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Does an increase in irradiance influence periphyton in a heavily-grazed woodland stream?

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Summary. Irradiance level and grazer density were manipulated in a factorial design to examine the relative effects of biotic and abiotic factors on periphyton biomass, productivity, and taxonomic structure in a heavily grazed, woodland stream. Irradiance levels were increased from 0.26 to 12.42 mol quanta/m^2/d by placing metal halide lamps over the stream. The major grazer in this system was the prosobranch snail *Elimia clavaeformis*. Its densities were reduced from ca. 750 individuals/m^2 to near zero by raising platforms off the stream bottom. Experimental treatments were maintained for 48 days. Biomass-specific carbon fixation rates increased significantly in response to higher light levels, indicating that periphyton communities were light-limited at this time of year. However, positive effects of irradiance on areal-specific carbon fixation and biomass were detected only when grazer density was reduced. Basal cells of the chlorophyte *Stigeoclonium* dominated communities exposed either to low light or high grazing pressure. When light was increased and grazer density reduced, large or upright diatoms became more abundant. Results from this study indicated that limitation of periphyton photosynthesis could be mitigated by increasing the levels of an abiotic resource (light) to this system, but that periphyton biomass was controlled by biotic interactions.

Key words: Herbivory – Light limitation – Periphyton – Snails – Streams

The structure and function of autotrophic communities can be influenced by abiotic and biotic factors, either alone or in tandem. Abiotic factors can be mediated through resource availability and hence are associated with "bottom-up" effects (McQueen et al. 1989). In lake pelagic zones, where much of the work has been done on the relative control of biotic vs abiotic factors on trophic level biomass, the abiotic resource that has attracted the most attention is inorganic nutrient concentration (e.g. Elliot et al. 1983; Vanni 1987). However, other abiotic factors may be important depending on the nature of the system being studied. For example, irradiance may be a limiting resource for plants in old fields (Tilman 1987) and it has been implicated as a limiting factor of algal communities in streams at certain times of the year (Triska et al. 1983; Hill and Harvey 1990).

Biotic effects are mediated through the influence of predators and hence, are associated with "top-down" interactions. Top-down forces are predicted to weaken as the food web becomes longer, but the trophic status of the system also will influence this interaction (McQueen et al. 1989), with top-down forces being dampened to a greater degree in more eutrophic systems. Presumably, higher nutrient levels result in enhanced primary production and autotrophic biomass, which in turn increase resistance to grazing by providing a large pool of organic matter (cf. O'Neill et al. 1975).

In lotic ecosystems, a rapidly developing body of work has shown that autotrophic communities can be controlled not only by physical and chemical factors (e.g. Elwood et al. 1981; Peterson et al. 1985; Grimm and Fisher 1986; Steinman and McIntire 1987; DeNicola and McIntire 1990), but also by biotic interactions (Lamberti and Resh 1983; Power et al. 1985; Steinman et al. 1987; Power 1990). Even simultaneous limitation by biotic and abiotic factors has been demonstrated (Hill et al. in press; Rosemond et al. submitted). There is a growing need to synthesize these diverse reports and put this information into some type of conceptual framework. Power (1990) applied the theory forwarded by Hairston et al. (1960) and Fretwell (1977), and subsequently expanded on in lake cascade models (Carpenter et al. 1985), to her work on biotic controls in a California river. The theory states that number of trophic levels in a food chain could be used to predict if autotrophic communities would be lush (and hence, presumably controlled by an abiotic resource) or barren (and hence,

controlled by biotic interactions). With an even number of levels, herbivores would control autotrophic biomass (barren), but with an odd number of levels autotrophs would be released from consumptive pressure (lush). Clearly, broad generalizations of this type can be abused at the ecosystem level (Yodzis 1988), and in this case the degree of "lushness" will be influenced not only by trophic level number, but also by the dynamics of the trophic level interactions. For example, mathematical models have indicated that it is possible that autotrophic biomass may be held at either very low (barren) or at relatively high (lush) levels by the herbivore, even when the food web consists of only two trophic levels; in these models, biomass level depended on whether or not the autotroph could respond to increasing values of nutrient input (or any other growth-limiting abiotic factor; DeAngelis et al. 1989).

The present study was designed to test the relative importance of abiotic vs biotic factors in controlling the biomass, structure and productivity of autotroph assemblages in Walker Branch. This oligotrophic stream is shaded by a dense riparian canopy from late spring through fall. An experimental nutrient enrichment study demonstrated that inorganic nutrients could limit periphyton biomass in Walker Branch (Elwood et al. 1981), but biomass accrual appears to be constrained ultimately by light level and herbivory (Rosemond et al. submitted). Given the extremely low irradiance levels in this stream during the summer and early fall, and the fact that light effects were reported to have a stronger influence on periphyton productivity than snail or fish effects in a nearby woodland stream (Hill and Harvey 1990), it was hypothesized that light is a limiting abiotic resource in Walker Branch (bottom-up effect) during the time of year when this experiment was conducted. Prior experiments have shown clearly that irradiance can influence periphyton taxonomic and physiognomic structure (Steinman and McIntire 1987), chemical composition (Steinman et al. 1988), and photosynthetic performance (Boston and Hill 1991).

The short food chain in Walker Branch consists at the bottom level of autotrophs and detritus, which are fed upon by herbivorous, detritivorous, or omnivorous invertebrates. Fish are observed in the stream, but they do not appear to be have much impact on the invertebrate communities. The dominant animal in the system is the grazing snail *Elimia clavaeformis*, and its densities can reach 2500 individuals/m^2 (T.D. Richardson, pers. comm.). Predators of *Elimia*, if present in the system, are not obvious and appear to have a minimal impact on snail biomass (analogous to a 2.5 link food chain; Fretwell 1987). Consequently, it was reasoned that herbivory also could be controlling periphyton biomass in this stream (top-down effect). If Fretwell's (1977) prediction is applicable to this system, I hypothesized that autotrophic communities would be influenced more strongly by biotic (i.e. herbivory) than abiotic controls, as Walker Branch appears to consist of an even number (two) of trophic levels.

Materials and methods

Study site. The experiment was conducted in a shallow pool (mean depth = 18 cm) in the first-order reach of Walker Branch, a woodland stream located on the U.S. Department of Energy's Oak Ridge reservation in eastern Tennessee. The experiment began on September 12, 1989. Instantaneous light level at 11:00 a.m. at the stream surface was 13 μmol quanta/m^2/s (determined with a Li-Cor Li-188B quantum meter), whereas the integrated light level for that date was 0.26 mol/m^2/d (using ozalid paper, Friend 1961). The riparian vegetation is dominated primarily by *Liriodendron tulipifera* L. (tulip poplar) and *Carpinus caroliniana* Walt. (ironwood). Detailed descriptions of Walker Branch are given in Curlin and Nelson (1968) and Johnson and Van Hook (1989).

Experimental design. Plexiglas platforms (20 × 20 cm) served as experimental units. Twelve platforms were used in total, and twenty-four unglazed ceramic tiles (2.54 × 2.54 cm) were attached to each platform with silicone sealant. Tiles had been in the stream for six months prior to the start of this experiment. The twelve platforms were exposed to one of four treatments: (1) high light, ambient (high) grazing pressure [HL/HG]; (2) high light, low grazing pressure [HL/LG]; (3) ambient (low) light, high grazing pressure [LL/HG]; and (4) low light, low grazing pressure [LL/LG]. This resulted in three replicate units per treatment.

Light level was increased by suspending two metal halide lamps with 400 Watt bulbs directly over the stream channel. Lamps were attached to an aluminum metal frame that protected them from the elements. Half (six) of the platforms were left exposed to the elevated irradiance level (HL) and the other half were covered with four layers of neutral density screen (attached to raised dowels glued into the corners of each platform so that the screening functioned as a tent). These screens reduced the irradiance level reaching the platform to the ambient level (LL) measured in the reach before the artificial lights were turned on. The lamps provided an instantaneous irradiance level of between 325 and 365 μmol/m^2/s and an integrated daily irradiance of 12.42 mol/m^2/d at the platform surfaces. Lamps were placed on a timer to provide a photoperiod of 10:14 L:D, a light regime that generated a cumulative daily flux equal to that measured in an open area exposed to full sunlight at the start of the experiment. A seine net was placed at the upstream end of the frame to collect coarse particulate matter. The net was cleaned daily of debris.

In addition, half of the LL and HL platforms were raised approximately 4 cm above the streambed, which effectively excluded the dominant grazing snail (*Elimia clavaeformis*) from the platform (LG). Exclusions were effected by threading a carriage bolt through the center of all platforms and attaching the bolt to a two-way clamp. The clamp was then attached to a metal bar that was suspended across the stream channel. Platforms could be raised or lowered by clamping the bolt to the bar at different heights. Daily checks were made to ensure that snails were absent from the raised platforms. Any snails present were removed with forceps. The other half of the platforms were left on the streambed, albeit still clamped to the suspended bar, to keep the platforms in place. Consequently, these platforms were exposed to grazing pressure by the benthic snails (HG). Platforms were aligned in three rows, with four platforms in each row. Hence, three metal bars were suspended across the channel and four platforms were clamped to each bar per row. Treatments were randomly assigned to each platform. The experiment was terminated on October 30, 1989 after 48 days, when ambient light levels began to increase with leaf fall.

Biomass measurement. Ash-free dry mass (AFDM) and chlorophyll *a* were measured on days 0, 8, 16, 29, and 48 of the experiment. Three tiles were removed randomly from each platform for biomass estimates. For AFDM estimates, tiles were scraped with a toothbrush, filtered onto pre-ashed Whatman GF/C filters, dried at 105° C for 24 h, weighed, ashed at 500° C for 4 h, and reweighed. For chlorophyll *a* estimates, tiles were extracted in 10 ml of DMSO for 24 h at room temperature. Extracts were analyzed spectropho-

tometrically before and after acidification for determining chlorophyll *a* and total phaeophytin, respectively (Shoaf and Lium 1976).

Production measurement. Areal and chlorophyll-specific carbon fixation rates were determined on days 8 and 29 of the experiment. Again, three tiles were removed randomly from each platform for photosynthetic measurements. Tiles were transported back to the laboratory (within 30 min of collection) and placed in glass chambers with one liter of filtered stream water. Submersible pumps were attached to each chamber, providing a mean current velocity of ca. 30 cm/s in each chamber. Chambers were placed in a large, fiberglass tank that served as a temperature-controlled water bath. For each incubation, the temperature of the water bath was set to within 1° C of that in Walker Branch at the time of collection. Irradiance was provided by a metal halide lamp suspended over the chambers. Differing degrees of neutral-density screening were placed directly over the chambers to generate light levels similar to those provided in the HL and LL treatments in the stream. Approximately 183 kBq of $NaH^{14}CO_3$ was added to each chamber and incubations lasted 3 h. Extraction and measurement of the isotope followed the methods described in Steinman et al. (1990).

Taxonomic structure. One tile was sampled from each platform on days 0, 8, 16, 29, and 48 to determine algal taxonomic structure. Tiles were scraped with a toothbrush and the slurry fixed in Lugol's solution. Algae were counted at 400X and 1000X with a Zeiss inverted microscope (Utermöhl 1958). In all cases, at least 300 cells were counted per sample. Only cells with distinct cell contents were included in the counts. Cell counts were converted to biovolume data using standard geometric formulae.

Statistical analysis. Differences among treatments were analyzed using a two-way analysis of variance or a repeated measures ANOVA. Prior to statistical analysis, tests for assumption of homogeneity of variance were conducted. If variances were heterogeneous, biomass and carbon fixation data were log-transformed and taxonomic data were arcsin-square root-transformed. Algal community structure was evaluated for each treatment on each sampling date by calculation of taxonomic similarity using the SIMI index. This measure ranges from 0 to 1, where a value of 0 indicates that a given pair of assemblages have no taxa in common, and a value of 1 indicates that the two assemblages have identical species compositions and proportional abundances (McIntire and Moore 1977).

Results

Treatment manipulations were effective at changing the irradiance and grazing regimes throughout the study. Irradiance levels in HL treatments were increased ca. 45X above ambient levels and ca. 24X above LL conditions (Table 1). Daily integrated irradiance under ambient conditions (i.e. about 10 m downstream of the manipulated area) was approximately half of that under LL at the start of the experiment, and about double that of LL at the end of the experiment. Increased irradiance under ambient conditions as the end of the experiment was attributable to reduced canopy cover as leaf fall increased. Snail densities on the HG platforms were about half of those under ambient conditions (Table 1) both at the start and end of the experiment. Snails were rarely observed on LG platforms.

Mean AFDM levels were higher in treatments with reduced snail densities throughout the experiment (Fig. 1a). Indeed, once treatments were initiated, snail

Table 1. Comparisons of environmental factors under ambient (i.e. site 10 m downstream of experimental area) and manipulated conditions at start and end of the experiment

	Irradiance ($mol/m^2/d$)	Snail Density ($individuals/m^2$)
12.9.89 (Start)		
Ambient	0.26	737
HL,HG	12.42	452
HL,LG	12.42	–
LL,HG	0.50	387
LL,LG	0.50	–
30.10.89 (end)		
Ambient	1.01	865
HL,HG	12.42	428
HL,LG	12.42	–
LL,HG	0.50	500
LL,LG	0.50	–

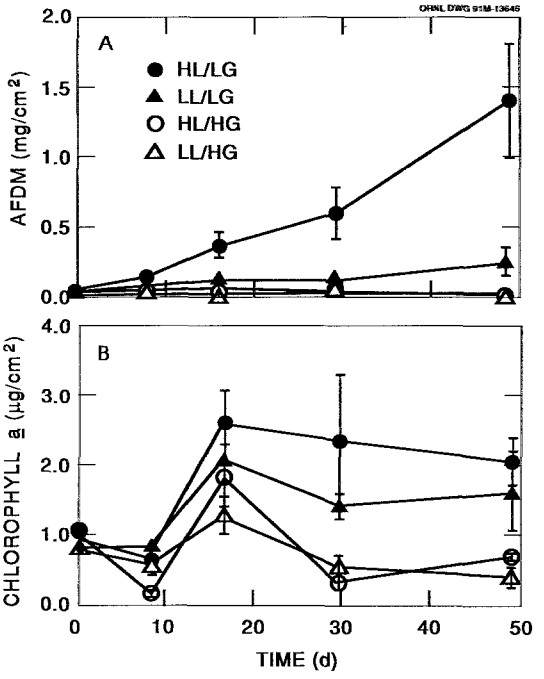

Fig. 1. Periphyton biomass levels in the different treatments over time. Data points are mean values ($n=3$) and error bars $=\pm 1$ SE. **(A)** Ash-free dry mass (AFDM); **(B)** Chlorophyll *a*

density had a significant, inverse effect on each sampling date (Table 2). Irradiance had a significant effect on most dates, as did the interaction term, which resulted from the positive effect of irradiance being more pronounced when snail density was reduced (Table 2). Chlorophyll *a* levels were significantly greater when snail density was reduced (Table 2, Fig. 1b). However, irradiance level had no significant influence on this parameter (Table 2). Areal-specific carbon fixation rates were not significantly affected by the treatments on day 8, although mean rates were highest in the HL/LG conditions (Table 2, Fig. 2a). On day 29, however, areal-specific carbon fixation rates were significantly influenced by irradiance and snail density. As with AFDM, a significant

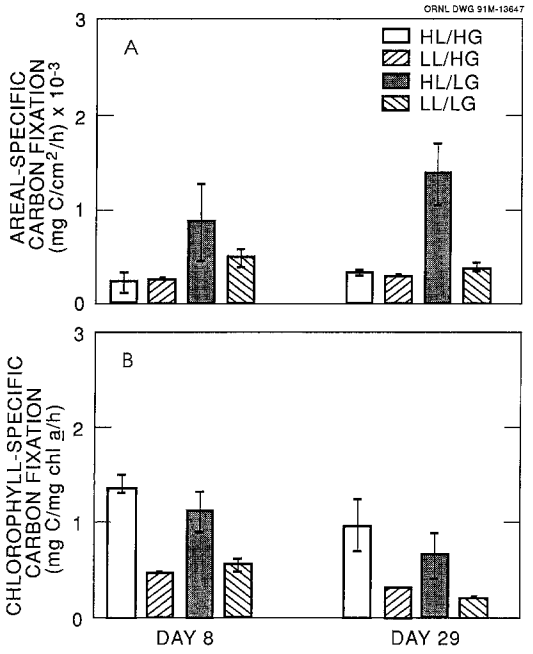

Fig. 2. Periphyton primary production in the different treatments over time. Data points are mean values ($n=3$) and error bars = ± 1 SE. (**A**) Areal-specific carbon fixation; (**B**) Chlorophyll-specific carbon fixation

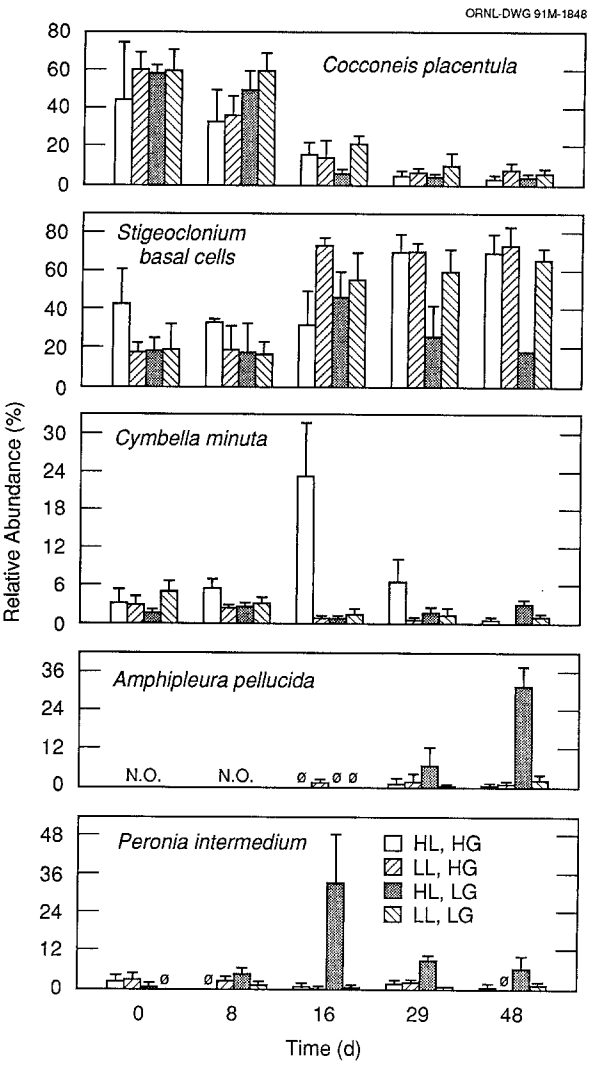

Fig. 3. Relative abundance (% of total community biovolume) of the five most abundant algal taxa in the different treatments over time. Data points are mean values ($n=3$) and error bars = ± 1 SE

interaction term resulted because the positive influence of light was more pronounced when snail densities were reduced.

Chlorophyll-specific carbon fixation rates were significantly greater with increased irradiance on both days 8 and 29 (Table 2, Fig. 2b). Snail density, however, had no apparent influence on this measure.

The five dominant algal taxa on the tiles included one green alga (*Stigeoclonium*) and four diatoms. *Stigeoclonium* was observed almost exclusively as basal cells or short (<10 cells long) filaments. Treatments had no significant effect on the relative abundance of *Stigeoclonium* through day 16 of the experiment (Table 2, Fig. 3). On days 29 and 48, its relative abundance was significantly greater in HG than LG treatments. In addition, *Stigeoclonium* relative abundance on day 48 was significantly greater in LL than HL conditions, although the significant interaction term indicated that the positive effect of reduced light was stronger under LG conditions.

The relative abundance of the prostrate diatom *Cocconeis placentula* declined throughout the experiment (Fig. 3). Overall, its relative abundance was significantly greater under reduced irradiance levels (Table 2). Treatments had a significant effect on the relative abundance of *Cymbella minuta* only on days 16 and 48 (Table 2, Fig. 3). On day 16, the extremely large relative abundance of *Cymbella* in HL/HG conditions accounted for the significant effects of high light and high snail density, and also accounted for the significant interaction term. On day 48, relative abundance of this taxon was increased by high irradiance and low snail densities.

Although relatively few *Amphipleura pellucida* cells were observed during the study, the large cell dimensions of this taxon resulted in it accounting for a substantial portion of community biovolume on days 29 and 48 (Fig. 3). *Amphipleura* was particularly abundant in HL/LG conditions, which explains the significant effects of light, snail density and the interaction term on day 48 (Table 2). The relative abundance of *Peronia intermedium* was similar to that of *Amphipleura*, exhibiting the greatest amounts in HL/LG treatments (Fig. 3). By day 16, *Peronia* relative abundance was significantly enhanced under high light and reduced snail conditions (Table 2). Significant interaction terms on days 16 and 29 resulted because the effect of increased light was more pronounced under reduced snail levels.

All pairwise comparisons of algal taxonomic structure except one were >0.80 (SIMI index) through day 29, suggesting that taxonomic composition was quite similar among all treatments. On day 48, however, taxonomic composition of communities exposed to HL/LG conditions diverged from communities exposed to all other treatments (Table 3; SIMI's from 0.48 to 0.51).

Table 2. Results of repeated measures ANOVA during the 48-d experimental period (F-values are listed; $*P<0.05$; $**P<0.01$; $***P<0.001$). Repeated measures ANOVA were performed on those parameters for which there was no significant treatment x time interaction. For parameters with a significant treatment x time interaction, results of ANOVA on individual sampling dates are given

Parameter	Time[a]	Treatment effects		
		Light	Snail	Light*Snail
Biomass				
AFDM	all (5)	10.99**	32.79***	12.40**
Chlorophyll *a*	all (5)	0.70	23.71**	0.40
Metabolism				
Areal carbon fixation	day 8	0.57	4.24	0.89
	day 29	11.80**	12.20**	9.26*
Chlorophyll-specific Carbon fixation	all (2)	136.27***	5.02	4.52
Taxonomic structure				
Stigeoclonium (basal)	day 0	1.10	1.25	0.55
	day 8	0.22	1.10	0.86
	day 16	2.90	0.01	1.34
	day 29	2.55	6.25*	2.56
	day 48	17.02**	20.75**	10.33*
Cocconeis placentula	all (5)	6.02*	3.31	0.02
Cymbella minuta	day 0	1.57	0.16	1.25
	day 8	1.34	1.06	2.75
	day 16	11.67**	12.18**	14.46**
	day 29	4.29	0.60	1.44
	day 48	9.10*	23.18**	0.11
Amphipleura pellucida	day 0	–	–	–
	day 8	–	–	–
	day 16	2.83	2.83	2.83
	day 29	1.78	0.26	3.11
	day 48	16.33**	30.42***	17.99**
Peronia intermedium	day 0	<0.01	14.39**	1.31
	day 8	0.10	47.11***	114.61***
	day 16	9.21*	7.13*	6.27*
	day 29	6.55*	3.52	14.42**
	day 48	7.98*	15.75**	2.67

[a] Time that measurements were made. "All" refers to use of all measurements (total number of dates when measurements were made is in parentheses) in a repeated measures ANOVA

Table 3. Similarity indices (SIMI) of algal taxonomic structure on day 48

	HL,HG	LL,HG	HL,LG	LL,LG
HL,HG	1.00			
LL,HG	0.98	1.00		
HL,LG	0.48	0.50	1.00	
LL,LG	0.98	0.99	0.51	1.00

Taxonomic structure of communities that were exposed to high snail densities was relatively unaffected by light regime, and similarly, structure of communities that were exposed to low light levels was relatively unaffected by grazing level.

Discussion

Biotic and abiotic constraints on periphyton biomass accrual function in fundamentally different ways. Biotic interactions (top-down) can directly reduce biomass levels via consumption or dislodgement (Hart 1985; Lamberti et al. 1989; Scrimgeour et al. 1991) but they have no direct effect on photosynthesis (although they often have an indirect effect; see below). Abiotic constraints (bottom-up) directly impact photosynthesis and hence have an indirect influence on biomass accrual as carbon fixation is translated into the elaboration of new tissue. Thus, it is important to keep in mind when discussing the relative roles of abiotic and biotic control on autotroph communities that abiotic factors regulate *potential* biomass levels, whereas biotic factors directly regulate *realized* biomass levels. This is particularly clear in the present data set because by increasing the level of a limiting abiotic factor, chlorophyll-specific production also was increased. However, biotic interactions dictated whether or not this increased production was translated into new biomass.

Biomass. The positive influence of light on AFDM was expressed only when grazing pressure was reduced. When snails were excluded, a 24X increase in light re-

sulted in a 3.6X increase in AFDM. Few other lotic studies have manipulated irradiance levels in situ. Gregory (1980) also placed artificial lights over a natural stream, but did not report changes in AFDM. When Triska et al. (1983) reduced light 92% and screened out most large invertebrates, a ca. 85% decline in AFDM was reported. AFDM levels under ambient grazing conditions in Walker Branch were on the low end compared to other heavily shaded, unmanipulated streams (Lyford and Gregory 1975; Feminella et al. 1989; Boston and Hill 1991). Whereas the extremely low irradiances presumably account for the low AFDM in streams of the Oregon Cascades (Lyford and Gregory 1975), heavy grazing pressure appears to be most responsible for low AFDM in Walker Branch, as AFDM did increase (albeit slowly) in LL treatments once grazers were removed (Fig. 1a).

Chlorophyll *a* also was influenced to a much greater degree by grazing than irradiance in the present study. Although overall mean levels of chlorophyll *a* were greater in high light than low light treatments within each grazing level, these differences were not significant. A possible explanation why irradiance significantly affected AFDM but not chlorophyll *a* is the demonstrated response of algae to increase their cellular pigment content under reduced photon flux densities (Richardson et al. 1983). Thus, even though increased light may have resulted in more algal biomass, detection of this response in the form of chlorophyll *a* may have been masked by greater pigment levels in cells exposed to low light levels. This pigment response may have been particularly extreme in the LL communities, as they were dominated by the chlorophyte *Stigeoclonium*. Falkowski (1980) noted that light-mediated changes in chlorophyll content per cell may be most acute in chlorophytes, although his analyses were based on marine phytoplankton, not lotic periphyton. In contrast to my results, Gregory (1980) reported that chlorophyll *a* was 5 times greater in the lighted reach than the unlighted sections. However, the algal communities in Gregory's study were dominated by diatoms, a class of algae that may have less flexibility than chlorophytes with respect to light-induced pigment changes (Falkowski 1980).

Ash-free dry mass increased at close to a linear rate in the HL/LG treatment. It is unknown how long this linear increase in biomass accrual could have been sustained in Walker Branch. Inorganic nutrient concentrations were very low throughout the experimental period ($\bar{X} \pm$ SE over 7 weeks: SRP $= 2.6 \pm 0.7$ µg/L; $NO_3 - N = 17.6 \pm 4.8$ µg/L; $NH_4 - N = 3.1 \pm 1.5$ µg/L) and possibly could have limited biomass accrual soon after day 48. Indeed, other studies in Walker Branch (Elwood et al. 1981; Rosemond et al. submitted) have suggested that periphyton communities are limited by nutrient supply. It appears that periphyton communities in this stream exist under conditions that are very close to some type of "switching point", where the proximate limiting resource may switch between light and nutrients depending on prevailing environmental conditions (Rosemond et al. submitted). Studies conducted in shaded streams of Oregon and California indicate that nutrient additions have little effect on periphyton biomass or productivity unless light is first increased (Gregory 1980; Triska et al. 1983; Hill and Knight 1988). However, the question regarding which abiotic resource limits periphyton biomass accrual in Walker Branch appears to be a moot one as long as snail densities remain high.

Productivity. Highest levels of areal-specific primary production occurred in HL/LG treatments. This is consistent with the AFDM data; systems that have more AFDM generally have greater areal-specific productivity simply because there is more biomass present to fix carbon. The highly significant relationship between light and chlorophyll-specific carbon fixation clearly indicated that periphyton production was light-limited during this time of year in Walker Branch. Under HG conditions, however, this stimulation was not reflected in areal-specific productivity. This was surprising, as one would expect that when biomass levels are similar (as they were between HL/HG and LL/HG), increased biomass-specific productivity should result in increased areal-specific productivity. The intense grazing pressure present in this system may have inhibited primary production (see below).

In contrast to the HG communities, increased chlorophyll-specific productivity under high light and reduced snail densities in LG communities was turned into greater biomass because reduced grazing allowed the fixed carbon to accrue, which in turn resulted in greater areal-specific productivity. This interaction between biomass accumulation and grazer activity is largely a function of autotroph productivity vs grazer ingestion rate and density. At high ingestion rates or densities, grazers can keep up with the productive capacity of the autotrophs, but as grazers become satiated or density is somehow reduced, the autotrophic productive capacity can exceed the consumptive demand of the herbivores and net biomass accrual occurs (Stewart 1987; Lamberti et al. 1989).

The effect of biotic interactions on primary production is complex and can change depending on grazing pressure, the level of abiotic resources, and how productivity is being evaluated. As stated above, herbivory has no direct impact on primary production, per se. Indirectly, biotic interactions usually decrease areal-specific productivity in periphyton assemblages simply because as grazing pressure increases, less biomass becomes present to fix carbon (Jacoby 1987; Mulholland et al. 1991; but see Flint and Goldman 1975). However, abiotic resource level complicates this scenario. As limiting resources are made available to the autotrophs, the productive capacity of the system increases and it may become possible for autotroph production to keep up or even "outrun" grazer demand (Stewart 1987; Lamberti et al. 1989; McCormick and Stevenson 1991). Once grazing pressure exceeds some threshold (which depends on grazer vagility, life history, and ingestion rates), they can once again attain the upper hand and keep biomass levels down irrespective of how plentiful the abiotic resources are (Steinman et al. 1987). Positive influences of grazers, such as nutrient cycling (Sterner 1986; Mulholland et al.

1991) or decreased self-limitation due to biomass cropping (Hill and Harvey 1990), may stimulate areal-specific production when abiotic resources are limiting, thereby compensating for the loss of production caused by grazers as they remove biomass. As grazing pressure increases, however, areal-specific production becomes constrained both by limiting abiotic resources and low biomass levels (Lamberti et al. 1989; Steinman et al. 1989).

Conversely, biomass-specific productivity often increases with greater grazing pressure because herbivores may (1) excrete nutrients to nutrient-limited periphytic cells (McCormick and Stevenson 1991), (2) remove dead or senescent cells (Lamberti et al. 1989), and (3) remove overstory cells, thereby reducing solute diffusion and light attenuation gradients in the periphyton mat (Riber and Wetzel 1987; Hill and Harvey 1990). Enhancement of primary production by grazing has been noted in coral reefs (Carpenter 1986), lakes (Berquist and Carpenter 1986), and terrestrial grasslands (McNaughton 1985), but degree of enhancement is often mediated by abiotic resources (e.g. nutrient levels in lakes; soil moisture in grasslands). In streams, stimulation of areal primary production by grazing is rare, and when reported is only in systems with light grazing pressure (Lamberti et al. 1989). In the present study, areal primary production was severely reduced by grazing and biomass-specific primary production was not increased in the high-grazed treatments. Indeed, biomass-specific production may even decline when grazing pressures are high (Hill et al. in press), although the mechanisms involved are unclear.

Taxonomic structure. Algal community structure data were consistent with previous studies that have found: (1) prostrate growth forms (e.g. *Stigeoclonium* and *Cocconeis*) are well adapted to high grazing pressure (Steinman et al. 1987; Hill et al. in press). Reduced relative abundances of *Cocconeis* at later dates in this experiment are presumably a function of it being overgrown by other species and its poor ability to immigrate (Stevenson and Peterson 1989); and (2) upright or large forms (e.g. *Amphipleura* and *Peronia*) are susceptible to grazing pressure. Large growth forms also may have a competitive advantage for light, as their higher profile will enable them to intercept irradiance before the lower profile cells (Hudon and Bourget 1983).

Because all treatments were heavily dominated by *Cocconeis* on days 0 and 8, and *Stigeoclonium* on days 16 and 29, it is not surprising that pairwise comparisons of all assemblages exhibited very high similarities on these dates. However, by day 48, large dissimilarities occurred because of dominance by *Amphipleura* and *Peronia* in HL/LG treatments but continued dominance by *Stigeoclonium* in all other treatments. It is interesting that *Stigeoclonium* dominated in treatments exposed to very different conditions. Given its ability to resist grazing, it is not surprising that this species dominated HG treatments, irrespective of light regime. However, it also dominated treatments with low light, irrespective of grazing regime. Either light levels were so low in Walker Branch that other species could not grow at a fast enough rate to supplant *Stigeoclonium*, or *Stigeoclonium* somehow inhibited growth of other species. Regardless of mechanism, this phenomenon resulted in the curious result of high similarities between assemblages exposed to high light, high grazing and those exposed to low light, low grazing.

Conclusions. Results from this study support (1) the ideas of Hairston et al. (1960) and Fretwell (1977) that autotroph biomass is controlled from above (biotic control) in food webs with an even number of trophic levels and (2) the expectation of McQueen et al. (1989) that top-down forces will be most detectable in short food chains. Although abiotic factors limited primary production in Walker Branch, relieving this limitation did not result in a high standing crop unless biotic control was simultaneously relieved. Thus, herbivore control was so complete in this system that autotroph biomass could not respond to increases in the levels of a growth-limiting abiotic resource. During those times of the year when grazing pressure is released, however (e.g. following leaf-fall or high discharge events), the controlling influence over autotrophs may switch from biotic to abiotic control.

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