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Nutrient induced changes in the species composition of epiphytes on *Cladophora glomerata* Kütz. (Chlorophyta)

Jane C. Marks[1] & Mary E. Power[2]
[1]*Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011, U.S.A. Tel+ 520-523-0918. Fax: +520-523-7500*
[2]*Department of Integrative Biology, University of California, Berkeley, CA 94720, U.S.A.*

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Abstract

Cladophora glomerata is a widely distributed filamentous freshwater alga that hosts a complex microalgal epiphyte assemblage. We manipulated nutrients and epiphyte abundances to access their effects on epiphyte biomass, epiphyte species composition, and *C. glomerata* growth. *C. glomerata* did not grow in response to these manipulations. Similarly, nutrient and epiphyte removal treatments did not alter epiphyte biovolume. Epiphyte species composition, however, changed dramatically with nutrient enrichment. The epiphyte assemblage on unenriched *C. glomerata* was dominated by *Epithemia sorex* and *Epithemia adnata*, whereas the assemblage on enriched *C. glomerata* was dominated by *Achnanthidium minutissimum*, *Nitzschia palea* and *Synedra* spp. These results indicate that nutrients strongly structure epiphyte species composition. Interactions between *C. glomerata* and its epiphytes were not affected by epiphyte species composition in our experiment but may be when *C. glomerata* is actively growing.

Introduction

Cladophora glomerata is a widely distributed filamentous green alga found in a diversity of aquatic ecosystems including eutrophic lakes, pristine coastal streams, and the marine inter tidal zone (Whitton, 1970; Sheath & Cole, 1992; Dodds & Gudder, 1992). *C. glomerata* grows under a wide range of nutrient regimes and hosts a taxonomically diverse and architecturally complex micro-algal epiphyte assemblage that varies among locations (Table 1 and references therein). Epiphyte species composition is known to respond to gradients of nutrients, light, current, conductivity and disturbance regimes within a habitat (Stevenson & Stoermer, 1982b; Luttenton & Rada, 1986; Jonsson, 1987; Hardwick et al., 1992; Bergey et al., 1995; O'Connell et al., 1997). Therefore, variation in physical factors (e.g. water chemistry) across habitats is likely to contribute to geographic variation in epiphyte assemblages on *C. glomerata* despite the common substrate. For example, *Epithemia* spp. tend to be dominant epiphytes only in habitats with low N:P ratios (some Western North American watersheds), whereas the epiphyte assemblages in habitats with higher N:P ratios (Great Lakes region) are dominated by *Cocconeis* spp., *Diatoma* spp., *Rhoicosphenia curvata* and *Gomphonema* spp. (Table 1 and J. C. Marks, pers. obs.).

C. glomerata and its epiphytes may interact negatively (e.g. competition for nutrients and light) or positively (e.g. *C. glomerata* provides substrate for epiphytes, epiphytes may leak nutrients benefiting *C. glomerata*). These interactions are likely to vary with nutrient concentrations, epiphyte density and epiphyte species composition. Furthermore, because the epiphytes on *C. glomerata* are an important food resource for grazers (Kupferberg et al., 1994), the nature of the interactions between *C. glomerata* and its epiphytes will likely depend on characteristics of the grazer assemblage. For example, Dudley (1992) and Kupferberg (1997) found that *C. glomerata* growth increased when herbivores significantly reduced epiphyte bio-

Table 1. A global survey of *Cladophora* epiphytes across freshwater habitats that have a wide range of nutrient concentrations[a]

Site & source	Nutrient levels	Major epiphytes
Western United States Watersheds		
Eel River, CA, U.S.A. This Study	NO_3_N: 7.9 μg L^{-1} NH_4-N: 6.3 μg L^{-1} S.R.P.[b]: 1.1 μg L^{-1}	*Cocconeis pediculus* Ehr.; *C. placentula* Ehr.; *Epithemia adnata* (Kütz.) Grun.; *E. sorex* Kütz.; *Rhoicosphenia curvata* (Kütz.) Grun.
Sycamore Creek, Arizona, U.S.A. (Busch & Fisher, 1981 Dudley, T. pers. comm.)	NO_3-N: 20 μg L^{-1} PO_4:-P 50 μg L^{-1}	*Cocconeis; Epithemia; Gomphonema; Navicula; Nitzschia; Synedra*
Madison River, Montana, U.S.A. (Dodds, 1991a,c)	NO_3_N: 6 μg L^{-1} NH_4-N: 12 μg L^{-1} S.R.P.: 25 μg L^{-1}	*Epithemia; Nitzschia fonticola* Grun.
Rattlesnake Creek, California, U.S.A. (Dudley, 1992)	NO_3-N: 26.6 μg L^{-1} PO_4-P: 10.84 μg L^{-1}	*Cocconeis*; *Epithemia*; *Gomphonema; Melosira*; *Mougeotia*; *Navicula*; *Rhoicosphenia curvata*; *Syndera ulna* (Nitz.) Ehr.
Colorado River, Glen and Grand Canyons, Arizona, U.S.A. (Hardwick et al., 1992) (Benenati et. al. 1998)	Not reported	*Amphora ovalis* var. *pediculus* Kütz.; *Cocconeis pediculus; Cymbella affinis* Kütz.; *Diatoma vulgare* Bory; *D. tenue* Ag.; *Fragilaria leptostauron* var *Dubia* Hust.; *F. ulna* Ehr.; *Gomphonema olivacium* (Lyngb.) Kütz.; *Nitzschia dissipita* (Kütz.) Grun.; *Rhoicosphenia curvata*
Great Lakes, United States and Canada Watersheds		
Grand Traverse Bay, Lake Michigan, U.S.A. (Lowe et al., 1982)	Not Reported	*Cocconeis pediculus*; *Diatoma vulgare*; *Rhoicosphenia curvata*
Upper Mississippi River, Wisconsin, U.S.A. (Luttenton & Rada, 1986)[c]	NO_3-N: 730-1830 μg L^{-1} NH_4-N: 8-239 μg L^{-1} PO_4-P: 3-127 μg L^{-1}	*Cocconeis pediculus*; *Diatoma vulgare*; *Rhoicosphenia curvata*
Tippecanoe River, Indiana, U.S.A. (McShaffrey & McCafferty, 1991)	Not Reported	*Achnanthes*; *Cocconeis*; *Fragilaria; Gomphonema*; *Melosira*; *Navicula*
Great Lakes and Upper St. Lawrence Seaway, U.S.A. (Sheath & Morison, 1982)	Not Reported	*Chamaesiphon; Cocconeis pediculus*; *Lyngbya diguetii* Gomont; *Lyngbya epiphytica* Hieronymus; *Rhoicosphenia curvata*
Lake Huron & Lake Michigan, U.S.A. (Stevenson & Stoermer, 1982 a & b) [d]	NO_3-N: 157-1475 μg L^{-1} NH_4-N: 7.7-172 μg L^{-1} S.R.P.: 3–150 μg L^{-1}	*Amphora perpusilla* (Grun.) Grun.; *Cocconeis pediculus*; *Cymbella prostrata* var *auerswaldii* (Rabh.) Reim comb.nov.; *Fragilaria brevistriata* Grun.; *F. pinnata* Ehr.; *Rhoicosphenia curvata*
St. Lawrence River, Canada (O'Connell et al., 1997)[e]	Not Reported	*Cocconeis pediculus; Achnanthes minutissima* (Kütz.);[f] *Rhoicosphenia abbreviata; Gomphonema minutum* (Ag.) Agardh

Continued on p. 189

Table 1. Continued.

Site & source	Nutrient levels	Major epiphytes
European Watersheds		
River Skawie, Poland (Chudyba, 1968)	Not Reported	*Cocconeis placentula* Ehrenb.; *Gomphonema olivaceum* (Lyngb.) Kütz.; *Rhoicosphenia curvata*
Langley Brook, England (Hawkes, 1964)	NH_4-N: 10,000 μg L^{-1}	*Cocconeis placentula*; *Rhoicosphenia curvata*; *Gomphonema olivaceum*
River Wear, England (Peabody & Whitton, 1968)	Not Reported	*Cocconeis pediculus*; *Rhoicosphenia curvata*
Other Watersheds		
Cape Maclear, Lake Malawi, Malawi, Africa (Haberyan & Mhone, 1991)	Not Reported	*Cocconeis*; *Cymbella*; *Epithemia*; *Navicula*; *Rhopalodia*
Kialing River, China (Jao, 1944)	Not Reported	*Cocconeis placentula*; *Diatoma vulgare*; *D. elongatum* (Lyngb.) C.Agardh; *Gomphonema olivaceum*; *Melosira varians* C.Agardh; *Synedra ulna*
Lake Thingvallavatn, Iceland (Jonsson, 1987)	Dissolved inorganic N: 0–29.7 μg L^{-1} PO_4-P: 8.4-17.1 μg L^{-1}	*Achnanthes cleveii* Grun.; *A. lanceolata* Bréb. ex. Kütz.; *A. minutissima* Kütz.; *A. pinnata* Hust.; *Cocconeis placentula* var *lineata* (Ehr.) V.H.; *Epithemia turgida* (Kütz.) Bréb.; *Gomphenema clevei* Fricke; *Rhoicosphenia curvata*

[a] Taxa are listed alphabetically. All taxa listed are diatoms (Bacillariophyta) except for *Chamaesiphon incrustens, Fischerella muscicola*, *Lyngbya diguetii* and *Lyngbya epiphytica* which are blue-greens (Cyanophyta) and *Mougeotia*, which is a green algae (Chlorophyta).
[b] S.R.P. = Soluble Reactive Phosphorus.
[c] This study reported 17 epiphyte species. Species included here constitute >95% of the epiphyte assemblage.
[d] These studies reported 245 epiphyte species. Species included here were reported as dominant taxa.
[e] This study reported 34 epiphyte species. Species included here were reported as dominant taxa.
[f] *Achnanthes minutissima* has been renamed *Achnanthidium minutissimum.*

mass. In contrast, Dodds (1991a) saw no effect of epiphyte removal and concluded that *C. glomerata* and epiphytes did not compete with each other in his system because *C. glomerata* was limited by nitrogen whereas the common epiphytes were limited by phosphorus.

Despite much speculation about the relationships between *C. glomerata* and its epiphytes, there have been no experimental studies that examine how nutrients and substrate affect *C. glomerata* epiphyte abundances and species composition. Nor have there been any studies that directly manipulate epiphyte density to determine how epiphyte density influences *C. glomerata's* response to nutrient enrichment. We manipulated nutrients and epiphyte abundances to assess their effects on epiphyte biomass, epiphyte species composition and *C. glomerata* growth. Understanding these direct effects is critical if we are to unravel the ways in which grazers and nutrients interact to influence dynamics of *C. glomerata* and its epiphyte assemblage. Specifically, we addressed the following questions: (1) Are epiphyte biovolume and species composition affected by nutrient availability? (2) Will highly epiphytized *C. glomerata* respond to nitrogen and phosphorus enrichment? (3) Will partial removal of epiphytes alter the response of *C. glomerata*' to nutrient enrichment? We predicted that epiphyte species composition would shift with changes in resource conditions. This would indicate that the epiphyte assemblage as a whole is not limited by any one nutrient but rather comprises species with different nutrient requirements so that dominance can change when resources change. We also predicted that high epiphyte abundances would both shade *C. glomerata* and block diffusion of nutrients to *C. glomerata* sufficiently to prevent its response to nutrient enrichment. Therefore,

we expected that *C. glomerata* growth would increase with nutrient enrichment only when epiphytes were reduced.

Study site and Methods

Study site and phenology of C. glomerata

We conducted this study in the South Fork of the Eel River in Mendocino County, California, where most precipitation falls between October and April. The concentrations of inorganic N and P in the river suggest that algal biomass is primarily limited by nitrogen (Table 1). *C. glomerata* blooms in late May following winter floods, grows throughout the summer; by mid July, its filaments can be several meters in length. In contrast, during drought years, *C. glomerata* biomass is greatly reduced (Power et al., 1996), and by midsummer primarily consists of short filaments attached to small cobbles and boulders. These short filaments become heavily epiphytized; individual *C. glomerata* cells can host over 50 epiphytic diatoms, and total epiphyte biovolume often exceeds that of *C. glomerata* (J. C. Marks, pers. obs.). The main epiphytic taxa are *Epithemia adnata* and *Epithemia sorex*, both of which have cyanobacterial endosymbionts that are capable of nitrogen-fixation (Floener & Bothe, 1980).

We conducted this experiment during a drought year, thus when *C. glomerata* biomass was relatively low. An unseasonably late spate (early June) further reduced *C. glomerata* biomass by detaching and exporting filaments during the peak of its growing season.

Enrichment experiment

We used a 3-way factorial design with 2 levels of nitrogen (ambient 7 μg/l and 300 μg/l $NaNO_3$), 2 levels of phosphorus (ambient <2 μg/l and 150 μg/l Na_2PO_4) and 2 epiphyte abundances (partially de-epiphytized *C. glomerata* and controls with ambient epiphyte densities). Each of the 8 treatments was replicated 4 times. Epiphytes were removed on day 0 by gently rubbing them off of the filaments manually. This resulted in a 50% decrease in the density of epiphytes (numbers per *C. glomerata* cell). Mean epiphyte densities at the start of the experiment were 12.3 epiphytes $*$ *C. glomerata* cell^{-1} (s.e.=3.8) for de-epiphytized *C. glomerata* and 23.2 epiphytes**C. glomerata* cell^{-1} (s.e.=2.9) for control *C. glomerata* (n=16 for each treatment). *Epithemia* spp. and *Cocconeis* spp. dominated both treatments.

On July 15, 1990, we placed rocks with attached *C. glomerata* in individual recirculating chambers in the Eel River. Our chamber design was a modification of chambers described by Rodgers et al. (1978). Chambers were constructed from 2 l (18 cm diameter, 10.5 cm depth) plexiglass water-tight containers. We inserted a recirculating water pump in each of the chambers by drilling a 2 cm diameter hole in the lid of each chamber and gluing the pumps to the lids. Each pump was individually wired to a voltage regulator that was positioned on shore and connected to a 12 volt battery. Each chamber was elevated on clay bricks so that the chamber was submersed while the lid/pump was kept out of water.

During each day of the experiment, we filled the chambers with river water and cleaned the chamber walls with a sponge. We excluded most grazers except for small grazers living in the water column (predominantly early instar midges and mayflies).

Microscopic examination of *C. glomerata* filaments on day 0 revealed that some filaments were undergoing zoosporogenesis.

We measured initial *C. glomerata* length (1–5 cm) by placing a sheet of plexiglass over each chamber, and tracing the rock shape and the outline of the floating attached filaments of *C. glomerata* filaments onto a sheet of acetate paper. The technique minimized physical disturbance of the *C. glomerata*-epiphyte assemblage. The procedure was repeated on day 21 and *C. glomerata* growth was quantified as the difference in mean length between the 2 sampling dates.

C. glomerata filaments were sub-sampled from each rock on days 0 and 21 of the experiment for epiphyte analysis. We mounted *C. glomerata* filaments on glass slides and analyzed epiphyte assemblages using an Olympus CH microscope at 400$\times$. We quantified epiphyte abundance by counting the epiphytes on 100–200 *C. glomerata* cells from each sample. More than 1000 epiphyte cells were counted in each sample, and identified to genus or species, with the exception of some pennate diatoms that were grouped together (species that were lumped together either at the genus or higher level responded similarly to nutrient treatments in other studies (Fairchild et al., 1985; Marks & Lowe, 1993). We then calculated the biovolume of each epiphyte taxon per cell of *C. glomerata* by multiplying the cell volume of each taxon by its relative abundance by the total number of epiphytes per *C. glomerata* cell.

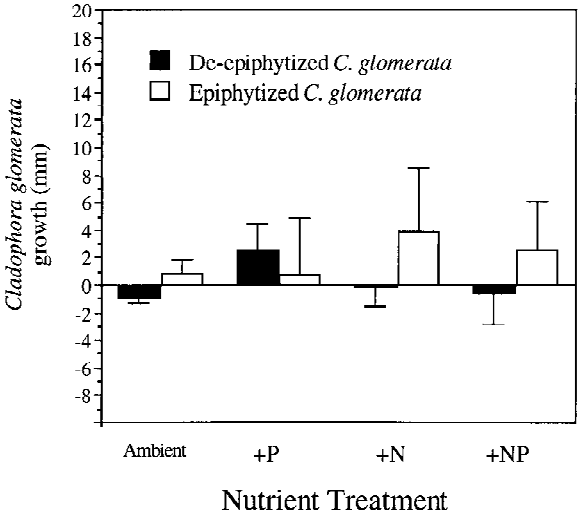

Figure 1. Mean change in *C. glomerata* filament length across nutrient and epiphyte treatments. Error bars represent one standard error. N=4 for each treatment. Statistics are reported in Table 2.

Data were analyzed with a three-way analysis of variance with nitrogen, phosphorus and epiphyte abundance as treatments and *C. glomerata* growth, epiphyte abundance, and the relative abundance of major epiphytic taxa as response variables. Sub-samples from the unenriched and nitrogen + phosphorus enriched treatments were also used for scanning electron microscopy (SEM), selecting replicates and views to illustrate 'typical' ephiphyte assemblages from these treatments (scanning electron micrographs were not used for quantitative assessments of treatment effects). Samples for Scanning Electron Microscopy were fixed in 2% glutaraldehyde (0.1 M Sodium cacodylate buffer, pH 7.2) mounted on stubs, critical point dried and sputter coated with gold palladium.

Results

Enrichment experiment

C. glomerata *response*

C. glomerata did not respond to either nutrient enrichment or epiphyte removal (Table 2, Fig. 1). Filament length decreased in a few replicates but most replicates showed either no growth or very small increases in filament length (Fig. 1). Growth was not significantly different from 0 in any treatment ($p>0.05$). *C. glomerata* on river substrates outside chambers did not show noticeable growth during this period (July 15–August 15).

Table 2. Results from three-way ANOVA assessing variation in *Cladophora* growth, epiphyte biovolume, and the relative abundance of three major epiphyte taxa across nitrogen, phophorus and epiphyte treatments. D.F.=1,24

Variable	Source	F-ratio	*P*
Cladophora	Epiphytes	0.9234	0.35
glomerata	N	0.0453	0.83
growth	P	0.1142	0.74
	Epiphytes*N	0.3141	0.58
	Epitphytes*P	0.8197	0.37
	N*P	0.4059	0.53
	Epiphytes*N*P	0.1187	0.73
Epiphyte	Epiphytes	1.906	0.18
Biovolume/	N	0.407	0.53
C. glomerata	P	1.675	0.21
Cell	Epiphytes*N	0.001	0.98
	Epiphytes*P	0.946	0.34
	N*P	2.41	0.13
	Epiphytes*N*P	0.244	0.63
%Relative	Epiphytes	1.475	0.24
Abundance	N	46.363	<0.001
Epithemia spp.	P	8.033	<0.001
	Epiphytes*N	2.769	0.11
	Epiphytes*P	0.196	0.66
	N*P	0.444	0.51
	Epiphytes*N*P	2.254	0.15
%Relative	Epiphytes	0.109	0.74
Abundance	N	29.472	<0.001
Achnanthidium minutissimum	P	2.128	0.16
	Epiphytes*N	0.740	0.40
	Epiphytes*P	0.143	0.71
	N*P	4.573	0.04
	Epiphytes*N*P	4.611	0.04
%Relative	Epiphytes	0.247	0.62
Abundance	N	24.336	<0.001
Pennate	P	0.056	0.82
Diatoms	Epiphytes*N	0.289	0.60
	Epiphytes*P	0.002	0.97
	N*P	0.236	0.63
	Epiphytes*N*P	0.048	0.83

Epiphyte response

Total epiphyte biovolume did not differ across nutrient treatment or epiphyte removal treatments (Table 2, Fig. 2). Epiphytes were able to re-establish high densities and a similar species composition after 21

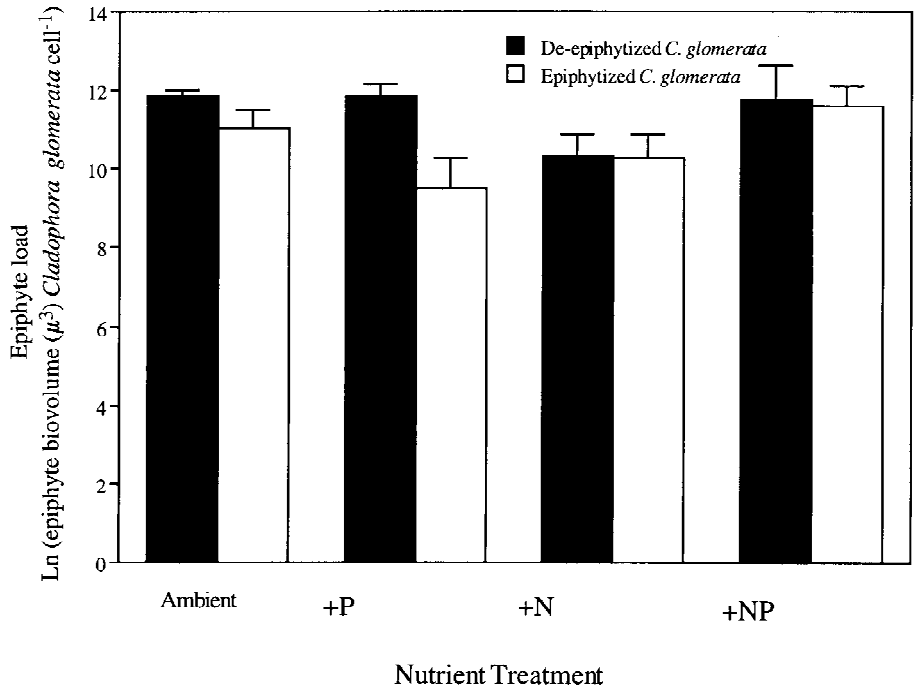

Figure 2. Mean epiphyte biovolume on day 21, across nutrient and epiphyte treatments. Error bars represent one standard error. N=4 for each treatment. Statistics are reported in Table 2.

days following a 50% removal. The epiphyte species assemblage did not respond to epiphyte removal, but changed dramatically with nutrient enrichment (Table 2, Fig. 3). Epiphyte assemblages on unenriched *C. glomerata* were dominated by *Epithemia* spp., primarily *E. adnata* and *E. sorex* (Table 2, Figs 3 and 4a), and both nitrogen and phosphorus enrichment significantly reduced the relative abundance of *Epithemia* spp. (Table 2). Treatments enriched with nitrogen were dominated by *Achnanthidium minutissimum (Kutz.) Czar.*

A. minutissimum, and other pennate diatoms, mostly *Nitzschia palea* and *Synedra* spp. (Figs 3 and 4b) responded positively to the +N and +NP treatments. Mean relative abundance of *A. minutissimum*, increased four-fold under nitrogen enrichment, ten-fold under nitrogen and phosphorus enrichment (from 3.2% in unenriched controls to 31% in nitrogen + phosphorus treatments), but did not respond to phosphorus enrichment alone (Table 2). Pennate diatoms responded only to nitrogen enrichment (Table 2, Fig. 3), increasing from a relative abundance of 1.2% on unenriched controls to 19% under nitrogen enrichment, and to 22% under nitrogen + phosphorus enrichment, but showed no response to phosphorus enrichment (<1.0%). The remaining epiphyte biovolume mostly comprised *C. pediculus*, *C. placentula* and *R. curvata*, taxa that did not respond to any treatment. Their relative abundances were highly variable even on control substrates. Together, the reported taxa accounted for over 95% of epiphyte biovolume.

Discussion

C. glomerata in our study did not grow measurably in response to either epiphyte reduction or nitrogen and phosphorus addition. It is possible that nutrients stimulated branching or larger cell size which did not lead to elongation of filaments. Although studies have shown that *C. glomerata* often responds positively to nutrient enrichment (see Dodds & Gudder, 1992 for review), other studies have shown that *C. glomerata* was not nutrient deficient or that nutrient deficiency changed seasonally within a site (Manuel-Faler et al., 1984; Dodds, 1991a). The lack of response to the factors we manipulated could indicate that other factors such as light, temperature or micro-nutrients limited growth, or alternatively, that *C. glomerata* was in an unresponsive life history stage during our experiment. Once *C. glomerata* undergoes zoosporogenesis,

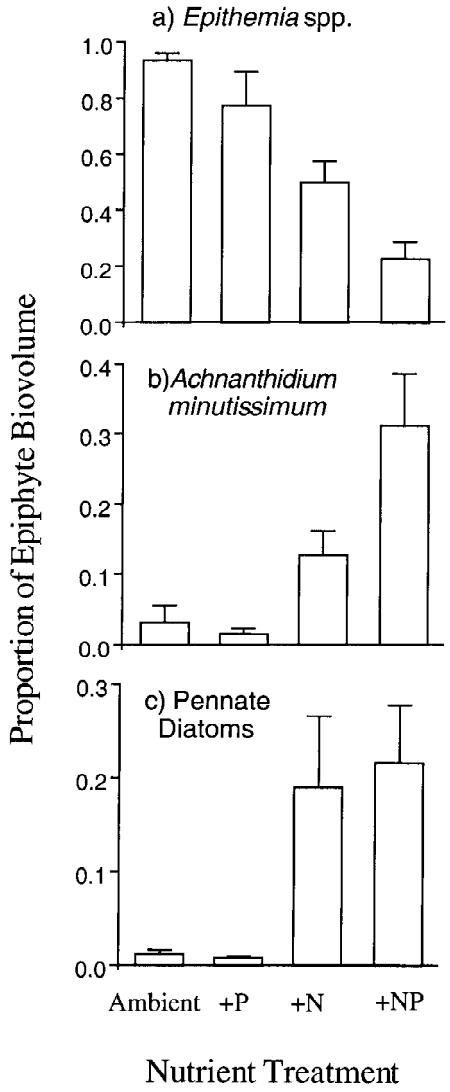

Figure 3. The relative abundances of the dominant epiphytic diatoms on control and nutrient enriched substrates after 21 days. Error bars represent one standard error. N=8 for each treatment. Data are pooled across epiphyte removal treatments. *Epithemia* spp. includes *E. adnata* and *E. sorex*. Pennate diatoms (other than *A. minutissimum*) primarily comprised *Nitzschia palea* and *Synedra* spp. Statistics are reported in Table 2.

it may greatly reduce growth, regardless of environmental conditions. Hoffman & Graham (1984) showed that zoosporogenesis is negatively correlated with dry weight production and is positively correlated with short day length and low light levels, suggesting that shading by dense epiphytes could induce zoosporogenesis. The initially high epiphyte abundances in our study may have induced zoosporogenesis, possibly reducing *C. glomerata's* ability to respond to nutrient enrichment. Because epiphytes grew back quickly in the epiphyte removal treatments, we were unable to determine the effect of prolonged epiphyte removal on *C. glomerata*. Studies that have shown a positive effect of epiphyte grazers on *C. glomerata* (Dudley, 1992; Kupferberg, 1997) have maintained grazing pressure (i.e. epiphyte removal) throughout the duration of the experiment, which differs from the one time 'pulse' removal that we performed.

In contrast to *C. glomerata* growth, epiphyte species composition responded strongly to nutrient enrichment, showing that the assemblage reflects the nutrient conditions of the host's habitat. The shift from an assemblage dominated by *Epithemia* spp. to one dominated by *A. minutissimum* and *N. palea* with nutrient enrichment has been seen in epilithic assemblages in other western North American watersheds (Peterson & Grimm, 1992; Marks & Lowe, 1993, Marks et al., 2000). While *Epithemia* species can thrive in low nitrogen habitats because of its nitrogen fixing endosymbiont (Floener & Bothe, 1980; Deyoe et al., 1992), *N. palea* and *A. minutissimum* do well in eutrophic habitats due to their fast maximal growth rates (Marks & Lowe, 1993).

The three major species that did not respond to any treatment, *R. curvata*, *Cocconeis pediculus* and *C. placentula*, constitute a substantial component of the *C. glomerata* epiphyte flora across a broad geographic range (Table 1). One property that might account for their cosmopolitan distribution is their close association with the host plant. The two *Cocconeis* species in particular are likely to gain nutrients from their host due to their prostrate growth form (Burkholder & Wetzel, 1990). This might buffer their susceptibility to changes in ambient water chemistry. *Cocconeis* species are often early colonizers of *C. glomerata* but decrease in abundance as *C. glomerata* becomes more highly epiphytized by other taxa. It is common to see a layer of dead *Cocconeis* species (empty frustules) beneath other epiphytes. These observations suggest that *Cocconeis* primarily benefits from the new substrate that growing *C. glomerata* provides. The third cosmopolitan epiphyte, *R. curvata* has an upright growth form but maintains contact with *C. glomerata* via a mucilaginous stalk. In contrast, other epiphyte species (*Epithemia* spp. *A. minutissimum* and *N. palea*) grow on top of each other and are often not in direct contact with the *C. glomerata*.

Shifts in the species composition of the epiphytes and shifts in the relative abundance of epiphytes and *C. glomerata* may have consequences for higher trophic

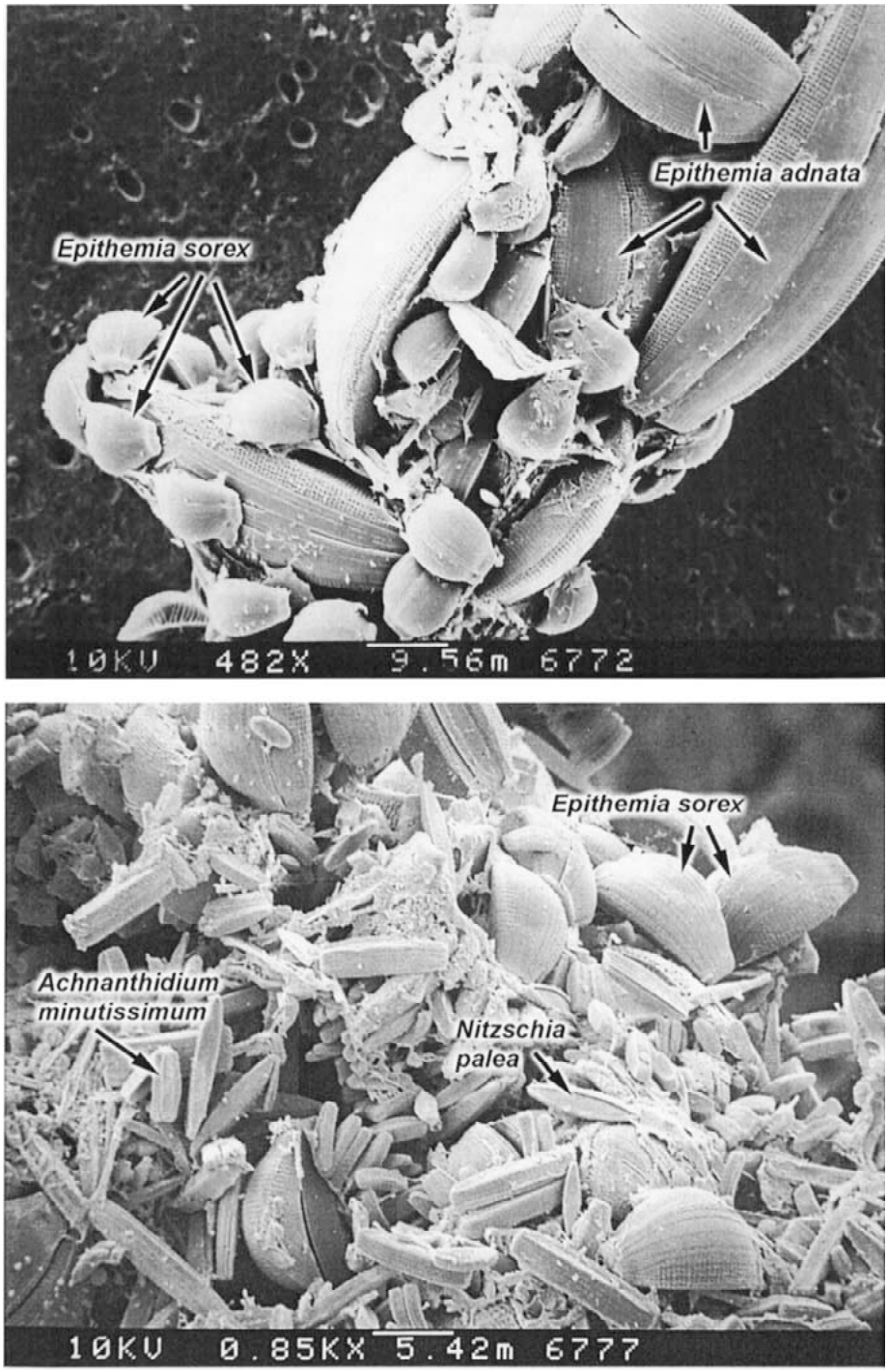

Figure 4. Scanning electron micrographs of *C. glomerata* and epiphyte assemblages from the unenriched (a) and nitrogen + phosphorus enriched (b) treatments, illustrating the shifts in epiphyte composition caused by nutrient enrichment. The *C. glomerata* filament representative from the unenriched control (a) is covered with *E. adnata* and *E. sorex* whereas the filament from the enriched treatment (b) has high densities of *A. minutissimum* and pennate diatoms in addition to *E. sorex*.

levels. For example, grazers often prefer epiphytes (particularly diatoms) over host plants because they have higher nutritional value and few structural defenses (Cattaneo, 1983; Bronmark, 1985; Kupferberg et al., 1994). We know of no studies that compare the nutritional quality or digestibility of different diatom species, but differences likely exist, and may depend on the nutrient environment. For example, in low nutrient habitats, *Epithemia* species may have higher cellular nitrogen content then other diatoms because of *Epithemia's* access to atmospheric nitrogen through its nitrogen-fixing endosymbiont. In addition to their nutrient content, epiphyte morphology may affect grazers. Loosely attached species are generally present on older *C. glomerata* cells that are highly epiphytized, and grazers often prefer loosely attached diatoms over prostrate forms because they are more easily harvested (Peterson, 1987; Dudley, 1992). Loosely attached diatoms were present in all nutrient treatments in our experiment, but the specific taxa with this morphology differed among nutrient treatments.

A recent survey of *C. glomerata* epiphytes in the St. Lawrence River points to their potential for monitoring water quality (O'Connell et al., 1997). Our experimental results support this idea. The rapid response of epiphytes to changes in nutrients indicate that epiphyte species composition could be a sensitive indicator of changes in water quality.

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