphorus addition. (+) = positive treatment effects, (−) = negative treatment effects. All taxa making up >5% average biovolume/treatment in >1 treatment/date are included. (±) Refers to interaction terms that reverse the sign of the main effect(s). A full ANOVA model (G, N, P, P × G, N × G, N × P, N × P × G) was tested for each species. Only those effects that were significant during either week 3 or week 7 are listed, otherwise "no effects" is listed. Degrees of freedom as in Table 2. (b) ANOVA results of percentage biovolume of different algal species from the 1989 experiment. Other notation as in Table 4a.

Species/ Treatment	Week 3		Week 7	
	F	*P*	*F*	*P*
(a) Log biovolume ANOVA				
Chlorophyta				
Draparnaldia sp.				
G	(−) 28.46	.0007	NS	
Stigeoclonium tenue				
(basal cells)	no effects		no effects	
G	(+)136.90	.0001	(+) 11.45	.01
N × G	NS		6.95	.03
Chrysophyta (Class: Bacillariophyceae)				
Achnanthes (all spp.)				
G	(−) 29.19	.0006	(−) 37.85	.0003
N	(+) 17.88	.003	(+) 20.80	.002
P	(+) 7.08	.03	(+) 6.14	.04
N × P	NS		11.80	.009
Cocconeis placentula				
G	NS		(−) 5.64	.04
Gomphonema (all spp.)				
G	(−)171.99	.0001	(−) 24.65	.001
Peronia intermedium				
G	(−)192.4	.0001	(−) 57.48	.0001
N	(+) 5.89	.04	(+) 8.06	.02
N × G	NS		(±) 6.72	.03
Melosira varians				
G	(−)293.42	.0001	(−) 58.57	.0001
P	NS		(+) 6.16	.04
Cyanophyta				
Chamaesiphon investiens				
G	(+) 44.40	.002	(+) 68.55	.0001
P	(−) 86.10	.0001	(−) 21.02	.002
P × G	(±) 78.51	.001	NS	
Heteroleibleinia sp.				
G	(+) 5.11	.05	NS	
N	(−) 9.59	.02	NS	
P	(−) 32.80	.0004	NS	
N × P	(±) 13.84	.006	NS	
P × G	(±) 15.86	.004	NS	
N × P × G	(±) 12.56	.008	NS	
Rhodophyta				
Audouinella sp.				
G	(+)336.05	.0001	NS	
N	NS		(−) 10.37	.01

Species/ Treatment	Week 3		Week 7	
	F	*P*	*F*	*P*
(b) Percentage biovolume ANOVA				
Chlorophyta				
Draparnaldia sp.				
	no effects		no effects	
Stigeoclonium tenue				
(basal cells)				
G	(+)136.90	.0001	(+) 11.45	.01
N × G	NS		6.95	.03
Chrysophyta (Class: Bacillariophyceae)				
Achnanthes (all spp.)				
G	(+) 24.48	.001	NS	
N	(+) 15.19	.005	(+) 10.93	.01
P	(+) 8.51	.02	NS	
N × P	6.89	.03	NS	
P × G	10.34	.01	NS	
N × G	12.16	.008	NS	
Cocconeis placentula				
G	(+)217.34	.0001	NS	
Gomphonema (all spp.)				
G	NS		(−) 9.45	.02
P	(−) 6.09	.04	NS	
Peronia intermedium				
G	NS		(−) 46.67	.0001
P	NS		(−) 5.45	.05
Melosira varians				
G	(−)136.04	.0001	(−) 25.77	.001
P	NS		(+) 11.35	.01
P × G	NS		6.35	.04
Cyanophyta				
Chamaesiphon investiens				
G	(+) 35.21	.0003	(+)140.33	.001
P	NS		(−) 35.84	.0003
P × G	NS		6.74	.03
Heteroleibleinia sp.				
G	(+)119.55	.0001	(+) 28.26	.0007
N	(−) 7.13	.03	NS	
P	(−) 15.74	.004	NS	
N × G	9.92	.01	NS	
Rhodophyta				
Audouinella sp.				
G	(+) 93.94	.0001	NS	
N	(−) 7.59	.03	(−) 5.91	.04
P	NS		(−) 5.39	.05
N × G	7.59	.03	NS	

TABLE 5. ANOVA results of measures of periphyton biomass from the midpoint (week 3) and end (week 7) of the 1990 experiment. Data are F values from ANOVA of chlorophyll a ($\mu g/cm^2$) from week 3 (CWK3) and week 7 (CWK7) and algal biovolume difference ($\mu m^3/mm^2$) from initial conditions from week 3 (BVOL3) and week 7 (BVOL7). G = grazing presence, (N + P) N and P addition. (+) = positive treatment effects, (−) = negative treatment effects.

Treatment	df	CWK3	CWK7	BVOL3	BVOL7
Overall	3	8.11**	23.04***	3.92†	5.56*
G	1	0.97	(−)11.83**	(−)4.50†	(−)7.74*
(N + P)	1	(+)18.66**	(+)50.49****	(+)7.10*	(+)8.15*
(N + P) × G	1	4.71	6.81*	0.15	0.80

† $P < .10$, * $P < .05$, ** $P < .01$, *** $P < .001$, **** $P < .0001$.

trient addition and snail removal, by themselves and together, to control conditions (grazed, low nutrient) using post-ANOVA Dunnett's tests (Table 7). Removing grazers resulted in significant increases in ASP, CSP, and total algal biovolume in the 1989 experiment under ambient stream water nutrient conditions. Nutrient addition (under grazed conditions) resulted in significant increases in ASP and chlorophyll a during both the 1989 and 1990 experiments. Although nutrient and grazing manipulations, by themselves, did not result in significant effects for all parameters, they always resulted in at least a 25% increase over controls. When ungrazed, (N + P) treatments were compared to controls, all differences were significant and the percentage increase in a particular parameter was typically at least twice that observed from removing grazers or adding nutrients singly (except for CSP).

We present a top-down index (TDI) which compares the strength of top-down control to the strength of bottom-up limitation for the parameters we measured:

$$\text{TDI} = \frac{(\text{ungrazed, low nutrient}) - (\text{control})}{[\text{grazed, (N + P)}] - (\text{control})},$$

where values in parentheses are the treatment means and the control is the unamended (grazed, low nutrient) treatment. This index is the ratio of the response when top-down constraint (via grazing) is eliminated to the response when bottom-up limitation (via nutrients) is eliminated. It does not take into account the interactive effects due to manipulations of both factors together, but rather indicates which factor, alone, had greater

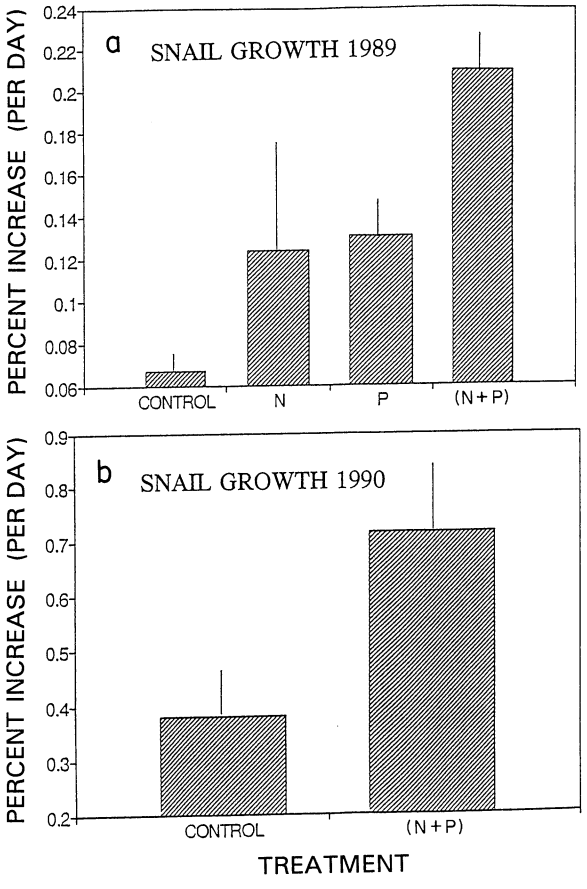

FIG. 5. Snail growth (% ash-free dry mass increase per day) from the 1989 (a) and 1990 (b) studies. Control = ambient stream water, N = addition of N, P = addition of P, (N + P) = addition of both N and P. Error bars = 1 SE. Note that ordinates have different scales.

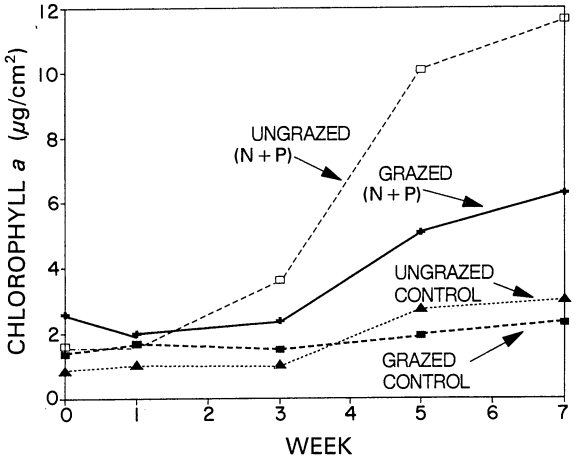

FIG. 6. Chlorophyll a level in periphyton during the 1990 study. Abscissa label, week, = number of weeks since treatments were started; week 0 = initial sampling. Ungrazed, (N + P) = ungrazed, N and P added; grazed, (N + P) = grazed, N and P added; ungrazed, control = ungrazed, ambient stream water; grazed, control = grazed, ambient stream water. Grazed = snails added at natural densities, ungrazed = snails not added.

TABLE 6. (a) ANOVA results of log biovolume of different algal species from the 1990 experiment. G = grazing presence; (N + P) = N and P addition. (+) = positive treatment effects, (−) = negative treatment effects. All taxa making up >5% average biovolume/treatment in >1 treatment/date are included. A full ANOVA model [G, (N + P), (N + P) × G] was tested for each species. Only those effects that were significant during either week 3 or week 7 are listed, otherwise "no effects" is listed. Degrees of freedom as in Table 5. (b) ANOVA results of percentage biovolume of different algal species from the 1990 experiment. Other notation as in Table 6a.

Species/ Treatment	Week 3		Week 7		Species/ Treatment	Week 3		Week 7	
	F	*P*	*F*	*P*		*F*	*P*	*F*	*P*
(a) Log biovolume ANOVA					(b) Percentage biovolume ANOVA				
					Chlorophyta				
Rhizoclonium hieroglyphicum (basal cells)	no effects		no effects		*Rhizoclonium hieroglyphicum* (basal cells)				
					G	NS		(+)	.02
					Chrysophyta (Class: Bacillariophyceae)				
Cocconeis placentula					*Cocconeis placentula*				
G	NS		(−) 9.91	.01	G	NS		(−) 14.85	.005
Diatoms (all spp.)					Diatoms (all spp.)				
G	(−) 5.92	.04	(−) 15.08	.005	G	NS		(−) 10.65	.01
(N + P)	(+) 8.63	.02	(+) 4.92	.06					
Epithemia intermedia					*Epithemia intermedia*				
G	(−) 4.37	.07	NS			no effects		no effects	
Gomphonema (all spp.)					*Gomphonema* (all spp.)				
G	NS		(−) 6.00	.04	G	NS		(−) 5.34	.05
(N + P)	NS		(+) 10.32	.01	(N + P)	NS		(+) 6.85	.03
Peronia intermedium					*Peronia intermedium*				
G	NS		(−)676.88	.0001		no effects		no effects	
(N + P)	NS		(+)676.88	.0001					
(N + P) × G	NS		676.88	.0001					
Melosira varians					*Melosira varians*				
G	NS		(−) 3.70	.09		no effects		no effects	
					Cyanophyta				
Chroococcus minutus					*Chroococcus minutus*				
G	NS		(+) 4.52	.07	G	NS		(+) 6.56	.03
(N + P) × G	NS		4.15	.08	(N + P) × G	NS		7.79	.02
Heteroleibleinia sp.					*Heteroleibleinia* sp.				
(N + P)	(+)12.23	.008	(+) 9.08	.02		no effects		no effects	
					Rhodophyta				
Audouinella sp.					*Audouinella* sp.				
	no effects		no effects		G	NS		NS	
					(N + P)	(−)10.62	.01	NS	

effects. A value of 1 indicates that top-down effects were equivalent to bottom-up effects, numbers > or < 1 indicate greater top-down or bottom-up control, respectively. For biomass parameters, the TDI was variable, ranging from 0.19 to 4.56 (Table 7). Bottom-up vs. top-down effects were stronger for chlorophyll *a* and the index was similar between experiments. Although bottom-up effects were also stronger for biovolume in the 1990 study, in 1989 grazing had much greater effects on biovolume than nutrient addition. The TDI was <1 for ASP and >1 for CSP. Because the TDI compares only the direct, singular effects of top-down vs. bottom-up factors, we also computed an index of the importance of interaction effects on biomass and productivity, the interaction coefficient (IC):

$$\mathrm{IC} = 1 - \frac{\{(\text{ungrazed, low nutrient}) - (\text{control})\} + \{[\text{grazed, (N + P)}] - (\text{control})\}}{[\text{ungrazed, (N + P)}] - (\text{control})},$$

where the values in parentheses are the treatment means and the control is defined as above. If the direct effects of nutrients and herbivores, together, explained the total response of a parameter, then IC = 0. As interaction effects become more important in explaining the total response, IC will increase, approaching a value of 1 when interaction effects account for the entire response. For the parameters we measured, the IC was generally >0.40, indicating that at least 40% of the total effects on primary producers in these studies were due to neither top-down nor bottom-up forces alone,

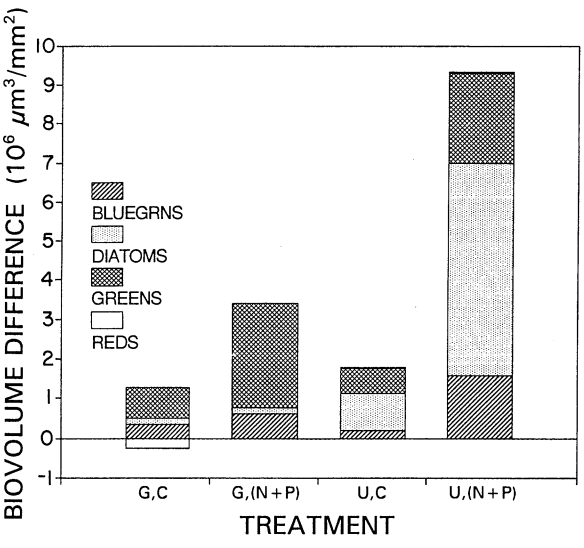

FIG. 7. Algal taxonomic composition and difference in total algal biovolume ($\mu m^3/mm^2$) from initial conditions for week 7 of the 1990 study. Treatments: G, C = grazed, ambient stream water; G, (N + P) = grazed, N and P added, U, C = ungrazed, ambient stream water; U, (N + P) = ungrazed, N and P added. Grazed = snails added at natural densities, ungrazed = snails not added. Bluegrns = biovolume of algae belonging to Division Cyanophyta; Diatoms = biovolume of algae belonging to Division Chrysophyta, Class Bacillariophyceae; Greens = biovolume of algae belonging to Division Chlorophyta; Reds = biovolume of algae belonging to Division Rhodophyta.

but their combined effects (Table 7). IC was low only for CSP, and combined with a TDI of 2.21, indicated that CSP was controlled mostly by direct top-down forces.

DISCUSSION

Comparison of the relative effects of N and P enrichment

Our results from the 1989 study suggest that both N and P limit algal productivity and biomass in WB; however, only P, and not N, had positive effects on periphyton nutrient content. Both nutrients are at low concentrations in the stream (inorganic N <50 μg/L, SRP <5 μg/L) with an average stream water atomic N:P ratio of 23:1 (range 12:1–48:1) for the study period in 1989 and 12:1 (range 6:1–19:1) for the study period in 1990. Based on a study by Schanz and Juon (1983), we would predict periphytic growth to be N limited in streams with N:P <10 and to be P limited with N:P >20. The N:P ratio in 1989 suggests stronger P than N limitation, but greater N limitation in 1990. We observed the greatest increases in algal biomass and productivity when both N and P were increased together, indicating co-limitation by both nutrients. The algal response to addition of either N or P alone in the 1989 study was small, probably due to constraints of low concentrations of the other nutrient.

TABLE 7. Percentage increases in biomass and productivity at the end of the 1989 and 1990 experiments due to removing top-down (− GRAZE) or bottom-up [+ (N + P)] constraints or both, and whether the corresponding means are different from control (grazed, low nutrient) by Dunnett's tests. Dunnett's test controls for experimentwise error rate of $*P < .05$. See *Results: Comparing top-down vs. bottom-up effects in both experiments* for explanation of top-down index (TDI) and interaction coefficient (IC).†

	Treatments				
Measures	− GRAZE	+ (N + P)	− GRAZE and + (N + P)	TDI	IC
ASP89	91*	183*	529*	0.48	.48
CSP89	54*	25	84*	2.21	.07
AFDM89	43	40	270*	1.06	.69
CHL89	27	132*	252*	0.21	.37
BVOL89	539*	118	1310*	4.56	.50
CHL90	32	174*	407*	0.19	.49
BVOL90	70	229	792*	0.31	.62

† ASP89 = area-specific productivity from the 1989 experiment (as ^{14}C uptake, $\mu g \cdot cm^{-2} \cdot h^{-1}$), CSP89 = chlorophyll-specific productivity from the 1989 experiment (as ^{14}C uptake, $\mu g \cdot \mu g^{-1} \cdot h^{-1}$), AFDM89 = periphyton ash-free dry mass from the 1989 experiment ($\mu g/cm^2$), CHL89 = chlorophyll *a* from the 1989 experiment ($\mu g/cm^2$), BVOL89 = total algal biovolume from the 1989 experiment ($\mu m^3/mm^2$), CHL90 = chlorophyll *a* from the 1990 experiment ($\mu g/cm^2$), BVOL90 = algal biovolume difference from the 1990 study ($\mu m^3/mm^2$).

The fact that we observed some positive effects of N addition on periphyton, even at low ambient levels of phosphorus, is contrary to the conclusions of Newbold et al. (1983*b*), showing no response in algal biomass (chlorophyll *a* or AFDM on Plexiglas slides) to enrichment of WB with ammonia-N. However, stream water N:P ratios in WB were higher (34:1, range 11:1–65:1) during the study by Newbold et al. (1983*b*) than during this study. Taken together, these studies indicate that in the same system, the limiting nutrient can vary from year to year and that small changes in the concentration of one limiting nutrient can induce limitation by another.

Top-down vs. bottom-up control

The results of these experiments indicate that the algal community in WB is under dual control from both the bottom up, via nutrient limitation, and from the top down, via consumption by herbivorous snails. For all parameters, the greatest effects were observed when levels of both grazing and nutrient concentrations were manipulated together. On average, biomass and productivity parameters increased by 520% in ungrazed, (N + P)-added treatments over controls, contrasted to average increases of 122% and 129% in these parameters over controls with either removal of snails or addition of nutrients alone, respectively. When both top-down and bottom-up effects have been tested together in other empirical studies, results have shown that both factors are important (Carpenter et al. 1987, Stewart 1987, Vanni 1987, Power 1990, Hansson 1992, Hill et al. 1992, Steinman 1992).

The TDI we presented suggests that relative strengths of top-down vs. bottom-up control were variable within and between experiments. The reason for this may partially lie in the fact that interaction effects (as shown by ICs, Table 7) were high, indicating that top-down and bottom-up effects alone were less important than their combined effects. Because our experimental design allowed us to examine both the independent and interactive effects of nutrients and herbivores, our results showed that neither nutrients nor herbivores had overwhelming control in this system, but that it was the interaction between these factors that ultimately determined algal biomass and productivity in WB.

However, there was some evidence from TDIs and results of ANOVAs that some characteristics of the algal community were affected more strongly by nutrient addition whereas other parameters were more strongly influenced by herbivores. Herbivore effects appeared to be more important than nutrient effects in determining algal community structure and to some extent, total algal biovolume. By the end of both the 1989 and the 1990 studies, ungrazed treatments were dominated by filamentous or erect diatoms and grazed treatments were dominated by chlorophytes and cyanophytes with prostrate morphologies. The differences between grazed and ungrazed treatments may be at least partially a result of a trade-off between algal species' resistance to grazing and nutrient-saturated maximum growth rates. In general, species that were negatively affected by snail grazing were positively affected by nutrient addition and those positively affected by grazing were negatively affected by nutrients. For example, there were positive effects of grazing on *Chamaesiphon investiens* biovolume, and negative effects of P addition, whereas there were positive effects of both N and P addition on species of *Achnanthes* and negative effects of grazing (Table 4a). Also, we found a negative correlation ($r = -0.83$, $P < .01$) between the (log) abundance of taxa in grazed, low nutrient treatments and their (log) abundance in ungrazed, (N + P) treatments from the last week of the 1989 study. This result further suggests that individual algal species that were abundant with grazers present were scarce when nutrients were at high levels and herbivores were removed. However, no such correlation was found from the 1990 study, for which there were fewer treatment effects on individual species than in the 1989 study.

These relationships are consistent with a conceptual model developed by Lubchenco and Gaines (1981), which presumes a trade-off between resistance to herbivory and competitive ability: herbivores preferentially consume "edible," fast-growing species, whereas those that are resistant to herbivory are slower growing. The basis of this tradeoff may be related to morphological differences. Algal taxa with upright, erect, or filamentous morphologies are more susceptible to removal by herbivores than taxa with prostrate morphologies but are superior to prostrate forms in capturing light and nutrients (e.g., they extend above the substratum and have greater surface-to-volume ratios) (Steinman et al. 1992). In this study, we found that grazing had a significant negative effect on chlorophyll-specific productivity, which may have been due to this trade-off and consequent morphological differences.

The negative effect of grazing on CSP is contrary to the positive effect of grazers on chlorophyll-specific or AFDM-specific productivity found in other stream studies (Gregory 1983, Lamberti and Resh 1983, Lamberti et al. 1987, Stewart 1987, Hill and Harvey 1990) but is consistent with results of Hill et al. (1992). In another study, we found that CSP was lower for a community comprised entirely of *Stigeoclonium tenue* than for a community of mixed diatoms, regardless of biomass level (high or low) (A. D. Rosemond and S. H. Brawley, *unpublished manuscript*). Basal cells of *S. tenue* were relatively more abundant in grazed vs. ungrazed treatments in the 1989 study and dominated grazed treatments in the study by Hill et al. (1992), indicating that it is a grazer-resistant species. This alga appears to persist with herbivores present but has an inherently slower growth rate than species (e.g., diatoms) that proliferate when herbivores are removed. In other studies (cited above) in which grazing increased biomass-specific productivity, grazing intensity may be less than it is in WB, allowing more, faster growing algal species to coexist with herbivores.

While herbivory had its greatest effects on species composition and CSP, measures of algal biomass were affected by both herbivory and nutrient addition, and particularly by their interaction. However, the relative effects of nutrients and herbivores on biomass parameters differed somewhat between the two experiments and changed during different times within a single experiment. Chlorophyll *a* was increased to a greater extent with addition of nutrients than removal of grazers and exhibited low TDIs (Table 7). Nutrients may have had greater effects than grazing on chlorophyll *a* because chlorophyll *a* per cell may have increased under high nutrient treatments at a greater rate than cell biovolume, which is suggested by our data (e.g., strong nutrient effects on chlorophyll but not biovolume). AFDM was positively affected by nutrients and negatively affected by grazing (Table 2) and responded equally to removal of grazers or additional of nutrients (TDI = 1.06, Table 7). Generally, there were greater grazing effects on most measures of algal biomass in the 1989 study compared with the 1990 study (e.g., greater absolute differences between grazed and ungrazed treatments, higher TDIs). This is not surprising, considering that the treatment manipulation of grazers was more effective in the streamside channels than in the in situ enclosures. In addition, the bedrock substrate used in the stream study contains more cracks and crevices than the relatively smooth surface of the tiles used in the streamside channels, providing a larger refugia for algal cells and thereby reducing effectiveness

of herbivores. But overall, nutrients and grazing together, had substantial effects on algal biomass in both studies, which has also been shown in other stream ecosystems (Stewart 1987, McCormick and Stevenson 1989, Winterbourn 1990).

Both top-down and bottom-up controls were also important in determining area-specific productivity, which was positively affected by both N and P additions and negatively affected by grazers. However, by far the greatest ASP was observed in treatments with both N and P added and grazers removed, indicating limitation by all factors in combination. Other studies have found positive nutrient effects (Marcus 1980, Bothwell 1985, Fairchild and Everett 1988) and negative grazing effects (Mulholland et al. 1983, 1991, Jacoby 1987) on ASP or periphyton growth rates, and when these factors have been tested simultaneously, both factors have been found to be important (Cuker 1983, Hill et al. 1992).

We observed (marginally significant) increases in snail mass resulting from nutrient enrichment, suggesting (1) herbivore and algal growth are tightly coupled and (2) that snail growth in this stream is food limited. These results imply both the importance of top-down control of the algae and bottom-up limitation of snail biomass in this stream. Mayflies that colonized channels were found in higher densities in nutrient enriched channels than in controls, which also suggests that grazers in WB may be food limited. Elwood et al. (1981), Perrin et al. (1987), Hershey et al. (1988), Hart and Robinson (1990), Winterbourn (1990), and Hill et al. (1992) have similarly observed increased densities or biomass of herbivores with addition of nutrients to streams or flumes.

It is unknown whether the observed increased growth of consumers in this or other studies was due to increased food quantity or food quality, as nutrients can affect both. In our study, P addition, but not N addition, increased indicators of food quality (%C, %N, and %P in periphyton). There were also positive effects of nutrients on food quantity; both N and P had positive effects on algal biomass in both the 1989 and 1990 studies and on ASP in the 1989 study. A study conducted on *E. clavaeformis* from a nearby stream indicated that these snails are extremely food limited under ambient conditions and suggests that quantity is more important: in a laboratory feeding experiment, snails grew better than potential competitors on food of similar quality, presumably by ingesting greater quantities (Hill 1992).

Determining top-down vs. bottom-up control in two-level systems

In contrast to the four-level pelagic and stream ecosystems studied to date (Carpenter et al. 1987, Power 1990), WB has apparently only two functional trophic levels. Based on simple food web models, removal of herbivores in two-level systems should result in increases in plant biomass. In this study, we found that removal of herbivores did not result in large increases in algal biomass, which is inconsistent with theories of Fretwell (1977, 1987). This two-level system appears "barren" (sensu Fretwell), but it is not only because of top-down control, as predicted from theory, but because of nutrient limitation as well. Also in systems with an even number of trophic levels, and in which herbivores respond to prey in a simple, density-dependent manner (as opposed to ratio-dependent), nutrient addition should result in an increase in the biomass of herbivores, but not plants (Power 1992). However, increases in plant biomass should be observed in systems with an odd number of trophic levels when nutrients are increased. We found this to be primarily true in this study, with large increases in algal biomass occurring in response to nutrient addition in ungrazed treatments (one trophic level) but not in grazed treatments (two trophic levels). Hansson (1992) similarly showed that phytoplankton increases were much greater in odd- (three) vs. even-numbered (two) trophic level lakes and enclosure experiments when nutrients were increased. However, differences in algal biomass between two- and three-level systems were reduced at the highest nutrient levels, suggesting that grazers may have been less effective in controlling algal biomass when nutrient levels were highest (Hansson 1992). In contrast, we found that differences in biomass between one- and two-level systems were greatest at high (N and P added together) vs. low (N or P added singly or no nutrients added) nutrient levels. Top-down control may have been strengthened in WB at high nutrient levels because of herbivore–nutrient interactions: the algal species most responsive to enrichment were also most susceptible to snail grazers.

The strong linkage between trophic levels characteristic of two-level systems such as WB may also affect their stability. Nutrient enrichments in other systems have resulted in instabilities due to "runaway" growth of producers, followed by increased herbivore growth and subsequent crashes in autotroph, and then herbivore populations (cf. DeAngelis et al. 1989). In this study, algal communities in ungrazed treatments experienced periods of blooms and subsequent sloughing (A. D. Rosemond, *personal observation*). Such biomass fluctuations occurred to a greater extent in high-nutrient than low-nutrient treatments, indicating reduced stability at higher nutrient levels. In contrast, algal biomass in grazed treatments, regardless of nutrient regime, changed little over time, indicating high stability. Characteristics of the herbivore in this system may prevent unstable cycles due to nutrient enrichment from occurring: *E. clavaeformis* is a highly effective herbivore, one capable of increasing feeding rates proportionately to increased autotroph productivity (Hill 1992), thereby stabilizing biomass.

The results of this study can be viewed in a framework depicting changes that occurred across simulta-

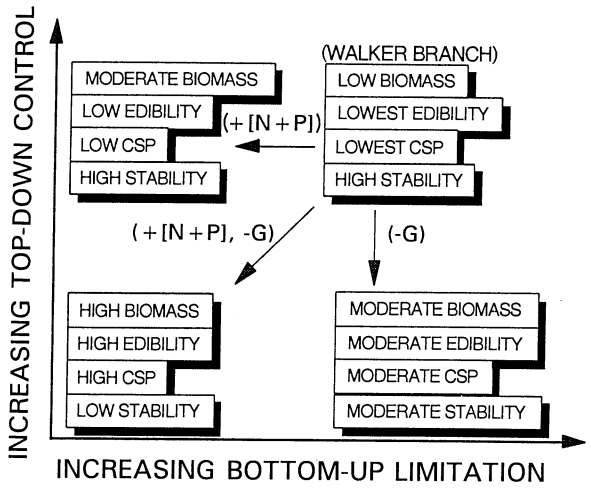

FIG. 8. Schematic indicating characteristics of Walker Branch periphyton (upper right-hand quadrant) placed within the framework of variation in the strengths of top-down control and bottom-up limitation. Characteristics of periphytic communities we observed in these experiments due to decreasing bottom-up limitation (nutrients added [+ (N + P)] treatments), decreasing top-down control (snail removal [− G] treatments), or decreasing both [+ (N + P) − G] are indicated in the upper left-hand, lower right-hand, and lower left-hand quadrants, respectively. CSP = chlorophyll-specific productivity.

neous gradients in control by top-down and bottom-up factors. The periphytic community typical of WB, which is under tight control by both herbivory and nutrients, is described in the upper right-hand quadrant of Fig. 8, with extremely low and stable biomass, and a community consisting largely of inedible (resistant or inaccessible) species having a low CSP. As bottom-up limitation is decreased [+ (N + P)], community composition stays the same, as it is largely controlled by herbivores, but some biomass accrual can take place, resulting in small increases in biomass. Herbivores maintain a low rate of CSP and high stability. Decreasing top-down control (− G) under low nutrient conditions (lower right-hand quadrant) results in community shifts that allow biomass (edible and resistant species) to accrue; however, biomass and CSP are still constrained by nutrient limitation. Decreasing top-down control (− G) under high nutrient conditions [+ (N + P)] (lower left-hand quadrant) results in extremely high and unstable biomass of algal species that are edible and have a high CSP. This framework illustrates that in low-nutrient, two-trophic level systems such as Walker Branch, top-down and bottom-up controls can both be important, thus imparting strong stabilizing effects on the algal community.

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