Grazer Control of Algae in an Ozark Mountain Stream: Effects of Short-Term Exclusion

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GRAZER CONTROL OF ALGAE IN AN OZARK MOUNTAIN STREAM: EFFECTS OF SHORT-TERM EXCLUSION[1]

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Abstract. Stony substrata in streams of the southwestern Ozark Mountains are covered with cyanobacterial felts dominated by *Calothrix* sp., an active nitrogen fixer. To study the effect of grazers on these producer assemblages, we exposed or protected periphyton from grazers for periods ranging from 4 to 33 d. When protected from grazing fishes and invertebrates, cyanobacterial felts are overgrown by turfs of benthic diatoms within 4–10 d. Diatom turfs also develop on bare substrata that are incubated in sites in the stream inaccessible to grazers. Diatom turfs exposed to grazing minnows are stripped off in 3–5 min, and when left exposed to grazers, are replaced by cyanobacterial felts within 11 d. Basal regeneration of *Calothrix* trichomes may contribute to their persistence under intense grazing.

Key words: algivorous minnows; cyanobacteria; diatoms; grazing; nitrogen fixation; overgrowth; Ozark Mountains; streams.

INTRODUCTION

Grazer-dependent plant assemblages occur in terrestrial (Harper 1977, McNaughton 1984) and marine (Paine and Vadas 1969, Lubchenco 1978, Paine 1980, Hay 1981, Steneck 1982, Lewis 1986) environments. Plants that dominate these assemblages resist grazing by virtue of toughness, unpalatability, or protected position of their regenerative tissues. In the absence of grazers, resistant species are frequently overgrown by faster growing, less protected species. Coevolution of resistant plant species with grazers that control their competitors has been posited for coralline algae (Stanley et al. 1983) and terrestrial grasses (McNaughton 1979).

In streams throughout the southwestern Ozark Mountains, rock and woody substrata are covered with dense black periphyton felts, except shortly after scouring floods. These felts clearly record grazing scars of algivorous minnows *Campostoma anomalum* (Rafinesque) and *C. oligolepis* (Hubbs and Greene), which occur in Ozark streams in schools of thousands, and in densities of up to 50 fish/m². Densities of fresh scars typically range from 1 to 4 scars/cm² in water deeper than 15–20 cm (Fig. 1A, Matthews et al. 1986). *Campostoma* graze less frequently in shallower water along channel margins. Felts in these areas are grazed by high densities (up to 8000 individuals/m²) of snails, *Elimia (Goniobasis) potosiensis* (Lea) and *Physella gy-*

rina (Say). Trails left by grazing snails can be readily distinguished from bite marks of grazing minnows (Fig. 1A, B).

The high densities of *Campostoma* and their grazing scars in many Ozark streams suggested that these fish might have strong effects on lotic communities in this region. This study reports the results of short-term (4–33 d) in situ experiments in the Baron Fork of the Illinois River in which substrata supporting stream periphyton were either protected from or exposed to grazing. The experiments tested the hypothesis that these dense, active grazers affected standing crops or composition of periphyton assemblages.

STUDY SITES

The Baron Fork of the Illinois River, 14 km east of Tahlequah, Oklahoma, USA (35°52′ N, 94°49′ E), is a clear fourth-order stream that flows over chert gravel and slate bedrock through deciduous forest and pastureland. At low flow during summer and autumn, stream width ranges from 5 to 15 m, and maximum depths in pools and riffles are typically ≈ 1.5 and 0.4 m, respectively. Between floods, discharge ranges from 0.1 to 0.3 m³/s¹.

METHODS AND RESULTS

To study the effects of grazers on periphyton, we used three fiberglass troughs, 4.70 m long × 0.61 m wide × 0.23 m deep. The floor of each trough was lined with unglazed clay tiles, each 232 cm² in area. Tiles were seasoned in troughs in a stream pool for 28 d, beginning on 31 August 1984. During this period, silt was deposited on the tiles and little periphyton developed. Troughs were then moved into riffles, and positioned parallel to the flow. Upstream and down-
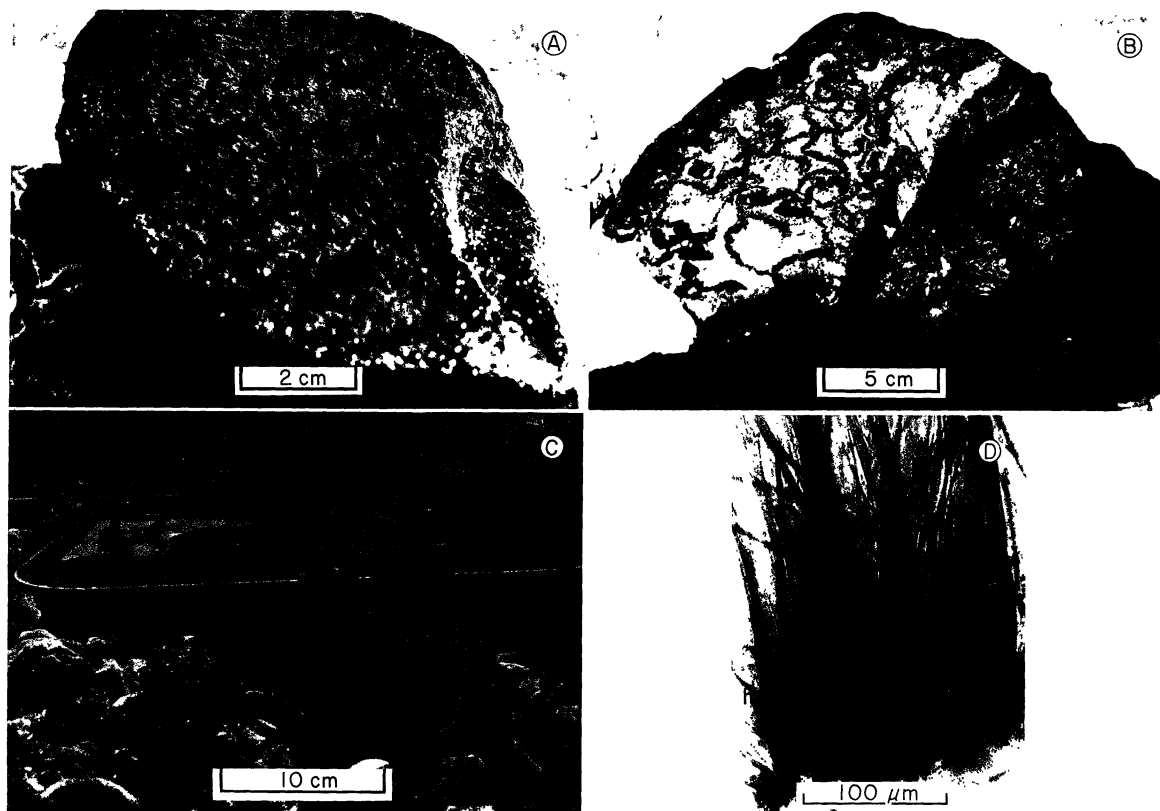
FIG. 1. (A and B): Stream cobbles showing (A) dark grazing scars of *Campostoma* spp. and (B) grazing trails of snails (*Elimia* [*Goniobasis*] *potosiensis*). The darkest areas are sites most recently grazed. (C): *Campostoma* feeding on diatom-covered tiles removed from troughs and placed in a tray on the streambed. Cyanobacterial felts on the streambed (foreground) were the normal foraging substrates for these minnows, but felts were ignored when diatom turfs were offered. (D): Photomicrograph (400×) of *Calothrix* filaments, showing basal heterocysts (h) and distally tapering trichomes.

stream walls were removed to enhance flow over tiles. Depths measured at 10 sites distributed evenly down the length of each trough were (mean ± SE): 21.5 ± 1.6 mm, 38.3 ± 2.8 mm, and 34.6 ± 2.2 mm. Corresponding surface flow velocities, estimated from six measurements of the time taken by floating objects to travel from the upstream to downstream ends of each trough, were 53 ± 2, 25 ± 1, and 25 ± 1 cm/s. Observations of floating objects indicated that surface velocities were relatively uniform throughout each trough. Troughs were shallow and essentially devoid of cover for fish. During frequent bankside observations, we never saw minnows inside troughs. Had *Campostoma* grazed inside, they would have left distinctive scars; these were observed on tiles along upstream and downstream edges of troughs (which fish could feed upon from outside the troughs) but never on interior tiles. Troughs were checked several times daily, and the few invertebrates that had entered were removed by hand, with the exception of chironomids, which oviposited on some tiles.

Soon after troughs were moved to flowing water, an olive-green algal turf developed on tiles. This turf was strikingly different from black felts on stream substrata. Microscopic inspection showed that the turf on tiles was dominated by the filamentous diatom *Melosira* sp., while black felts on natural stream cobbles were composed largely of the cyanobacteria *Calothrix* sp. and *Phormidium* spp. Diatoms in troughs grew extremely rapidly, forming turfs 8 cm thick only 10 d after being placed in fast flow. Felts on stream substrata outside troughs were never thicker than 1 mm.

Diatom turfs, rather than cyanobacterial felts, might have developed in troughs because of differences (1) between clay tiles and natural substrata; (2) in initial inoculation from a stream pool for tiles, from riffles for cobbles; (3) between physical or chemical conditions in troughs and in the stream; or (4) in grazing pressure. To assess the relative importance of these factors, we transferred tiles with diatom turfs from troughs to the streambed, and cobbles with cyanobacterial felts from the streambed to the troughs. In addition, bare cobbles from dry gravel bars were incubated in troughs. Flat slate and chert cobbles similar in thickness to clay tiles were used so that flow within troughs was only minimally altered.

TABLE 1. Proportional composition (proportional cover of an ocular grid) of periphyton sampled from natural (cobble) and artificial (tile) substrata in the Baron Fork, and from the guts of the grazing minnow *Campostoma*.

	Periphyton*					
	Cyanobac-teria		Diatoms			Other algae
Treatment	Cal	Ph, L	Mel	Cym	Misc.	
a. Cobbles from streambed incubated in troughs						
0 d (n_s† = 6, n_c† = 7504)	0.71	0.17	0.02	0.03	0.03	0.04
4 d (n_s = 2, n_c = 2260)	0.65	0.08	0.07	0.11	0.05	0.04
10 d (n_s = 6, n_c = 7576)	0.53	0.13	0.05	0.19	0.07	0.03
Surface of felt only, sampled after						
4 d (n_s = 2, n_c = 2244)	0.20	0.06	0.09	0.49	0.12	0.04
10 d (n_s = 3, n_c = 3823)	0.11	0.03	0.13	0.65	0.07	0.01
Bare cobble from dry bar, after						
10 d (n_s = 3, n_c = 4457)	0.02	0.03	0.19	0.12	0.62	0.02
b. Tiles incubated in troughs						
33 d, no exposure to grazers (n_s = 2, n_c = 4457)	0.00	0.03	0.62	0.08	0.22	0.05
20 d, exposed on streambed 5 min, re-incubated 13 d (n_s = 3, n_c = 3776)	0.01	0.06	0.30	0.20	0.27	0.16
c. Tiles exposed to grazers						
on streambed for 11 d after developing a diatom turf during 23 d of trough incubation (n_s = 4, n_c = 5904)	0.02	0.39	0.00	0.12	0.05	0.42
in trough at edge positions accessible to *Campostoma* (n_s = 3, n_c = 3507)	0.03	0.36	0.00	0.34	0.10	0.17
d. Gut contents of *Campostoma* (n_s = 17, n_c = 7055)	0.43	0.02	0.02	0.38	0.11	0.04

* Cyanobacteria include *Calothrix* (*Cal*), *Phormidium*, and *Lyngbya* (*Ph, L*); diatoms include *Melosira* (*Mel*), *Cymbella* (*Cym*), and miscellaneous diatoms; "Other algae" are primarily miscellaneous Chlorophyceae.

† n_s = numbers of cobbles, tiles, or guts sampled (10 subsamples were examined from each); and n_c = cell counts on which proportions were based.

Periphyton on tiles and cobbles was sampled using an aspirator with a glass pipette fitted on the intake. During sampling, substrata were transferred to shallow still water so that material detached by the pipette would not be lost to the flow. A flexible circular template 3.14 cm² in area was pressed to the substratum and periphyton within was simultaneously scraped and sucked into the aspirator vessel. Samples were immediately preserved in 2% formalin, and identified later at 400× magnification. Relative abundances of periphyton taxa were quantified using an ocular Whipple grid as a two-dimensional transect (Jones 1968). This method scores the number of grid intersections that overlie particular taxa, thereby taking into account both the numbers of individuals and the sizes of cells or colonies in quantifying proportional composition of the periphyton sample. From 100 to 213 intersections were scored per subsample, and 10 subsamples were examined per sample (Table 1).

Periphyton felts sampled in autumn 1984 from chert and slate cobbles taken directly from the stream were dominated by the cyanobacteria *Calothrix* sp., *Phormidium* sp., and *Lyngbya* sp. (Table 1a). (Cyanobacteria also dominated felts in autumn 1985, when 46 cobbles from three riffles over an 800-m reach of the Baron Fork were sampled. Three subsamples were examined per cobble. Of a total of 17 106 cells counted, 86% were cyanobacteria [29% *Calothrix* sp., 57% *Phormidium* or *Lyngbya* spp.]; 3% were diatoms [0.1% *Me-losira* sp., 2% *Cymbella* spp., and 1% miscellaneous genera including *Synedra*, *Fragilaria*, and *Navicula* spp.]).

When cobbles from the stream with similar felts were incubated in troughs, the felts were visibly overgrown with turfs of olive-green filaments after only 4 d. These turfs were composed largely of diatoms, with *Melosira* sp. and *Cymbella* spp. particularly abundant (Table 1a). Proportions of diatoms in periphyton on incubated felts were significantly higher and proportions of cyanobacteria were significantly lower than on felts sampled directly from the streambed (t = 2.44 and t = 2.55, respectively, $P < .02$ from t tests on arcsine square-root transformed data [Sokal and Rohlf 1969]). After 10 d of incubation, the proportion of diatoms on incubated stream cobbles had increased and the proportion of cyanobacteria was correspondingly reduced (Table 1a). When stream cobbles incubated 4 and 10 d were aspirated superficially by drawing the pipette tip lightly across the felt surface, instead of removing periphyton down to the rock substratum as was done for other samples, samples were enriched with diatoms (Table 1a), indicating that diatoms were colonizing surfaces of cyanobacterial felts. Diatoms also flourished on bare streamside cobbles taken from dry gravel bars, after these had incubated 10 d in troughs (Table 1a).

Unglazed clay tiles that had incubated for 33 d in troughs with no exposure to grazers developed floras that were 92% diatoms; of these, *Melosira* was pre-

dominant (62% of the total flora, [Table 1b]). When tiles were transferred from troughs to the streambed, *Campostoma* stripped off diatom turfs within 3–5 min (Fig. 1c), leaving only a thin green skin. Some tiles that had been stripped by *Campostoma* were re-incubated in troughs; these tiles regrew diatom-dominated turfs within 13 d (Table 1b). When tiles that had supported diatom turfs were subjected to chronic grazing by *Campostoma* on the streambed, cyanobacterial felts visible to the naked eye developed after 11 d, and microscopic examination revealed significant increases in cyanobacteria and decreases in diatoms ($t = 1.98$, $P < .05$ for arcsine square-root tranformed data); *Melosira* became undetectable (Table 1c). These results showed that differences in algal floras were not due to differences between colonization history or materials of artificial and natural substrates. However, the possibility remained that different conditions in troughs and on the streambed contributed to development of the different floras.

During the course of the experiment, *Campostoma* began to graze on tiles along the edges of troughs. Grazing scars were first noted on tiles along the upstream and downstream edges of all three troughs from 5 to 7 October. Minnows did not enter troughs, so thick diatom turfs persisted on more interior tiles. Except for their exposure to grazing, conditions for tiles situated at the upstream and downstream ends of troughs were very similar to conditions within troughs: depth was only a few millimetres greater, and surface velocity was not detectably different. Nevertheless, where minnows removed the diatom turf from tiles at the ends of troughs, a visible cyanobacterial felt developed within 8 d after grazing scars were first noted, and proportions of cyanobacteria were higher than proportions in samples from interior tiles (Table 1c).

Gut contents of *Campostoma* (also quantified by the method of Jones [1968]) were composed largely of diatoms and cyanobacteria, but proportions of diatoms were high ($t = 2.14$, $P < .05$ from t tests on arcsine square-root transformed data) relative to their abundance in felts on natural stream substata where minnows grazed (Table 1d). *Campostoma* may have enriched their diets with diatoms by cropping the tops of felt surfaces, much as superficial aspiration increased proportions of diatoms in samples from incubated felts. Diatoms are generally considered to be superior to cyanobacteria as food for grazers (Cummins 1964, Calow 1973, Moore 1975, Porter 1977, Gregory 1983, Lamberti and Moore 1984, Hart 1985). *Calothrix* filaments in *Campostoma* guts, however, appeared digested: their cell walls were ruptured, and the color of cell contents had changed from blue-green to reddish brown.

DISCUSSION

Persistence of cyanobacterial felts in Ozark streams where grazing pressure is intense is likely related to their prostrate filaments, production of mucilage, and,

in *Calothrix,* to clumping of trichomes into tufts with basal regeneration. Cell division in *Calothrix* is commonly restricted to the lower parts of filaments, often within several cells of terminal heterocycsts (Smith 1950; B. A. Whitton, University of Durham, *personal communication*). Superficial grazing by fish or snails would remove attenuated, distal portions of trichomes, and would leave basal regenerative portions. In the lagoon of Aldabra Atoll, intertidal mats of the cyanobacterium *Scytonema* sp. have erect filaments that often show evidence that terminal parts have been grazed (B. A. Whitton, University of Durham, *personal communication*). Mats of *Calothrix* embedded in the cyanobacterium *Pleurocapsa* persist in hot springs of the western United States, where grazing by thermophilic ostracods eliminates other cyanobacteria capable of overgrowing these species (Wickstrom and Castenholz 1985).

Grazer-resistant and dependent cyanobacteria have functional analogs among the coralline algae, turf-forming seaweeds, and terrestrial grasses (Harper 1977, Lubchenco 1978, Paine 1980, Hay 1981, Steneck 1982, McNaughton 1984, Lewis 1986), which persist under grazing because of basal regeneration. Characteristics that protect these plants from grazers also retard their growth, and render them susceptible to overgrowth by competitors in the absence of grazing. Basal growth and packing of branches into compact tufts, for example, slow the growth of seaweeds by reducing light penetration and nutrient diffusion (Hay 1981). While maintenance of lawns of plants with basal regeneration under intense grazing has been documented in terrestrial grasslands and marine communities, it has not to our knowledge been reported in nonthermal freshwater habitats, where heavy grazing often produces periphyton assemblages dominated by small, adnate diatoms (Gregory 1983, Lamberti and Resh 1983, Hart 1985).

In addition to forming tufts with basal regeneration, *Calothrix* secretes copious mucilage. The functions of cyanobacterial mucilage are not well understood, but resistance to grazing is one hypothesized advantage (Fay 1983). Mucilaginous coats over *Calothrix* felts, however, rapidly collect seston, including diatoms capable of overgrowing felts. Mucilage secretion by these cyanobacteria may therefore increase their dependence upon grazers.

Grazers-induced changes in the structure of periphyton assemblages may produce ecosystem-level effects. Diatom turfs that replaced cyanobacteria in the absence of grazers were much more loosely attached to substrata. Export and suspension of biomass from these turfs could have far-reaching effects on water clarity (Ozark streams with cyanobacterial felts are extremely clear), and on availability and quality of food for suspension feeders. *Calothrix* and many other periphytic cyanobacteria actively fix nitrogen (Fay 1983), and grazers that uncover them may enhance nitrogen loading of rivers and streams. On the Great Barrier Reef,

for example, rates of nitrogen fixation increased up to 27-fold in areas where grazing fishes removed macrophytic algae, and activity of nitrogen-fixing cyanobacteria was increased (Wilkinson et al. 1985). In Ozark rivers, we have yet to learn whether nitrogen fixation is actually slowed by overgrowth, and whether community primary productivity is nitrogen limited. If both conditions apply, grazers such as snails and *Campostoma* could enhance primary productivity by maintaining high proportions of nitrogen fixers in producer assemblages. On the other hand, diatom turfs could be more productive if diatoms maintained intrinsically higher growth rates than cyanobacteria, or if thick turfs cycled nitrogen or other nutrients more tightly, reducing spiral length (Webster 1975, Newbold et al. 1982), than thin cyanobacterial felts. Much remains to be learned about linkages between community-level and ecosystem-level processes in rivers and streams. Ozark ecosystems, where biotic interactions produce strong effects on the structure of lotic communities, are promising arenas for investigation of the consequent dynamics.

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