AN ABSTRACT OF THE THESIS OF

Alan D. Steinman for the degree of Doctor of Philosophy in Botany and Plant Pathology presented on June 18, 1987.

Title: Effects of Current Velocity, Irradiance, and Herbivory on Algal Assemblages in Laboratory Streams.

Redacted for Privacy

Abstract approved: ______________________
C. David McIntire

Effects of current velocity, irradiance, and grazing on the biomass, taxonomic structure, physiognomy, and chemical composition of lotic algal assemblages were investigated. Four experiments, lasting 32 to 75 days, were conducted in laboratory streams to determine how these factors affect algal assemblages singly, and in concert with each other.

Regardless of light level, low current velocities (5 $cm \cdot s^{-1}$) enhanced initial rates of colonization, presumably because of high settling rates. However, in streams exposed to equal irradiances, greater biomass levels eventually developed in streams with high current velocities (15 $cm \cdot s^{-1}$). Few taxonomic differences could be attributed solely to current velocity regimes.

Algal assemblages exposed to high (400 and 150) as opposed to low (50 and 15 $\mu E \cdot m^{-2} \cdot s^{-1}$) irradiances were characterized by higher biomass, a greater amount of filamentous chlorophytes, and lower concentrations of total lipid and the 18:1 and 20:5 fatty acids.

The physiognomy of the assemblage was also more complex at high irradiances.

Effects of grazing on taxonomic structure were primarily a function of algal growth form and herbivore feeding behavior. Large, overstory cells were vulnerable to grazing and decreased in relative abundance as grazing pressure increased, while small, adnate cells increased in relative abundance. The snail *Juga silicula* had little effect on algal dynamics at low densities (125/stream = $62/m^2$), although at higher snail densities (500 and 1000/stream) and at all densities of the caddisfly *Dicosmoecus gilvipes*, grazing resulted in low algal biomasses and a dominance of adnate cells. Fatty acids were more robust indicators of algal taxonomic structure than amino acids.

A separate experiment showed that at densities of 500 snails/stream ($250/m^2$), algal biomass levels were similar in grazed and ungrazed streams by day 43 in channels exposed to 100 and 400 $\mu E \cdot m^{-2} \cdot s^{-1}$. At 15 $\mu E \cdot m^{-2} \cdot s^{-1}$, algal biomass levels were similar (and low) throughout the experiment. Grazing reduced amounts of taxa with large growth forms, regardless of irradiance level.

A detailed process model of herbivory was developed, which allows both quantitative (i.e. biomass) and qualitative (i.e. taxonomic and chemical composition) components to be assessed. The proposed model can be used to generate hypotheses about how algal assemblages respond to current velocity, irradiance, and grazing in natural streams.

EFFECTS OF CURRENT VELOCITY, IRRADIANCE, AND HERBIVORY ON ALGAL ASSEMBLAGES IN LABORATORY STREAMS

by

Alan D. Steinman

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Completed June 18, 1987

Commencement June 1988

APPROVED:

Redacted for Privacy

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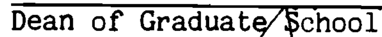

Date thesis is presented June 18, 1987

Typed by Alan D. Steinman for Alan D. Steinman

ACKNOWLEDGEMENTS

I wish to acknowledge my major professor, Dave McIntire, whose guidance, insight, tolerance, and unique perspective on science contributed substantially both to this dissertation and my growth as a biologist.

The content and shape of this dissertation were profoundly influenced by the members of the Stream Team at O.S.U. Stan Gregory and Gary Lamberti were generous with their time and ideas, and many of the conclusions drawn in this thesis reflect a synthesis of their perspectives with my own. Linda Ashkenas provided a theoretical and technical expertise which improved this dissertation greatly, and her willingness to plot the figures in Chapter VII is sincerely appreciated. In addition, I am appreciative of the aid received from Judy Li, Randy Wildman, Karan Fairchild, and Dean DeNicola.

Sincere thanks also go to Roney Cargill formerly of the Stream Team, Bob Lowry in the Dept. of Agricultural Chemistry at O.S.U., and Bob Becker in the Dept. of Biochemistry at O.S.U. The collective expertise of these generous people allowed me to pursue the biochemical avenues that this dissertation traveled along.

In the Botany Department, Al Soeldner's magic touch with the SEM, Harry Phinney's help with identification of algal specimens and loans of phycological treatises, and Nancy Bobadillo's help with typing sundry tables helped make this work possible. All their help is greatly appreciated.

Input from my other committee members, Jane Lubchenco, Jack Lattin, and Norm Anderson also improved this dissertation.

Leslie Kershaw Steinman provided an understanding and warm environment to return home to. Her patience, love, and humor helped keep me sane through some trying times. Finally, I'd like to acknowledge the contribution of my folks. My father taught me the value of personal integrity and hard work, but also the need to temper work with fun. I consider myself fortunate to have inherited my mom's positive attitude to life and joy of discovering knowledge. I thank her for her wisdom in adopting a laissez-faire approach to my upbringing, which I'm sure was not easy for her, but which allowed me to develop in my own way. Her influence and presence are never far away from my consciousness.

CONTRIBUTION OF AUTHORS

C. David McIntire, R. R. Lowry, Stan Gregory, Gary Lamberti, and Linda Ashkenas appear as co-authors on at least some of the manuscripts in this dissertation.

C. David McIntire helped with data collection, statistical analyses, data interpretation, and conceptual development of the thesis topic.

R. R. Lowry provided expertise with lipid analyses and aided me in the interpretation of lipid data.

Stan Gregory, Gary Lamberti, and Linda Ashkenas all worked on the herbivory project, from which the research in this dissertation was generated. They provided numerous ideas on experimental design, helped with the experimental set-up and maintenance, aided in the interpretation of data, and provided comic relief.

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I. EFFECTS OF CURRENT VELOCITY, IRRADIANCE, AND HERBIVORY ON ALGAL ASSEMBLAGES IN LABORATORY STREAMS

INTRODUCTION

Approaches to the study of benthic lotic communities generally fall into two classes: (1) an organismal approach, where the emphasis is placed on the biology of the individual or population, and (2) a process orientation, where the emphasis is placed on a systematic series of actions relevant to the dynamics of the lotic system (e.g. primary production or herbivory, McIntire 1983). This dichotomy reflects the fact that stream ecologists often ask questions at different scales of organization, and also suggests that there is a need for an integrated approach to the study of these communities.

The work of Linnaeus (1753) is commonly regarded as the start of the modern organismal approach to the botanical kingdom. Although Linnaeus recognized 14 genera of algae in *Species plantarum*, only four genera can be considered as being valid in the current sense (Papenfuss 1955). The genus *Conferva* was usually applied to filamentous forms, *Ulva* was given to membranous types, *Fucus* was used for fleshy morphologies, and *Chara* was regarded as a special form or excluded from the algae in subsequent works (Papenfuss 1955). Thus, morphology played a major role in the early taxonomic studies of algae. When Harvey (1836) recommended dividing the algae into four divisions based on color (Melanospermae: brown

algae; Rhodospermae: red algae; Chlorospermae: green algae; and Diatomaceae: diatoms and desmids), a biochemical character was also introduced into algal classification and study.

The study of algal ecology lagged behind that of taxonomy and systematics. By the late nineteenth and early twentieth centuries, however, descriptive surveys of lotic algae were becoming common. Publication of floristic surveys, with attendant physical data regarding the stream, reflected the organismal approach of (botanical) lotic ecologists (e.g. Kofoid 1903, Fritsch 1906, Brown 1908, Pearsall 1923, Eddy 1925, Budde 1930, Butcher 1932). Indeed, surveys of lotic algae are still being conducted (e.g. Rushforth et al. 1986, Sheath et al. 1986b), and they provide valuable information about regions which have been infrequently studied or have undergone ecological change. With the advent of modern instrumentation, organismal approaches to the study of lotic algae are shifting away from floristic surveys and placing more emphasis on cytology (e.g. Hymes and Cole 1983), ultrastructure (e.g. Broadwater et al. 1986), physiology (e.g. Livingstone et al. 1984, Jasper and Bothwell 1986) and biochemistry (e.g. Millie 1986).

Unlike the organismal approach, the process orientation promotes a holistic approach to the study of communities, and often operates at a level of resolution incompatible with individuals or populations (see McIntire 1983). One of the earliest and best known examples of a process approach to ecology was Elton's (1927) work on food chain dynamics. The concept of energy flow in ecosystems

was refined further by Lindeman (1942), who also arranged the biotic components of ecological systems into trophic levels. The study of lotic systems from a trophic level perspective eventually followed (e.g. Odum 1957, Warren et al. 1964, McIntire 1983), and resulted in the designations of autotrophic and heterotrophic stream systems, and autochthonous and allochthonous sources of energy in streams. The autotrophy/heterotrophy and autochthonous/allochthonous dichotomies are both compatible with the process point of view, and as a consequence, measurements of primary production and community respiration, size classification of allochthonous organic matter, and gravimetric and colorometric measurements of plant material have become common procedures in the study of benthic communities in lotic ecosystems. Indeed, most recent paradigms in stream ecology have been based on a process approach (e.g. river continuum concept, Vannote et al. 1980; nutrient spiralling, Elwood et al. 1983; serial discontinuity, Ward and Stanford 1983; and riparian control, Cummins et al. 1983), indicating how pervasive (and useful) the process orientation has become in this field.

Organismal and process approaches ask questions at different levels of resolution, and as a consequence, provide information about different scales of organization. Research that integrates both approaches may provide new and useful information on lotic ecosystem structure and function. Although the stream model of McIntire and Colby (1978) examined ecosystem dynamics from a process perspective, its conceptual framework theoretically allows

for the consideration of both structural and functional attributes, including both quantitative (i.e. biomass) and qualitative (i.e. taxonomic composition and physiological status) components of the state variables associated with each process (McIntire 1983). This integrated conceptual framework has been adopted in this dissertation, where a series of experiments were conducted that allowed the integration of the quantitative and qualitative aspects of primary producers. In this case, the herbivory subsystem from McIntire and Colby's stream model (1983) was the target system under investigation. This system decomposes into the grazing and primary production subsystems. Grazing includes processes associated with the flow of energy from living aquatic plants to macroconsumers (McIntire and Colby 1978), while primary production represents the production dynamics of autotrophic organisms (McIntire 1973).

The primary objective of the research reported in this dissertation was to examine the effects of current velocity, irradiance, and grazing on quantitative (biomass) and qualitative (taxonomic, physiognomic, and chemical structure) aspects of the primary production subsystem of lotic ecosystems. The integration of these results into a more detailed model of McIntire and Colby's periphyton subsystem (1978) was a secondary objective. The research approach adopted for this dissertation was experimental in nature, involving the use of laboratory streams and ceramic tiles as a standard substrate for colonization. The dissertation has been

divided into ten chapters. The first chapter is the introduction. The following six chapters detail the experimental research conducted. Altogether, four separate experiments were carried out: (1) effects of current velocity and irradiance on algal community structure (Chapter 2); (2) effects of irradiance alone on algal taxonomic and physiognomic structure (Chapter 3) and chemical composition (Chapter 4); (3) effects of grazing by different densities of a snail and a caddisfly on algal taxonomic and physiognomic structure (Chapter 5) and chemical composition (Chapter 6); and (4) effects of irradiance and grazing on algal community structure (Chapter 7). A synthesis section attempts to integrate the experimental results from Chapters 2-7 (Chapter 8), and that is followed by the bibliography (Chapter 9) and appendices (Chapter 10).

II. EFFECTS OF CURRENT VELOCITY AND LIGHT ENERGY ON THE STRUCTURE OF ALGAL ASSEMBLAGES IN LABORATORY STREAMS

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ABSTRACT

Effects of current velocity and light energy on the taxonomic and physiognomic characteristics of algal assemblages were investigated in laboratory streams. The initial rate of colonization was related to current velocity, while the effects of light energy accounted for differences in species composition by the end of the experiment. Although the laboratory systems had many species in common during the early stages of colonization, the experimental treatments generated differences in rates of community development. *Synedra* spp. were the early colonizers of the substrate, followed by an understory of *Achnanthes* spp. After day 16, *Stigeoclonium tenue* developed in the streams exposed to the higher photon flux density, but was rare in the shaded streams. The applicability of traditional successional theory to developmental patterns in lotic algal assemblages is discussed.

INTRODUCTION

Components of community structure in lotic periphyton assemblages include taxonomic composition, biochemical composition, and growth form (physiognomy). Many studies of such assemblages have emphasized production dynamics by analyzing changes in algal biomass and rates of primary production (McIntire and Phinney 1965, Power and Matthews 1983, Lamberti and Resh 1983, McAuliffe 1984a, Jones et al. 1984). However, reports of selective consumption of certain algal taxa by herbivores (Moore 1975a, 1977, Gray and Ward 1979, Sumner and McIntire 1982) and the modification of algal communities by grazers (Hart 1985) indicate that knowledge of taxonomic composition can enhance understanding of mechanisms associated with plant-animal interactions. Moreover, the morphology of feeding structures in aquatic invertebrates often delimits the size, shape, and location of food that can be ingested (Cummins and Klug 1979). Consequently, food availability is closely related to the micro-physiognomy (e.g. adnate diatoms, stalked diatoms, or filamentous algae) of the periphytic food resource (Gregory 1983).

This study investigated the effects of current velocity and light energy on the successional development of lotic algal assemblages in relation to the taxonomic and physiognomic components of community structure. The research approach was experimental, involving the use of laboratory streams and ceramic tiles as a standard substrate for colonization. Species

composition of the experimental algal assemblages was monitored during community development, and corresponding structural characteristics were examined with scanning electron microscopy (SEM).

MATERIALS AND METHODS

The Laboratory Streams

The laboratory streams were made of fiberglass and were similar in design to the experimental systems described by McIntire et al. (1964). Each stream was 3 m in length, 0.6 m wide, and 20 cm deep, and consisted of two parallel channels with openings in a center partition at each end. The streams were supplied by well water which was circulated by rotating paddle wheels connected to a variable speed motor. Water was exchanged in each stream at a rate of 1.5 $L \cdot min^{-1}$; water temperature remained constant at 13°C ± 1 in each stream throughout the experimental period. Chemical analysis of the well water indicated that nutrient concentrations were relatively high (orthophosphate: 0.19 $mg \cdot L^{-1}$; silica: 19.2 $mg \cdot L^{-1}$; NH_3-N: 0.01 $mg \cdot L^{-1}$; NO_3-N: 6.25 $mg \cdot L^{-1}$). Light energy was provided by 16 1000-watt Metalarc lamps (Sylvania Corp.), each mounted in a symmetrical Maxigro reflector. A system of timers controlled photoperiod to produce alternating light-dark periods of 12 h each. The bottom of each stream was lined with unglazed ceramic tiles, 7.5 cm x 7.5 cm, which provided a surface for colonization and units for periodic sampling. Smaller tiles (1.2 cm x 1.2 cm), which were spaced among the larger tiles, served directly as SEM sampling units for the investigation of the physiognomic characteristics of periphyton assemblages.

Experimental Design

The experiment was initiated on February 12, 1985, and

continued for 32 days. Approximately 4 months before the experiment, rocks with associated periphyton were transferred from four lotic ecosystems in Benton County, Oregon (Rock Creek, Oak Creek, Berry Creek, and the Willamette River) to an outdoor channel at the laboratory. At the beginning of the experiment, periphyton was scraped from an arbitrarily selected subset of these rocks and homogenized for 30 s in a 3.8-L Waring blender. This treatment produced a uniform algal suspension with minimal disruption of the cell walls. Subsequently, each laboratory stream was inoculated with a 1-L subsample of this suspension.

The experimental design involved 12 laboratory streams subjected to four combinations of light energy and current velocity, with three replications of each treatment. Biomass accumulation was monitored in all 12 streams, while taxonomic and physiognomic structure of the algal assemblages were studied in eight streams (two replications of each treatment). The treatment photon flux densities and velocities were: (1) 450 $\mu E \cdot m^{-2} \cdot s^{-1}$, 15 $cm \cdot s^{-1}$ (treatment 450:15); (2) 450 $\mu E \cdot m^{-2} \cdot s^{-1}$, 5 $cm \cdot s^{-1}$ (treatment 450:5); (3) 50 $\mu E \cdot m^{-2} \cdot s^{-1}$, 15 $cm \cdot s^{-1}$ (treatment 50:15); and (4) 50 $\mu E \cdot m^{-2} \cdot s^{-1}$, 5 $cm \cdot s^{-1}$ (treatment 50:5). The high photon flux density was obtained by adjusting the height of the lamp fixtures, while the low photon flux density was achieved by placing green Chicopee screen (73%) over the streams. Current velocity was controlled by setting the speed of the paddle wheels to conform to the two treatment velocities. Photon flux densities were chosen to simulate irradiance levels that occur naturally in the streams from

which the algae were collected. The current velocities employed were similar to those found during low flow conditions in natural streams.

Sampling

For estimates of biomass accumulation, a random sample of three 7.5 cm x 7.5 cm tiles was obtained from each stream on days 8, 16, 24, and 32. Biomass, expressed as ash-free dry weight, was determined by the method described by McIntire and Phinney (1965).

For the quantitative analysis of species composition, two 7.5 cm x 7.5 cm tiles were selected at random from each of eight streams, i.e. two for each treatment, on days 2, 4, 8, 16 and 32. Periphyton assemblages were removed from the tiles with a razor blade and fixed immediately in Lugol's solution. The organisms were allowed to settle in 50 mL chambers, and 500 algal units were counted at 400X magnification with a Nikon MS inverted microscope (Utermöhl 1958). During this procedure, diatoms were lumped in one category, and all other taxa were identified to species. An algal unit was an individual cell or valve, if the taxon was a unicellular form, or an individual filament or colony in the case of multicellular taxa. For the filamentous and colonial taxa, the total number of cells in each algal unit was also estimated for the calculation of biovolumes. After the counts were completed, each sample was pipetted into a flask and boiled in concentrated HNO_3. The clean diatom frustules that resulted from this treatment were mounted on microscope slides in Cumarone resin (Holmes et al.

1981), and 300 valves were identified and counted at 1,250X magnification with a Zeiss RA microscope. The proportions of the diatom taxa in this sample were used to estimate the abundances of these taxa in the corresponding count of 500 algal units. Specifically, $N(500)_j = T(500) \times P(300)_j$, where $N(500)_j$ was the estimated number of units that belonged to the j-th diatom taxon in the count of 500, T(500) was the total number of diatom units in the count of 500, and $P(300)_j$ was the proportion of units in the count of 300 that belonged to the j-th taxon. Biovolumes for each taxon were calculated by multiplying an estimated mean volume per algal unit by the number of algal units in the count of 500. Mean volumes were based on standard geometric formulae and, whenever possible, measurements of at least 10 cells for each taxon.

Sampling for the examination of physiognomic properties involved the removal of two of the smaller (1.2 cm x 1.2 cm) tiles from each stream on days 1, 2, 4, 8, 16 and 32. These tiles, which served as samples for SEM, were freezed-dried immediately in liquid N_2. After sublimation, the samples were coated with Au-Pd by vacuum evaporation and examined with an Amray 1000-A SEM at 20 kV.

Data Analysis

Treatment effects on biomass accumulation were examined with a 2-way analysis of variance (Snedecor and Cochran 1967). Species compositions of the algal assemblages were compared with the SIMI measure of similarity (McIntire and Moore 1977). This measure, which can range from 0 to 1, gives greatest weight to dominant taxa. A value of 0 indicates that a given pair of assemblages have

no taxa in common, while a value of 1 indicates that the two assemblages have identical species compositions and proportional abundances. In this study, SIMI values were based on biovolumes. Statistical analyses were performed with a CYBER 170/720 computer and an IBM PC using the program AIDN and the MGLH module of SYSTAT (SYSTAT, Inc. 1984).

RESULTS

Biomass and Species Composition

Periphyton biomass increased in the 12 streams between the start of the experiment and day 24 (Fig. II.1). At day 8, there were small treatment-associated differences in mean biomass, with the highest values occurring in streams subjected to treatment 450:5. Moreover, an analysis of variance indicated that on day 8, the interaction between light level and current velocity was statistically significant ($P < 0.03$). On days 16 and 32, mean biomasses in streams exposed to 450 $\mu E \cdot m^{-2} \cdot s^{-1}$ were significantly higher ($P < 0.01$) than those in streams receiving 50 $\mu E \cdot m^{-2} \cdot s^{-1}$; the effects of current velocity and the interaction between current velocity and light level were not significant for samples obtained on those days ($P > 0.13$). On day 24, the mean biomass in streams subjected to treatment 450:15 was from 3 to 10X higher than mean biomasses measured in streams with the other treatments. This pattern was associated with a significant interaction between light level and current velocity ($P < 0.01$). The combination of relatively high biomass and high current velocity in streams with treatment 450:15 resulted in a biomass decrease between days 24 and 32, and corresponded to a period of high export.

Treatment effects on the taxonomic composition of the experimental algal assemblages are summarized in Table II.1. The estimated mean biomass of filamentous green algae was greater in the streams receiving photon flux densities at 450 $\mu E \cdot m^{-2} \cdot s^{-1}$ than

in the streams subjected to 50 $\mu E \cdot m^{-2} \cdot s^{-1}$. Moreover, the ratio of the pooled mean biomasses of filamentous chlorophytes in streams exposed to the two light levels (450/50) was 15.76. When the data were pooled by current velocity for these taxa, the corresponding ratio (15/5) was 0.97, indicating that filamentous green algae were equally abundant relative to velocities of 5 and 15 $cm \cdot s^{-1}$. The seven most common diatoms exhibited several different patterns of response to the experimental conditions: *Synedra ulna* and *Fragilaria vaucheriae* had relatively high mean biomasses at both the higher light level and higher current velocity; *S. rumpens* var. *familiaris* and *Nitzschia oregona* had greater mean biomasses at the higher light level and lower current velocity; the mean biomasses of *Nitzschia dissipata* had a negative relationship with light energy and current velocity; *Nitzschia linearis* had greater mean biomasses at the lower current velocity while *Achnanthes lanceolata* had lower mean biomasses at the lower current velocity.
Successional changes in the taxonomic structures of the experimental algal assemblages were examined by the calculation of the SIMI index for all data pooled by sampling date, i.e. data for all samples obtained on a particular date were combined and treated as one sample (Table II.2). SIMI values for the pooled data indicated that there was a gradual change in taxonomic composition between days 2 and 32, with the notable exception of the comparison between days 4 and 8 for which there was relatively little difference. Also, there was a relatively rapid change in the average composition during the initial stage of colonization

(between days 2 and 4). An interaction between current velocity and successional changes was evident by analyzing the data from the two current velocities separately while pooling by sampling date. At the lower velocity, there was a rapid change in the composition of the algal assemblages early in the experiment followed by a period of relatively little change (Table II.3). In contrast, successional changes at the higher velocity were more gradual (Table II.4).

Effects of light energy and current velocity on taxonomic composition were less evident than temporal changes during community development. The SIMI value was relatively high (0.896) for the comparison of all samples pooled into two groups representing 450 and 50 $\mu E \cdot m^{-2} \cdot s^{-1}$. When the samples were pooled into two groups on the basis of current velocity, they were even more similar (SIMI = 0.983).

Structural Characteristics

SEM analysis revealed treatment-related effects on the physiognomic characteristics of the experimental periphyton assemblages. Successional patterns on days 1, 4, 8, 16 and 32 are illustrated in Figs. II.2-21.

On day 1 (Figs. II.2-5), 24 h after inoculation, the algal accumulations consisted of diatoms, and occurred primarily in streams with the lower current velocity (Figs. II.2 and II.5). Although other studies have shown bacteria and fungi to be conspicuous constituents during the initial stage of colonization

(Geesey et al. 1978, Hoagland et al. 1982), the presence of these organisms was not obvious in the electron micrographs during early stages of community development. Tile surfaces were examined at a magnification of 10,000X in an attempt to detect bacteria and organic films. Comparisons between sample tiles and unused tile surfaces revealed some isolated bacterial mats, but there was no evidence of organic coatings or widespread bacterial colonization.

On day 4 (Figs. II.6-9), diatoms dominated the flora, again with most growth in streams with treatments 450:5 and 50:5 (Figs. II.6 and II.9). Moreover, the diatoms at this time were represented by several growth forms. Rosettes of *Synedra ulna*, chains of *Synedra rumpens* var. *familiaris*, and adnate unicells of *Achnanthes lanceolata* were present in streams with treatment 450:5 (Fig. II.6), while a stalked *Cymbella turgidula* and chains of *Fragilaria vaucheriae* were observed in samples from treatment 50:5 (Fig. II.9).

Algal growth was evident in all the experimental streams by day 8 (Figs. II.10-13), although the greatest accumulation of cells was observed on tiles from treatment 450:5 (Fig. II.10). The assemblage associated with treatment 450:5 was characterized by rosettes of *Synedra* and an understory of *Achnanthes lanceolata*. Tiles from treatment 50:5 had a relatively dense population of *Synedra ulna* and some other small adnate diatoms (Fig. II.13), while tiles from the faster current velocity (treatments 450:15 and 50:15) supported a similar, but sparser assemblage of diatoms (Figs. II.11 and II.12). Unlike treatment 450:5, assemblages on

tiles from the other treatments had not formed an understory layer of diatoms by day 8.

By day 16 (Figs. II.14-17), tiles from treatment 450:5 were covered by populations of Synedra and Fragilaria (Fig. II.14), and branches of the green alga Stigeoclonium tenue were evident among a diverse assemblage of diatoms on tiles from treatment 450:15 (Fig. II.15). In the streams receiving the lower photon flux density (treatments 50:15 and 50:5), a dense understory of Achnanthes lanceolata was present beneath a canopy of Synedra spp. (Figs. II.16 and II.17).

At the end of the experiment (day 32), Stigeoclonium tenue formed an extensive reticulum on tiles from the streams exposed to the higher photon flux density (Figs. II.18 and II.19). In contrast, algal assemblages from treatments 50:5 and 50:15 retained a dense understory of Achnanthes lanceolata and an upper layer of larger diatoms, primarily Synedra ulna, S. rumpens var. familiaris, and Melosira varians (Figs. II.20 and II.21).

To examine the vertical structure of a mature periphyton assemblage, a longitudinal section (i.e. perpendicular to the tile surface) was prepared by removing part of the biomass from a tile surface with a razor blade. In this case, the assemblage was obtained from treatment 450:15 on day 32 (Fig. II.22). Small, adnate diatoms were still visible on the scraped section of the tile, while a loosely aggregated wall of mostly Synedra cells was evident at the face of the sectioned material. The height of the

exposed layer was equivalent to the thickness of approximately 85 cells of *Synedra ulna*, the dominant species. Therefore, Figure II.22 indicated that mature, ungrazed periphyton assemblages in lotic systems can consist of a thick, relatively unstructured pile of cells.

DISCUSSION

Results of earlier SEM studies have suggested that periphyton assemblages follow a predictable series of seral stages after colonization, resulting in a successional sequence that is analogous to patterns in terrestrial ecosystems (Hudon and Bourget 1981, Hoagland et al. 1982, Korte and Blinn 1983). More specifically, the hypothesis corresponding to these studies suggests a sequence of stages consisting of (1) an organic matrix and bacteria; (2) relatively small, adnate diatoms with a low vertical profile; (3) short vertically-oriented diatoms (often stalked); and (4) long, filamentous algae. However, it is not yet clear how often this expected sere occurs in natural streams and to what degree the predicted trajectory is vulnerable to modification by various environmental and stochastic processes. For example, deviations from the hypothetical sequence were observed by Hamilton and Duthie (1984) who failed to find either an organic film or bacterial colonization on granite substrates introduced into a Quebec stream. They attributed this departure to the high surface tension of the granitic material. In the present study, SEM indicated that bacterial colonies were sparse during early colonization (stage 1), observations which may have been related to the paucity of a suitable inoculum in the water supply. Nonetheless, because bacterial presence is a well documented phenomenon in past studies, further analyses seem warranted (e.g. epiflourescence microscopy) to assess the quantity and role of

bacteria in our laboratory system.

The early colonization of large rosette- and chain-forming species of *Synedra* followed by the development of an understory of *Achnanthes* spp. on the ceramic tiles represented a different physiognomic sequence than the pattern observed by Hoagland et al. (1982) in a lentic habitat. In the latter study, vertical community structure changed from assemblages of relatively small, low profile taxa to a stratified organization consisting of a well-defined overstory and understory. In the laboratory streams, early colonization of *Synedra* spp. may have been related to (1) the high relative abundance of the genus in the inoculum (species pool); (2) differential sinking rates within the species pool favoring early settlement of the genus; and (3) an elongate shape with a relatively large surface area available for attachment. The longitudinal section of a mature periphyton assemblage (Fig. II.22) revealed that, at least in the laboratory systems, the analogy between vertical stratification in lotic periphyton and higher plant communities is equivocal.

During early stages of colonization, treatment effects on periphyton assemblages in the laboratory streams were less obvious than temporal changes. However, examination of the SEM tiles and SIMI values indicated that the treatments did have some impact. In particular, tiles subjected to the higher current velocity had slower initial rates of community development. McIntire (1966) found that periphyton biomass accumulated more rapidly on glass microscope slides at a current velocity of 9 $cm \cdot s^{-1}$ than at 38

cm$\cdot$s^{-1} during the first 15 days of colonization, after which time, the biomass was higher on slides exposed to the higher velocity. Stevenson (1984) found a larger biomass of diatoms on substrates in protected sites than on those that were exposed to a faster current in the main channel. These data and the results of the present experiment indicate that a fast current inhibits initial colonization, but once established, the growth of a periphyton assemblage may be enhanced by rapid exchanges of nutrients and dissolved gasses between algal cells and the moving aquatic medium (Whitford and Schumacher 1964).

The relatively rapid change in community composition between days 2 and 4 in the streams with low current velocity (Table II.3) may be a consequence of autogenic processes (Stevenson 1983). Once cells attach to the tile surface, eddy formation can occur downstream of the attached particles, which may enhance community production (Stevenson 1983). In addition, the attached cells may exude mucilage, which may have a major influence on the developmental pattern in periphyton assemblages (Stevenson 1983; Roemer et al. 1984). In this study, relatively little mucilage was associated with the early colonizers of the tiles, possibly because the dominant taxa at this stage were araphid forms. However, after the assemblages became more mature, mucilage apparently contributed to the establishment of a stable reticulum and facilitated particle attachment.

The effects of light energy accounted for notable differences

in species composition by the end of the experiment. In particular, the relatively high abundances of filamentous green algae in streams exposed to high photon flux densities were consistent with the findings of other studies (e.g. McIntire 1968, Lyford and Gregory 1975, Shortreed and Stockner 1983). Tolerance of low photon flux densities by prostrate diatoms may have adaptive significance because of their vulnerability to shading by other cells and detritus (Hudon and Bourget 1983). The abundance of the prostrate diatoms Nitzschia dissipata and Achnanthes lanceolata on tiles exposed to the low light treatment tended to support this contention. However, other adnate diatoms, e.g. Nitzschia oregona (this study) and several species of Nitzschia (Antoine and Benson-Evans 1983), apparently were indifferent to treatment effects of light energy, suggesting that other factors were important in influencing community structure.

Horn (1976) introduced three alternative theoretical structures to account for successional changes in natural communities, concepts that are closely related to the facilitation, tolerance and inhibition models of succession discussed by Connell and Slatyer (1977). The successional sequences observed by Hudon and Bourget (1981), Hoagland et al. (1982), and Korte and Blinn (1983) were characterized by the development of organic and bacterial films before the establishment of benthic algal assemblages. However, the results of these studies do not necessarily correspond to the facilitation model, as it is uncertain how bacterial and organic films are related to algal

colonization. Moreover, our results and observations by Hamilton and Duthie (1984) indicate that algal biomass can accumulate rapidly on surfaces without a well-developed bacterial flora. Evidence for the tolerance model, i.e. the competitive hierarchy of Horn (1976), is lacking in natural streams, although this may be because lotic periphyton assemblages are being perturbed at such frequent intervals that competitive interactions cannot be demonstrated. In laboratory streams, where disturbance can be controlled and mature assemblages can form, there is a tendency for filamentous forms to dominate when light energy is relatively high (McIntire 1968, this study), suggesting a competitive advantage by these forms. The inhibition model or chronic, patchy disturbance pattern (Horn 1976) is consistent with the spatial heterogeneity and patchy distribution of algal assemblages sometimes observed in natural streams, where frequent disturbances generate open areas for recolonization.

Unlike the clean ceramic tiles used in the present experiment, substrates in natural streams, even after a period of scouring, are usually never devoid of living organisms. Studies by Wehr (1981) and Steinman (1983) have indicated that propagules of stream algae exist on substrates throughout the year, albeit in low concentrations at times. The reproductive success of these propagules, which is dependent on changing physical, chemical, and biological factors, will strongly influence successional patterns. When the influences of environmental variables exhibit spatial or

temporal irregularities, such heterogeneity promotes a variety of algal assemblages within relatively small localized areas of habitat. An interesting scientific question, which will be addressed in future studies, is whether spatial heterogeneity in lotic periphyton assemblages results from a mosaic of different seral stages of the same successional trajectory or instead, the patches themselves are on different trajectories. In this experiment, species compositions were similar in all the streams during early stages of colonization. However, the subsequent appearance of filamentous green algae in streams exposed to the higher photon flux density makes it questionable whether all the experimental systems were on the same successional trajectory by the conclusion of the experiment.

In summary, the taxonomic structure of lotic periphyton assemblages is apparently determined by (1) the composition of the species pool; (2) dispersal and colonization rates of the taxa in the pool; (3) competitive interactions among the community constituents; (4) herbivory; (5) the chemical and physical environment, including substrate type; and (6) spatial and temporal patterns of disturbance. In such assemblages, generation times of the dominant organisms are short relative to cyclic seasonal changes in the system, and the biological products of mortality are usually exported from the site of generation (McIntire 1966). As a consequence, successional trajectories of lotic periphyton are rarely able to evolve to a "climax" stage without interruption.

ACKNOWLEDGMENTS

We are very grateful to Linda Ashkenas, Randy Wildman, Karan Fairchild, and Al Soeldner for their excellent technical assistance, and to two anonymous reviewers whose comments helped improve this manuscript. Stan Gregory and Gary Lamberti kindly provided the periphyton biomass data, and collaborated with the authors on the design of the experiment. This study was supported by research grant No. BSR-8318386 from the National Science Foundation and by a Sigma Xi Grant-In-Aid.

Table II.1 Abundance of selected algal taxa in eight laboratory streams (4 treatments and 2 replications) expressed as the mean biomass ($g.m^{-2}$) of days 8, 16, and 32. Biomass of each taxon on each sampling day was estimated by multiplying the corresponding proportion of the community biovolume by the total community biomass. The ratios are the quotients of the pooled mean biomasses in the streams subjected to the two light levels (450/50) and the two current velocities (15/5). Treatment designators are defined in the text.

Taxon	Treatment									
	450:5		450:15		50:5		50:15		Ratio 450/50	Ratio 15/5
	1	2	1	2	1	2	1	2		
Filamentous Chlorophyta[a]	4.98	6.34	4.42	5.53	0.11	0.06	0.05	1.13	15.76	0.97
Bacillariophyta:										
Synedra ulna (Nitzsch) Ehr.	3.04	3.36	7.37	4.22	0.52	1.35	1.17	0.56	5.00	1.61
S. rumpens var. *familiaris* (Kütz.) Hust.	1.48	2.18	1.62	0.52	0.78	0.49	0.46	0.38	2.75	0.60
Fragilaria vaucheriae (Kütz.) Peters.	0.47	0.41	0.89	0.45	0.25	0.18	0.10	0.22	2.96	1.27
Nitzschia oregona Sov.	0.19	0.52	0.23	0.14	0.12	0.14	0.06	0.09	2.63	0.54
N. dissipata (Kütz.) Grun.	0.03	0.05	0.03	<.01	0.11	0.04	0.02	0.04	0.57	0.39
N. linearis W. Smith	0.50	0.74	0.54	0.56	0.76	0.57	0.64	0.13	1.11	0.73
Achnanthes lanceolata (Bréb.) Grun.	0.55	0.61	1.95	2.39	2.15	1.18	1.35	1.21	0.93	1.54

[a] includes *Stigeoclonium tenue* (C.A. Ag.) Kütz., *Ulothrix zonata* (Weber & Mohr) Kütz., *U. tenerrima* Kütz., and *Klebsormidium fluitans* Kütz.

Table II.2 Matrix of similarity values (SIMI) for 40 experimental algal samples pooled by sampling date.

Day	4	8	16	32
2	0.674	0.732	0.490	0.352
4		0.939	0.871	0.589
8			0.855	0.548
16				0.800

Table II.3 Matrix of similarity values (SIMI) for 20 experimental algal samples pooled by sampling date. Samples were subjected to a current velocity of 5 $cm \cdot s^{-1}$.

Day	4	8	16	32
2	0.558	0.383	0.359	0.285
4		0.944	0.889	0.557
8			0.895	0.522
16				0.793

Table II.4 Matrix of similarity values (SIMI) for 20 experimental algal samples pooled by sampling date. Samples were subjected to a current velocity of 15 $cm \cdot s^{-1}$.

Day	4	8	16	32
2	0.760	0.711	0.553	0.398
4		0.785	0.818	0.571
8			0.684	0.475
16				0.687

Figure II.1 Biomass accumulation of algal assemblages (expressed as ash-free dry weight) in laboratory streams subjected to treatments 450:5, 450:15, 50:5, and 50:15 during 32-day experimental period.

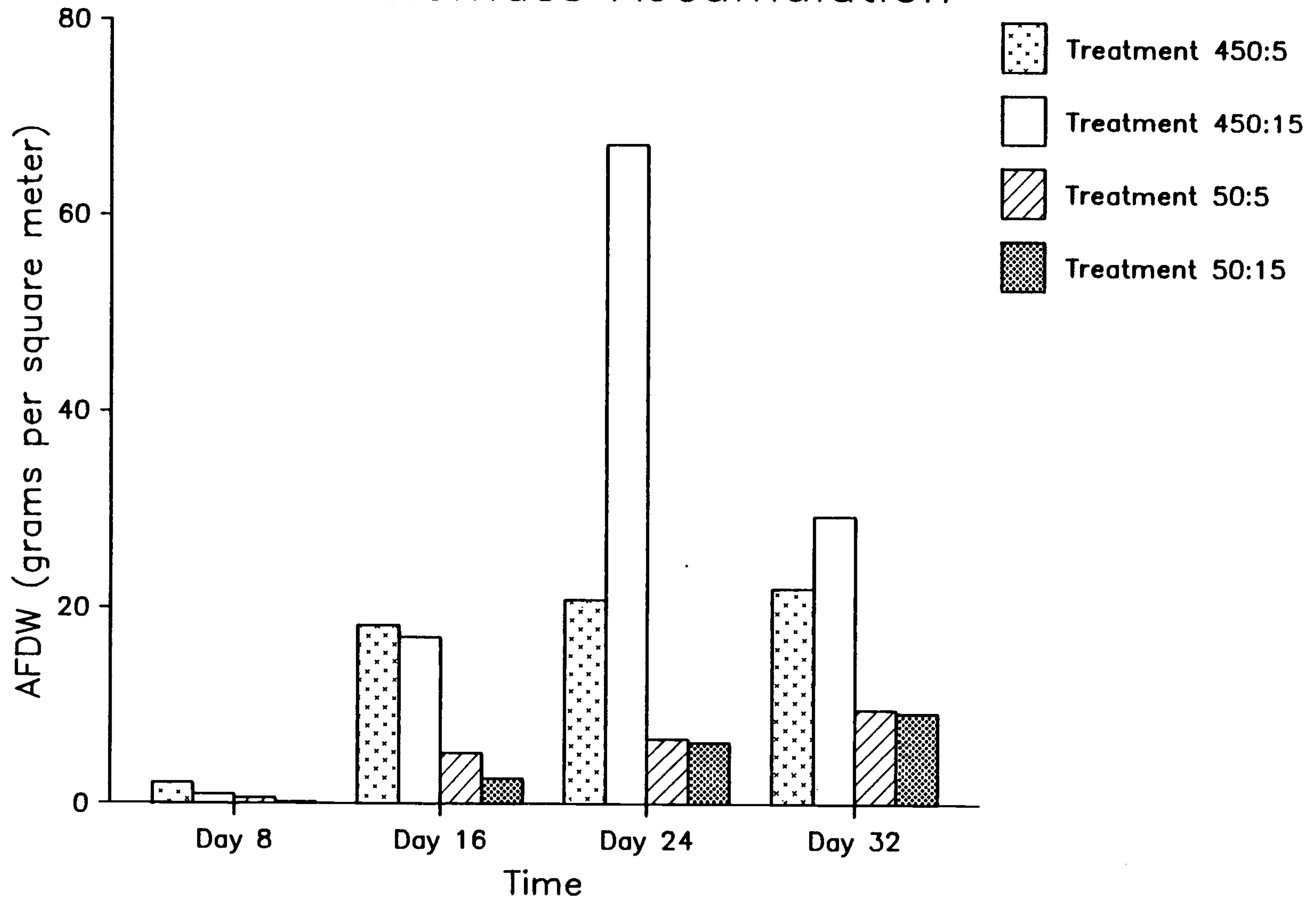


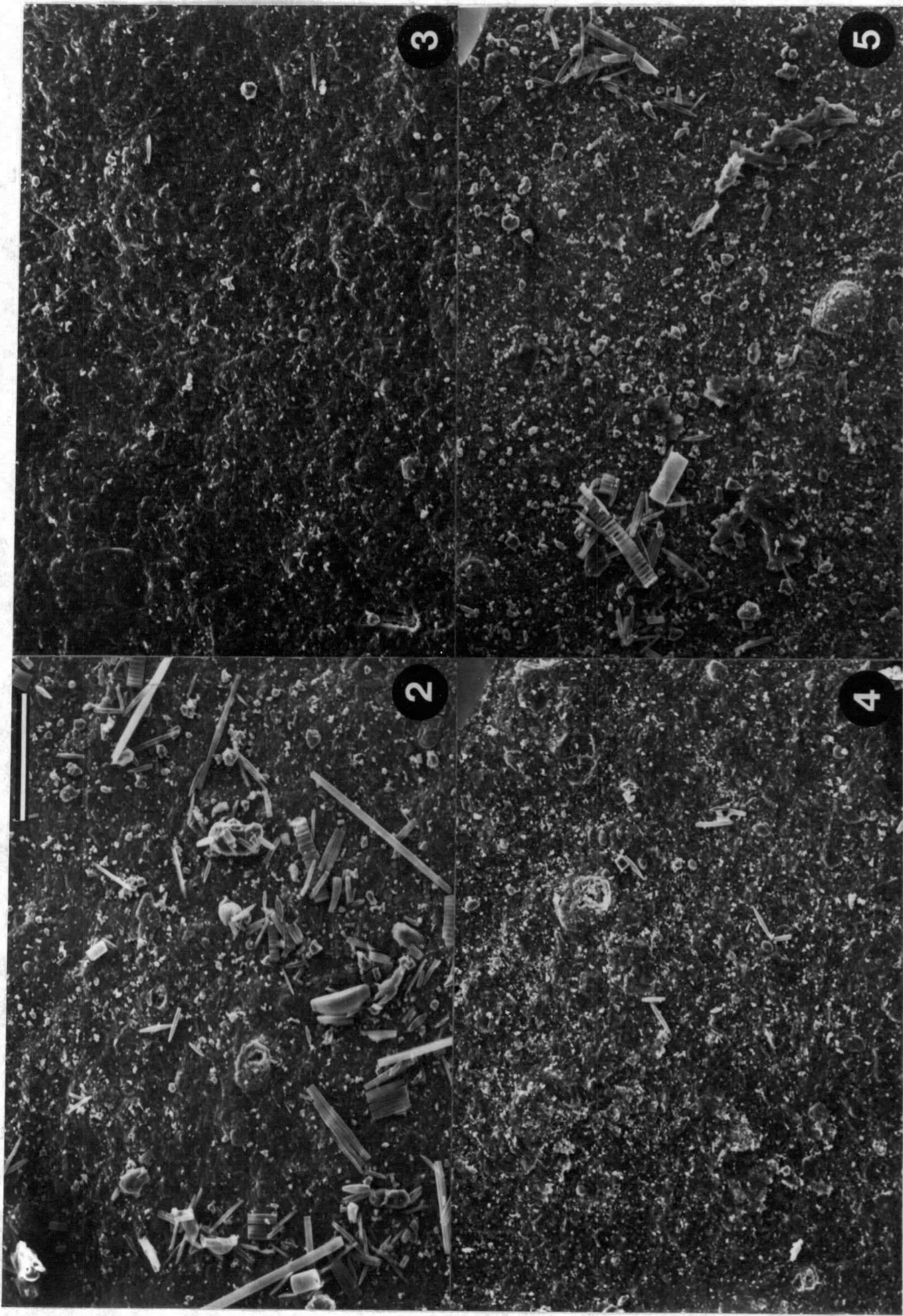
Figure II.1

Figure II.2 SEM of algal assemblage at day 1. Treatment 450:5. Limited diatom flora consisting of small chains and adnate unicells. Scale = 100 µm.

Figure II.3 SEM of mostly barren tile surface at day 1. Treatment 450:15. Scale = 100 µm.

Figure II.4 SEM of algal assemblage at day 1. Sparse assemblage of adnate diatoms. Treatment 50:15. Scale = 100 µm.

Figure II.5 SEM of algal assemblage at day 1. Diatom assemblage similar to that in Figure 2. Treatment 50:5. Scale = 100 µm.



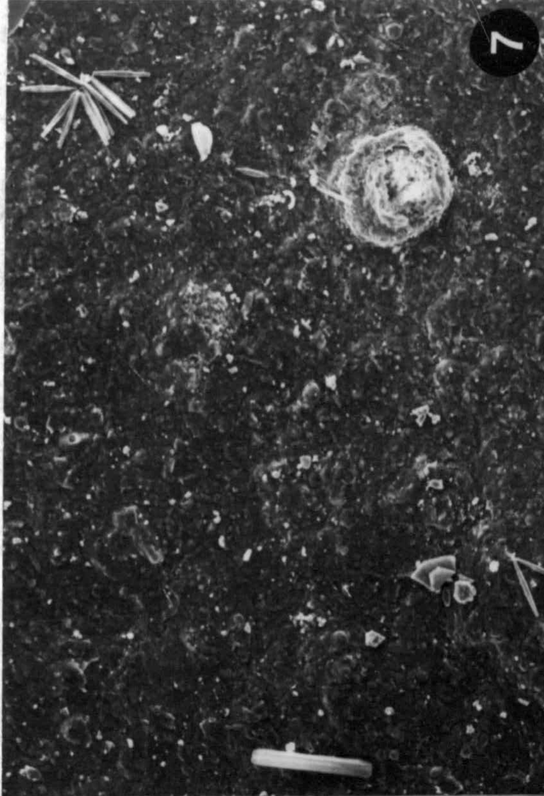
Figures II.2-5

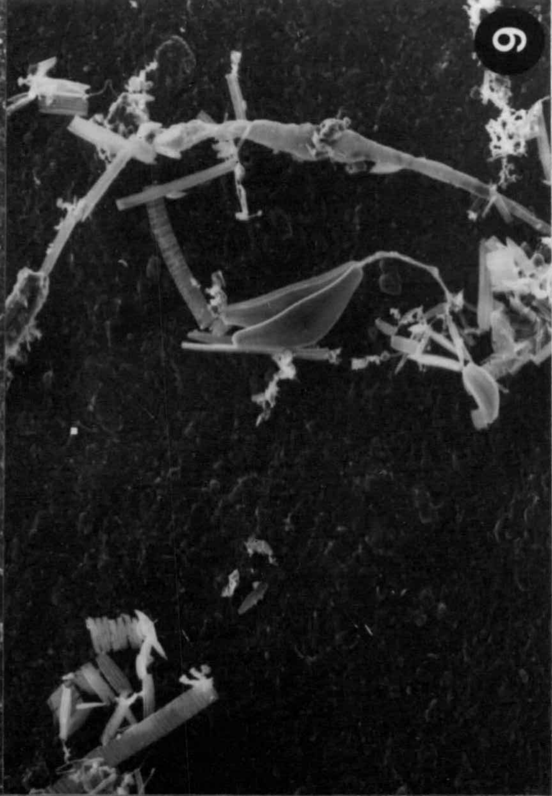
Figure II.6 SEM of algal assemblage at day 4. Note rosettes of _Synedra ulna_, chains of _S. rumpens_ v. _familiaris_, and unicells of _Achnanthes lanceolata_. Treatment 450:5. Scale = 100 µm.

Figure II.7 SEM of sparse diatom assemblage at day 4. Treatment 450:15. Scale = 100 µm.

Figure II.8 SEM of algal assemblage at day 4. Note similarity to assemblage in Figure II.7. Scale = 100 µm.

Figure II.9 SEM of algal assemblage at day 4. Note chains of _Fragilaria vaucheriae_ and stalked _Cymbella turgidula_. Treatment 50:5. Scale = 100 µm.





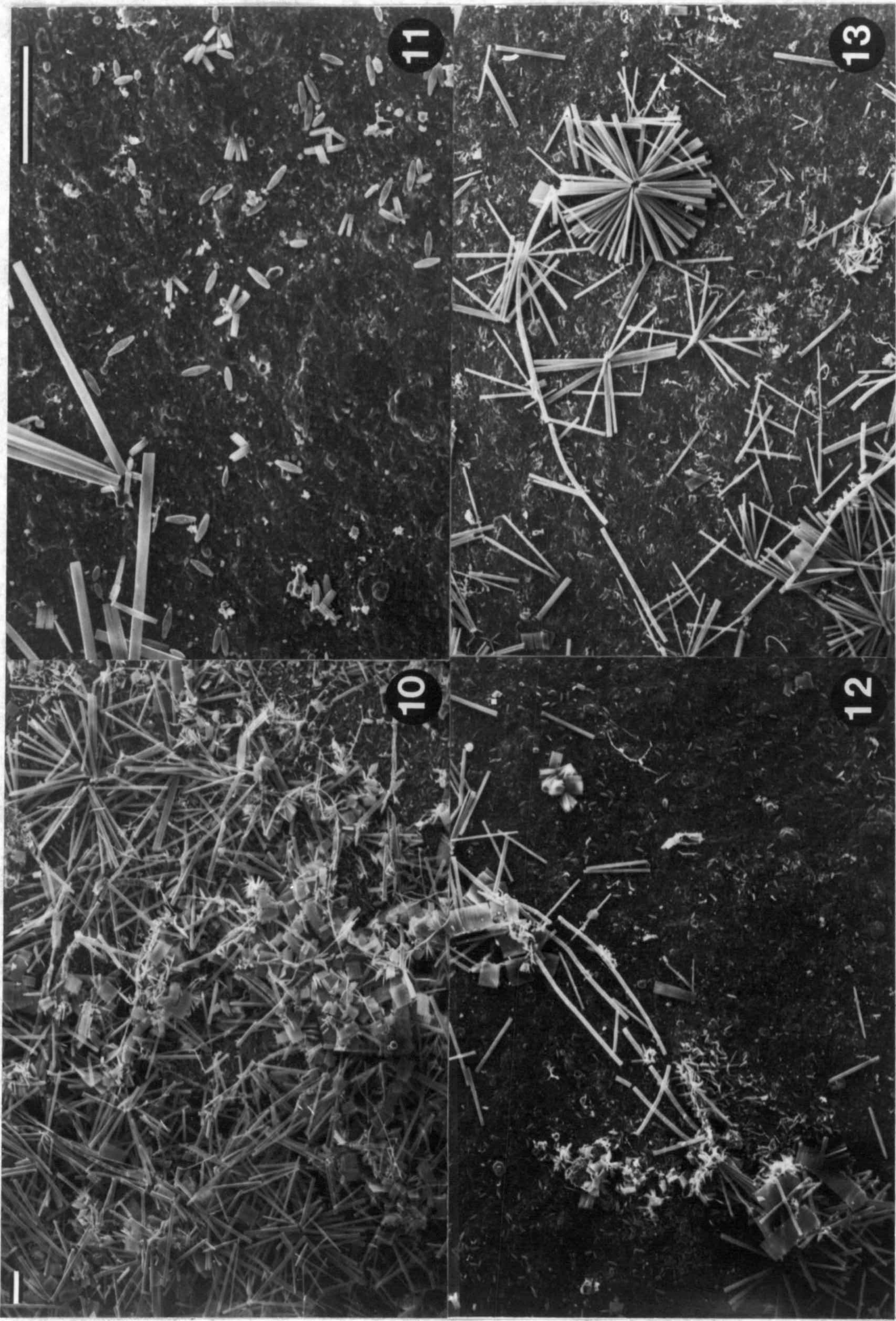
Figures II.6-9

Figure II.10 SEM of algal assemblage at day 8. Note understory of *Achnanthes lanceolata* in lower right corner and overstory of *Synedra* and *Fragilaria* spp. Treatment 450:5. Scale = 100 μm.

Figure II.11 SEM of algal assemblage at day 8. Scattered unicells of *A. lanceolata* and colonies of *S. ulna*. Treatment 450:15. Scale = 100 μm.

Figure II.12 SEM of algal assemblage at day 8. Clusters of *Fragilaria* spp., chains of *Synedra* spp. and *Melosira varians* and various unicells present in limited amounts. Treatment 50:15. Scale bar in Figure II.10 applies here and = 100 μm.

Figure II.13 SEM of algal assemblage at day 8. Rosettes of *S. ulna* evident with understory of various species. Treatment 50:5. Scale bar in Figure II.11 applies here and = 100 μm.



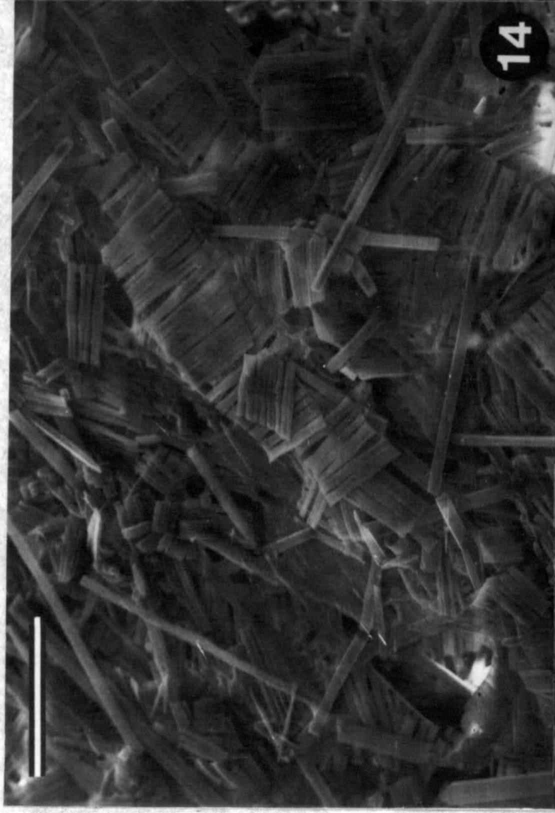
Figures II.10-13

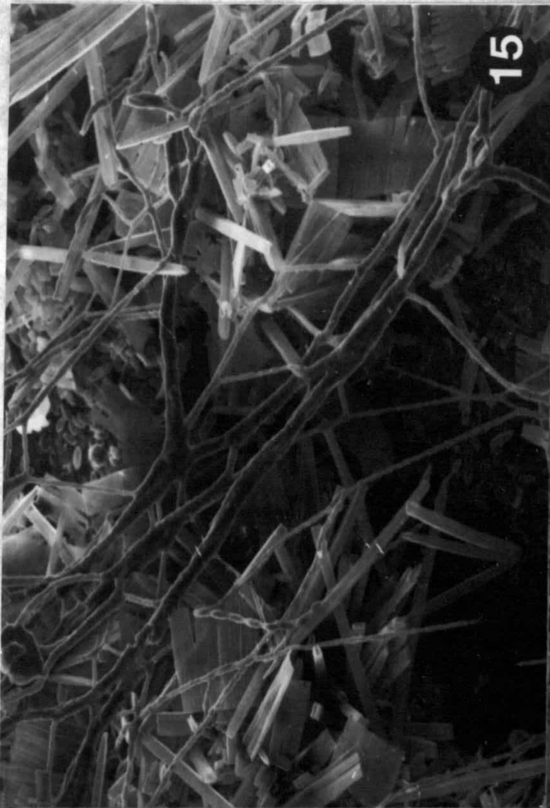
Figure II.14 SEM of algal assemblage at day 16. Chains of *Synedra* and *Fragilaria* spp. form dense cover. Treatment 450:5. Scale bar = 100 µm.

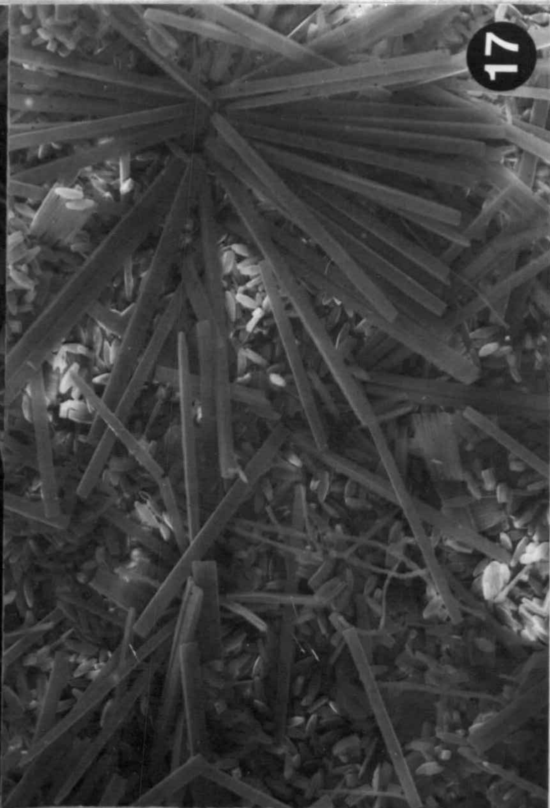
Figure II.15 SEM of algal assemblage at day 16. *Stigeoclonium tenue* filaments associated with an assemblage of diatoms. Note understory of *A. lanceolata* at bottom of micrograph. Treatment 450:15. Scale = 100 µm.

Figure II.16 SEM of algal assemblage at day 16. Dense understory of *A. lanceolata* exists beneath the rosettes of *Synedra* spp. Treatment 50:15. Scale = 100 µm.

Figure II.17 SEM of algal assemblage at day 16. Note similarity to assemblage in Figure II.16. Scale = 100 µm.







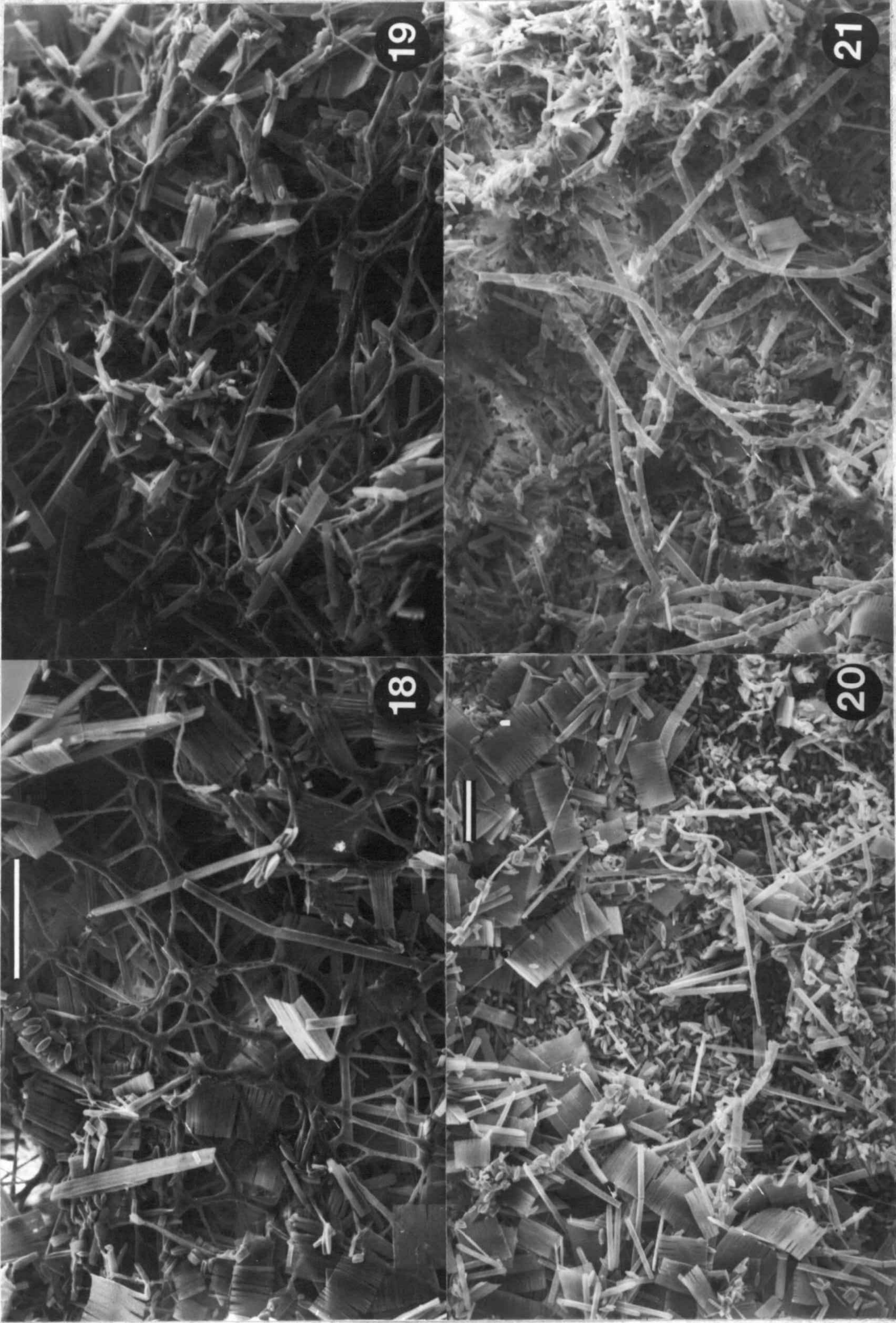
Figures II.14-17

Figure II.18 SEM of algal assemblage at day 32. Stigeoclonium tenue filaments are evident. Treatment 450:5. Scale = 100 µm.

Figure II.19. SEM of algal assemblage at day 32. Note similarity to assemblage in Figure II.18. Treatment 450:15. Scale bar in Figure II.18 applies here and = 100 µm.

Figure II.20 SEM of algal assemblage at day 32. Chains of Synedra and Fragilaria spp. overlay dense understory of A. lanceolata. Treatment 50:15. Scale bar = 100 µm.

Figure II.21 SEM of algal assemblage at day 32. Dense accumulation of A. lanceolata beneath chains of Melosira varians. Treatment 50:5. Scale = 100 µm.



Figures II.18-21

Figure II.22 SEM of longitudinal section of periphyton assemblage at day 32 from treatment 450:15. Note lack of well-defined vertical structure. Dominant taxon is *Synedra ulna*. Scale = 100 μm.

Figure II.22

III. EFFECTS OF IRRADIANCE ON THE COMMUNITY STRUCTURE AND BIOMASS OF ALGAL ASSEMBLAGES IN LABORATORY STREAMS

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ABSTRACT

Studies in natural streams have implicated irradiance as a factor which has a strong influence on the dynamics of algal communities. In this study, laboratory streams were used in a replicated, experimental design to investigate whether differences in algal biomass, taxonomic structure, and physiognomy result from exposure to different irradiances. Effects of four photon flux densities (15, 50, 150, and 400 $\mu E \cdot m^{-2} \cdot s^{-1}$) on locally collected benthic stream algae were monitored over a 48-day period. Biomass increased in all streams during the experiment, but the streams exposed to the highest irradiance had 25x more biomass at the end of the experiment than the channels exposed to the lowest irradiance. Although diatoms were the dominant algal class in all streams, the relative abundance of chlorophytes was much greater in streams exposed to 150 and 400 $\mu E \cdot m^{-2} \cdot s^{-1}$ than in channels treated with 15 and 50 $\mu E \cdot m^{-2} \cdot s^{-1}$. Detrended correspondence analysis indicated that the successional trajectories of assemblages exposed to low irradiances were quite distinct from those of assemblages treated with high irradiances. Observations of assemblage physiognomy by scanning electron microscopy revealed that at low irradiances, a densely packed understory of adnate diatoms, with a few overstory diatoms, covered the tile surface. At high irradiances, tiles were overlaid with thick algal mats, composed of filamentous and coenobic chlorophytes and diatoms of various growth forms (rosette, chain-forming, and solitary). The experimental

results suggested that differences in biomass and community structure among the laboratory assemblages were a direct result of light energy, and that irradiance is a major factor influencing algal dynamics in lotic ecosystems.

INTRODUCTION

Irradiance is the primary source of energy for algal assemblages in lotic ecosystems. Hence, streams that have received an increase in light energy often exhibit a corresponding increase in primary production (McIntire 1966; Gregory 1980; Triska et al. 1983; Duncan and Brusven 1985). In addition, studies of streams that have had their drainage basins logged have concluded that increases in algal biomass are attributable to high irradiance levels (Lyford and Gregory 1975, Shortreed and Stockner 1983, Duncan and Brusven 1985). Light has also been proposed as a major determinant of algal community structure in streams (McIntire 1968; Whitton 1972; Antoine and Benson-Evans 1983; Sheath and Burkholder 1985). Moreover, taxonomic composition and physiognomic structure of the algal community are closely related to trophic interactions, as such properties may influence patterns of export and the flora's susceptibility to grazing by aquatic invertebrates (Sumner and McIntire 1982; Gregory 1983; Hart 1985; Steinman unpubl. data). Steinman and McIntire (1986), using laboratory streams, found that current velocity and irradiance interacted in a complex fashion to influence the dynamics of algal assemblages. In that experiment, only two irradiance levels (50 and 450 $\mu E \cdot m^{-2} \cdot s^{-1}$) were used, and as a consequence, the effects of very low and intermediate light levels on algal assemblages were not examined. In addition, their use of two different flow regimes complicated interpretation of the effect of irradiance alone. Therefore, the present study was

conducted to examine the effects of irradiance on attached algal assemblages in more detail.

The present study was designed to examine the following hypotheses: (1) that algal biomass accumulation in lotic systems is affected by irradiance; and (2) that successional changes in lotic algal assemblages are closely related to the level of irradiance. More specifically, this research investigated the effects of four levels of irradiance on the biomass, taxonomic structure, and physiognomy of algal assemblages in laboratory streams. Photon flux densities were selected to include levels that correspond to both light saturation and potential light limitation of photosynthesis. Species composition and biomass of the experimental assemblages were monitored over 48 days, and corresponding physiognomic properties were examined by scanning electron microscopy (SEM).

MATERIALS AND METHODS

The design of the laboratory streams was described by Steinman and McIntire (1986). Well water was exchanged in each stream at a rate of 1.5 $L \cdot min^{-1}$, and water temperature remained constant at 14 ± 1 °C throughout the experimental period. Nutrient concentrations in the well water were relatively high (orthophosphate: 0.096 $mg \cdot L^{-1}$; silica: 19.187 $mg \cdot L^{-1}$; NO_3-N: 6.499 $mg \cdot L^{-1}$; NH_3: 0.002 $mg \cdot L^{-1}$). Streams were housed indoors and the sole source of light energy was provided by 16 1000-Watt Metalarc lamps (Sylvania Corp.), each mounted in a symmetrical Maxigro reflector. Timers were set to produce 8 h of light and 16 h of darkness each day. The bottom of each stream was lined with 7.5 cm x 7.5 cm unglazed, ceramic tiles, which provided a surface for colonization and units for periodic sampling. Smaller tiles (1.2 cm x 1.2 cm) were spaced among the larger tiles, and served as sampling units for the investigation of assemblage physiognomy by scanning electron microscopy (SEM).

At the beginning of the experiment (April 7, 1985), the laboratory streams were inoculated with one liter of an algal suspension obtained by scraping rocks from four local streams (Steinman and McIntire 1986). The experimental design involved 12 streams exposed to four different levels of light energy, with three replications of each treatment. Photon flux densities (PFD) of 400, 150, 50 and 15 $\mu E \cdot m^{-2} \cdot s^{-1}$ were obtained by adjusting the height of the lamp fixtures and by placing green Chicopee screen with the appropriate mesh size over the streams. A PFD of 400 μE

$m^{-2} \cdot s^{-1}$ is at or near the saturation intensity of photosynthesis for benthic algal assemblages (McIntire 1968; Jasper and Bothwell 1986). The other PFD were chosen to simulate irradiance levels that occur naturally in the streams from which the algae in this experiment were collected. Current velocity in all streams was maintained at 10 $cm \cdot s^{-1}$. The experiment ended after 48 days.

For estimates of biomass accumulation, a random sample of three 7.5 cm x 7.5 cm tiles was obtained from each stream on days 8, 16, 32, and 48. Biomass was determined by the method of McIntire and Phinney (1965).

For the quantitative analysis of species composition, two 7.5 cm x 7.5 cm tiles were randomly selected from each of the twelve streams on days 8, 16, 32 and 48. Algae were scraped from tiles with razor blades, fixed in Lugol's solution, settled in 50 mL chambers, and 500 algal units were counted at 400X magnification with a Nikon MS inverted microscope (Utermöhl 1958). During this procedure, diatoms were lumped in one category, and all other taxa were identified to species. An algal unit was an individual cell or valve, if the taxon was a unicellular form, or an individual filament or colony in the case of multicellular taxa. For the filamentous and colonial taxa, the total number of cells in each algal unit was also estimated for the calculation of biovolumes. After the counts were completed, each sample was pipetted into a flask and boiled in concentrated HNO_3. The clean diatom frustules that resulted from this treatment were mounted on microscope slides in Cumarone resin (Holmes et al. 1981), and 300 valves were

identified and counted at 1,250X magnification with a Zeiss RA microscope. The proportions of the diatom taxa in this sample were used to estimate the abundances of these taxa in the corresponding count of 500 algal units. Specifically, $N(500)_j = T(500) \times P(300)_j$, where $N(500)_j$ was the estimated number of units that belonged to the j-th diatom taxon in the count of 500, T(500) was the total number of diatom units in the count of 500, and $P(300)_j$ was the proportion of units in the count of 300 that belonged to the j-th taxon. Biovolumes for each taxon were calculated by multiplying an estimated mean volume per algal unit by the number of algal units in the count of 500. Mean volumes were based on standard geometric formulae.

Sampling for the examination of physiognomic characteristics involved the removal of two 1.2 cm x 1.2 cm tiles from each stream on days 2, 4, 8, 16, and 32. These tiles were immediately freeze-dried in liquid N_2. After sublimation, the samples were coated with Au-Pd by vacuum evaporation and examined with an Amray 1000-A SEM.

Treatment effects on biomass accumulation at the end of the experiment were examined with a one-way analysis of variance (Snedecor and Cochran 1967). Successional changes in the species composition of the algal assemblages were examined by detrended correspondence analysis (DCA), an ordination procedure (Hill and Gauch 1980). In this case, species abundance was based on relative biovolume, and successional trajectories were obtained by plotting the sample scores for DCA axes 1 and 2.

RESULTS

Algal biomass increased during the 48-day experimental period in all streams (Fig. III.1). An analysis of variance indicated that the treatment mean biomasses at the end of the experiment were not equal ($P < 0.01$). Moreover, a linear component of variance was highly significant ($P < 0.01$) and accounted for 94.1% of the treatment sum of squares. Therefore, algal biomass in the laboratory streams on day 48 was roughly proportional to treatment PFD.

The biomasses of the five dominant taxa on each sampling day were estimated by multiplying a taxon's proportion of the community biovolume by the total community biomass (Fig. III.2). _Achnanthes lanceolata_ and _Synedra ulna_, the dominant diatoms, had the highest biomasses in streams receiving 400 $\mu E \cdot m^{-2} \cdot s^{-1}$. However, the prostrate _A. lanceolata_ continued to accumulate biomass in all treatments throughout the experiment, whereas the rosette-forming _S. ulna_ reached a maximum mean biomass by day 16 in streams exposed to the two higher PFD and thereafter decreased or changed very little in abundance. The cyanophyte _Phormidium tenue_ exhibited little biomass until day 32, when it began to increase in all streams except those subjected to 15 $\mu E \cdot m^{-2} \cdot s^{-1}$. The _Scenedesmus_ populations also failed to show much biomass accumulation until day 32. However, between days 32 and 48, biomass of this taxon increased rapidly in the streams exposed to 150 and 400 $\mu E \cdot m^{-2} \cdot s^{-1}$. The filamentous chlorophytes included _Stigeoclonium tenue_, _Ulothrix_

zonata, U. tenerrima, and Klebsormidium fluitans. These taxa exhibited biomass maxima on day 32 in the streams receiving 150 and 400 $\mu E \cdot m^{-2} \cdot s^{-1}$, and thereafter decreased, concomitant with the increase in Scenedesmus spp.

Based on cell numbers, the relative abundance of A. lanceolata increased in the streams exposed to the two lower PFD (Fig. III.3), although this pattern is not apparent in Figure III.2 because of the low biomass in these streams. While biomass data provided information related to production rates and bioenergetics, cell counts gave an indication of the relative abundance of the units of genetic information in the system. Synedra ulna exhibited relatively high biomasses in the streams exposed to 150 and 400 $\mu E \cdot m^{-2} \cdot s^{-1}$, but its relative abundance based on cell numbers was virtually unaffected by light level. In the case of Phormidium tenue and Scenedesmus spp., the relative abundances of cells were low (<2%) until after day 32. By day 48, the highest relative abundances for these taxa were found in streams exposed to 50 and 400 $\mu E \cdot m^{-2} \cdot s^{-1}$, respectively. The relative abundances of the filamentous chlorophytes varied during the experiment, reaching maximum values at the highest light level on day 32.

SEM analysis of samples obtained on day 8 revealed an understory of adnate Achnanthes lanceolata and an overstory of mostly Synedra ulna on tiles exposed to 15 $\mu E \cdot m^{-2} \cdot s^{-1}$ (Fig. III.4) and 50 $\mu E \cdot m^{-2} \cdot s^{-1}$ (Fig. III.5). Even greater accumulations of Synedra spp. and Fragilaria spp. were observed on tiles from the streams receiving 150 $\mu E \cdot m^{-2} \cdot s^{-1}$ (Fig. III.6) and 400 $\mu E \cdot m^{-2} \cdot s^{-1}$

(Fig. III.7).

There was still limited diatom development by day 16 on the tiles exposed to the lowest PFD (Fig. III.8), although diatom growth was relatively dense on tiles exposed to 50 $\mu E \cdot m^{-2} \cdot s^{-1}$ (Fig. III.9). In comparison, denser accumulations of filamentous green algae and diatoms covered the entire surface area of the tiles exposed to 150 and 400 $\mu E \cdot m^{-2} \cdot s^{-1}$ (Figs. III.10 and III.11, respectively).

A dense understory of _A_. _lanceolata_ covered the tile surface on day 32 in streams exposed to the lowest PFD (Fig. III.12) with a few _Fragilaria_ chains and _Synedra_ _ulna_ cells providing an overstory. A similar type of physiognomy was apparent on the tiles subjected to 50 $\mu E \cdot m^{-2} \cdot s^{-1}$ (Fig. III.13), although the understory appeared denser and more diverse (note the mound-like morphology). At 150 and 400 $\mu E \cdot m^{-2} \cdot s^{-1}$ (Figs. III.14 and III.15), the assemblages consisted of a thick layer of diatoms and associated green algae, such as _Scenedesmus_ (Fig. III.17). Figure III.16 shows a reticulum of unknown origin, similar in gross appearance to Fig. 46 of Hoagland et al. (1982). This type of structure, along with organic debris and mucilage, may be important in facilitating colonization by algae.

The mean successional trajectories for the algal assemblages associated with four light treatments are illustrated in Figure III.18. The ordination clearly showed that assemblages exposed to low irradiances (15 and 50 $\mu E \cdot m^{-2} \cdot s^{-1}$) followed different

successional trajectories than those exposed to high irradiances (150 and 400 $\mu E \cdot m^{-2} \cdot s^{-1}$). The assemblages subjected to 150 $\mu E \cdot m^{-2} \cdot s^{-1}$ initially developed along a trajectory similar to the one followed by the low light assemblages, but reversed themselves at day 16. By day 48, their successional trajectory paralleled that of the assemblages exposed to 400 $\mu E \cdot m^{-2} \cdot s^{-1}$.

DISCUSSION

Previous investigations have indicated that light energy can have an important influence on the production dynamics of algal assemblages in lotic environments. In prior studies where light reaching the stream surface has been increased, algal biomass has also increased (McIntire 1968; Lyford and Gregory 1975; Murphy and Hall 1981; Shortreed and Stockner 1983; Lowe et al. 1986; Steinman and McIntire 1986). The results of the present study were consistent with this pattern, as higher photon flux densities resulted in greater algal biomasses. It is clear that biomass production was severely light limited at photon flux densities below 50 $\mu E \cdot m^{-2} \cdot s^{-1}$, and still was not saturated at a PFD of 150 $\mu E \cdot m^{-2} \cdot s^{-1}$. It is unknown whether or not 400 $\mu E \cdot m^{-2} \cdot s^{-1}$ represented a saturating irradiance for biomass production in these assemblages, because experiments were not conducted at a higher irradiance. However, a number of investigations have indicated that photosynthetic saturation by attached algae tends to occur at irradiances that are approximately 10-20% of incident sunlight (i.e. 200-400 $\mu E \cdot m^{-2} \cdot s^{-1}$). Jasper and Bothwell (1986) determined that optimal light levels (I_k) for photosynthesis by (suspended) periphyton from streams in British Columbia exceeded 400 $\mu E \cdot m^{-2} \cdot s^{-1}$ from April through September, but were below 300 $\mu E \cdot m^{-2} \cdot s^{-1}$ during November through March. In addition, I_k values for assemblages in the present study, as determined in enclosed, recirculating chambers, were between 200 and 400 $\mu E \cdot m^{-2} \cdot s^{-1}$ (S. V. Gregory, pers.

comm.), an intensity range that corresponds to levels noted by McIntire et al. (1964) and Turner et al. (1983). Based on these data, it is hypothesized that biomass production was light-saturated at a PFD of 400 $\mu E \cdot m^{-2} \cdot s^{-1}$ in this study. However, saturation irradiances may vary depending upon the previous light history (Beadall and Morris 1976; Jasper and Bothwell 1986) and nutrient status (Morris 1981) of the algal assemblage.

Light energy also influences the taxonomic structure of lotic algal assemblages. Filamentous chlorophytes have increased in abundance after canopy removal by logging (Lyford and Gregory 1975; Stockner and Shortreed 1976; Shortreed and Stockner 1983; Lowe et al. 1986), suggesting that these algae may be adapted to utilize high irradiances more efficiently than other taxa. For example, chlorophytes may have higher maximum rates of photosynthesis than species in other algal classes. Steinman and McIntire (1986), using laboratory streams, also observed that chlorophytes were more abundant at 450 than at 50 $\mu E \cdot m^{-2} \cdot s^{-1}$ after 32 days of growth. In the present study, the relative abundance of green algae again were greater in streams exposed to the higher treatment irradiances (i.e. 150 and 400 $\mu E \cdot m^{-2} \cdot s^{-1}$). However, chlorophyte relative abundances were similar at 150 and 400 $\mu E \cdot m^{-2} \cdot s^{-1}$, indicating that a PFD of 150 $\mu E \cdot m^{-2} \cdot s^{-1}$ was sufficient to stimulate growth of green algae. An alternative hypothesis to account for the increased abundance of chlorophytes in streams after the canopy is removed by logging suggests that these taxa may be restricted to habitats where the blue and red wavelengths of the visible light spectrum

are abundant. The major pigment of light absorption for photosynthesis in both riparian vegetation and green algae is chlorophyll a. Under shaded conditions, light energy reaching a stream may be impoverished with respect to the blue and red wavelengths because of absorption by chlorophyll a in the leaves of the surrounding riparian vegetation. As chlorophytes lack the pigment diversity of other common stream algae (Lowe et al. 1986), they may become both quantitatively and qualitatively light-limited under shaded conditions. In the present study, it is probable that blue and red light was absorbed by the green screening material, which may in turn have restricted the growth of chlorophytes in the shaded laboratory streams.

The greater relative abundances of the adnate diatom *Achnanthes lanceolata* at relatively low light levels suggested that this taxon may be tolerant of low light intensities. If so, such tolerance may represent an adaptive strategy (Hudon and Bourget 1983), as adnate diatoms are vulnerable to shading by an overstory of detritus and other algal cells. However, this pattern does not occur universally among adnate species, as factors such as current velocity and genetic variation among different taxa may result in low relative abundances at low PFD (Steinman and McIntire 1986). In contrast to *A. lanceolata*, *Synedra ulna* reached its maximum relative abundance during an early stage of succession in all laboratory systems. This taxon apparently can colonize bare substrate quickly, regardless of irradiance (Oemke and Burton 1986, Steinman and McIntire 1986), perhaps because of its large surface

area which may enhance attachment.

The abundance of Phormidium tenue and Scenedesmus spp. during the late stages of succession may be an example of a facilitation effect (Connell and Slatyer 1977). Filaments of Phormidium may require a well-developed mucilagenous matrix or a well-colonized substrate surface before a sizable population can develop. In this study, Scenedesmus coenobia were found growing as loosely arranged colonies within structurally complex algal mats. Presumably, the mat provided cover and prevented the coenobia from being dislodged by shear stress, as these taxa lack a mechanism to adhere firmly to substrate. Therefore, the relative abundances of Scenedesmus may remain low until algal mats of a certain size and structural complexity have developed. If facilitation was necessary, then the large relative abundances of Scenedesmus at high PFD may not have been due to these taxa responding positively to high light. Rather, their high abundances would have been a function of the positive response of filamentous algae to high irradiances, which in turn provided a suitable microhabitat for the growth of Scenedesmus. In fact, Antoine and Benson-Evans (1983) found that Scenedesmus spp. grew better at irradiances of 5.5 $W \cdot m^{-2}$ (ca. 25 $\mu E \cdot m^{-2} \cdot s^{-1}$) than at 29.1 $W \cdot m^{-2}$ (ca. 134 $\mu E \cdot m^{-2} \cdot s^{-1}$) in white light. However, Scenedesmus has obtained high relative abundances at much earlier times (e.g. day 8) in other experiments in laboratory streams (Steinman et al. submitted [b]), suggesting that facilitation is not required for growth by these taxa, or at least that facilitation by filamentous chlorophytes is not required.

Alternatively, the algal inoculum at the start of the experiment may have had low amounts of Phormidium and Scenedesmus (accounting for their low relative abundances through day 32). Once settled, however, these taxa may have exhibited high growth rates (accounting for their high abundances on day 48).

The physiognomy of a periphyton assemblage can affect current velocity (Reiter and Carlson 1986), mediate competitive interactions within the assemblage (Cathy Pringle unpubl. data), and determine the assemblage's susceptability to grazing by aquatic invertebrates (Gregory 1983; Steinman and McIntire unpubl. data). Therefore, it is important to understand how assemblage physiognomy varies under different conditions. In this study, the pattern of early colonization at all light levels included the formation of large rosette- and chain-forming colonies of Synedra spp. followed by the development of an understory of Achnanthes spp. At the higher light levels (i.e. 150 and 400 $\mu E \cdot m^{-2} \cdot s^{-1}$), the successional sequence continued with the development of dense diatom accumulations followed by the growth of filamentous green algae and ultimately, of masses of Scenedesmus spp. The development of a structurally complex physiognomy under high irradiance is consistent with the findings of Lowe et al. (1986), even though the taxa comprising their lotic assemblages were considerably different from those in this study.

Benthic assemblages in streams often consist of a mosaic of algal patches in an array of successional states (Busch 1978;

Fisher 1983). However, it is unclear whether the patches represent different seral stages of one successional trajectory or instead, the patches are on separate successional trajectories. Results from this study indicate that algal assemblages were developing along separate successional trajectories after 48 days, apparently in response to different light regimes. In a natural stream, spatial and temporal variation in light energy, current velocity, nutrient supply, substrate complexity, and patterns of herbivory may generate even greater differences among the patches than in the laboratory streams. However, data from this study clearly demonstrate that differences in irradiance alone can account for large differences in algal biomass, taxonomic composition, and physiognomy.

ACKNOWLEDGEMENTS

We are very grateful to Linda Ashkenas, Karan Fairchild and Al Soeldner for their technical assistance. Stan Gregory and Gary Lamberti kindly provided the biomass data, and collaborated with the authors on the design of the experiment. Scott Overton kindly advised us on statistical analyses. Comments by Roger Green and two anonymous reviewers improved this manuscript. This study was supported by research grant No. BSR-8318386 from the National Science Foundation and by a Sigma Xi Grant-In-Aid.

Figure III.1 Biomass accumulation of algal assemblages (expressed as ash-free dry weight) in laboratory streams.

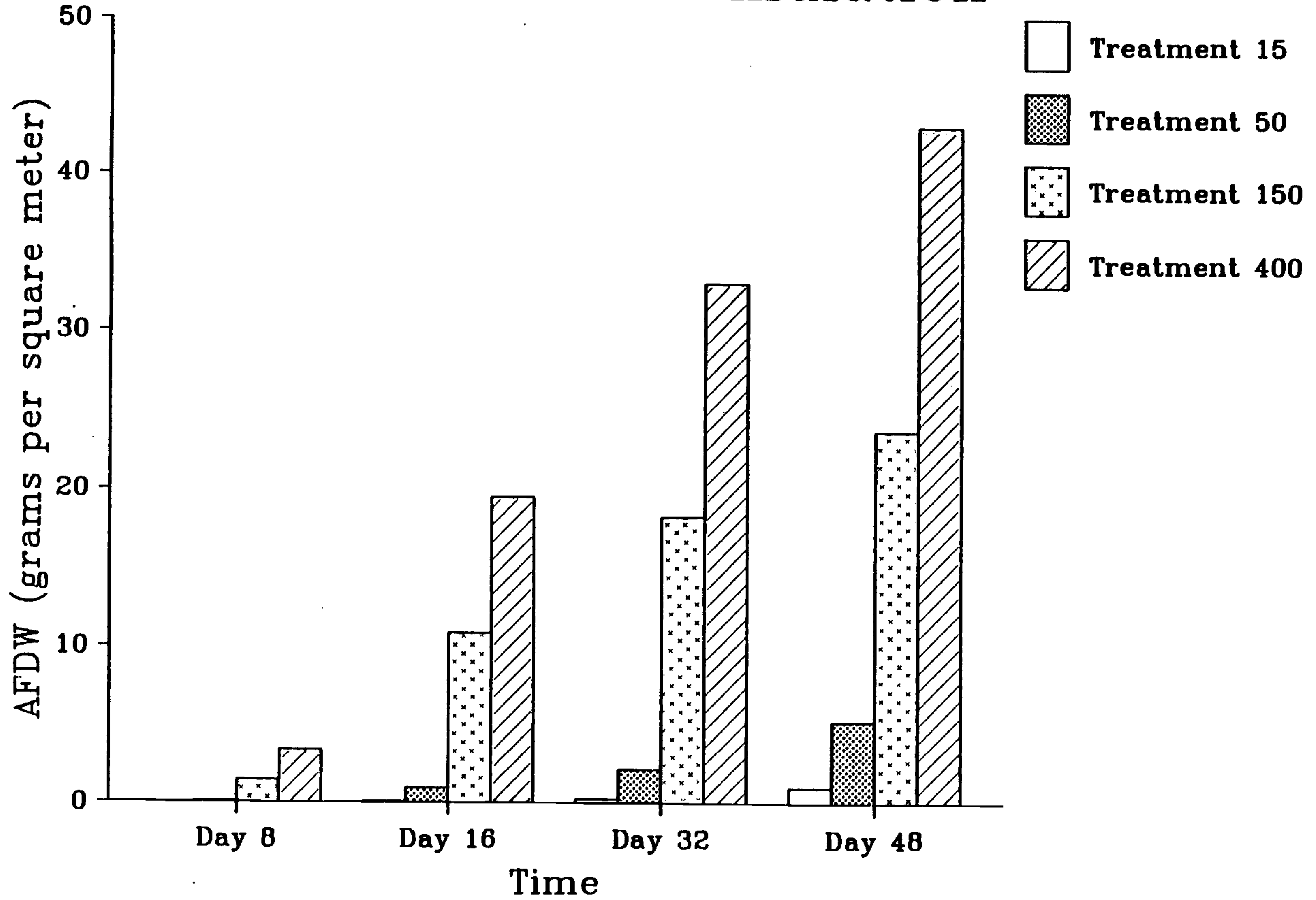


Figure III.1

Figure III.2 Biomass of five dominant taxa (estimated by multiplying a taxon's proportion of community biovolume by the total community biomass) in laboratory streams. Note the scale on the ordinate axis varies with taxon.

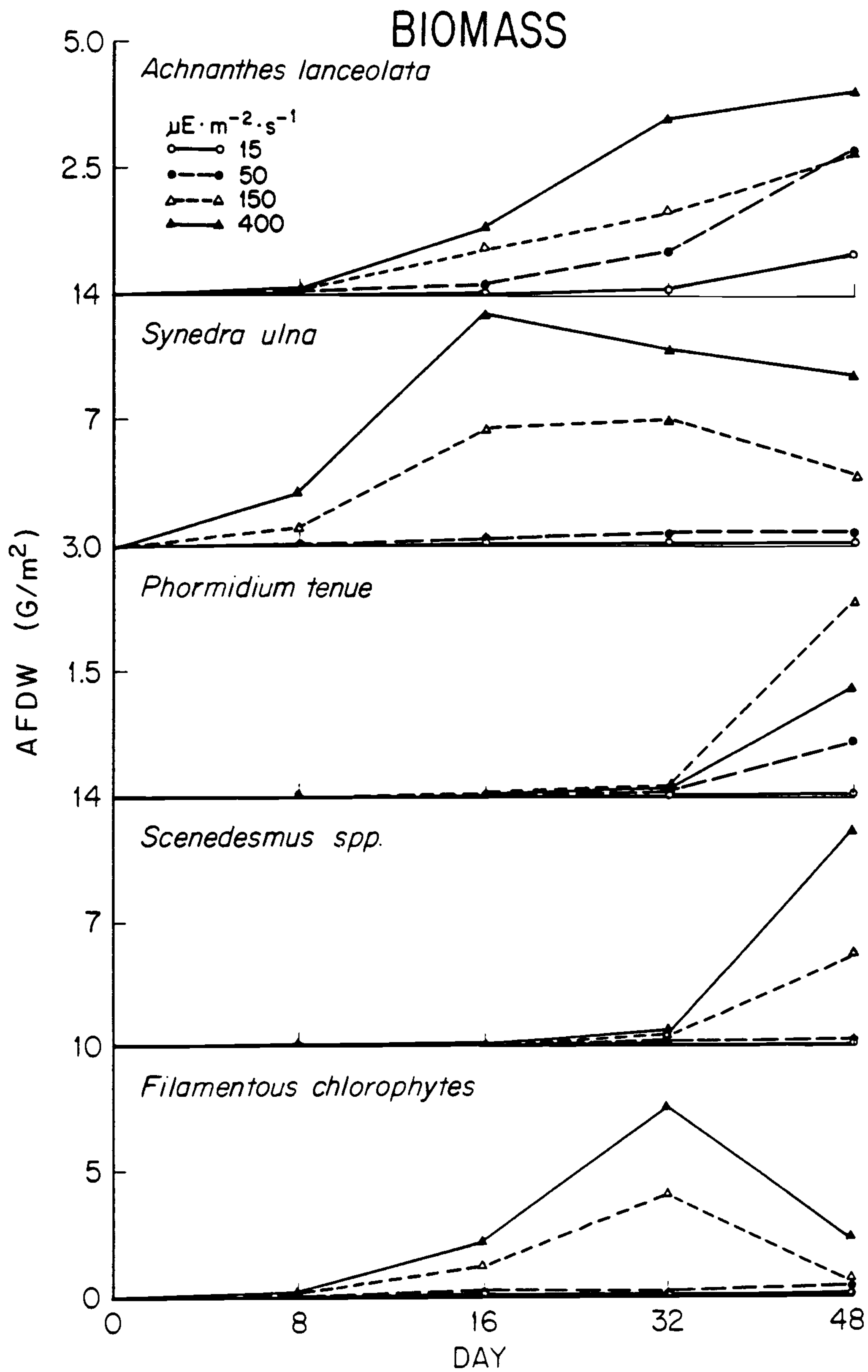


Figure III.2

Figure III.3 Relative abundance of five dominant taxa (based on a taxon's proportion of total cells in each assemblage on a sampling day) in laboratory streams. Note the scale on the ordinate axis varies with taxon.

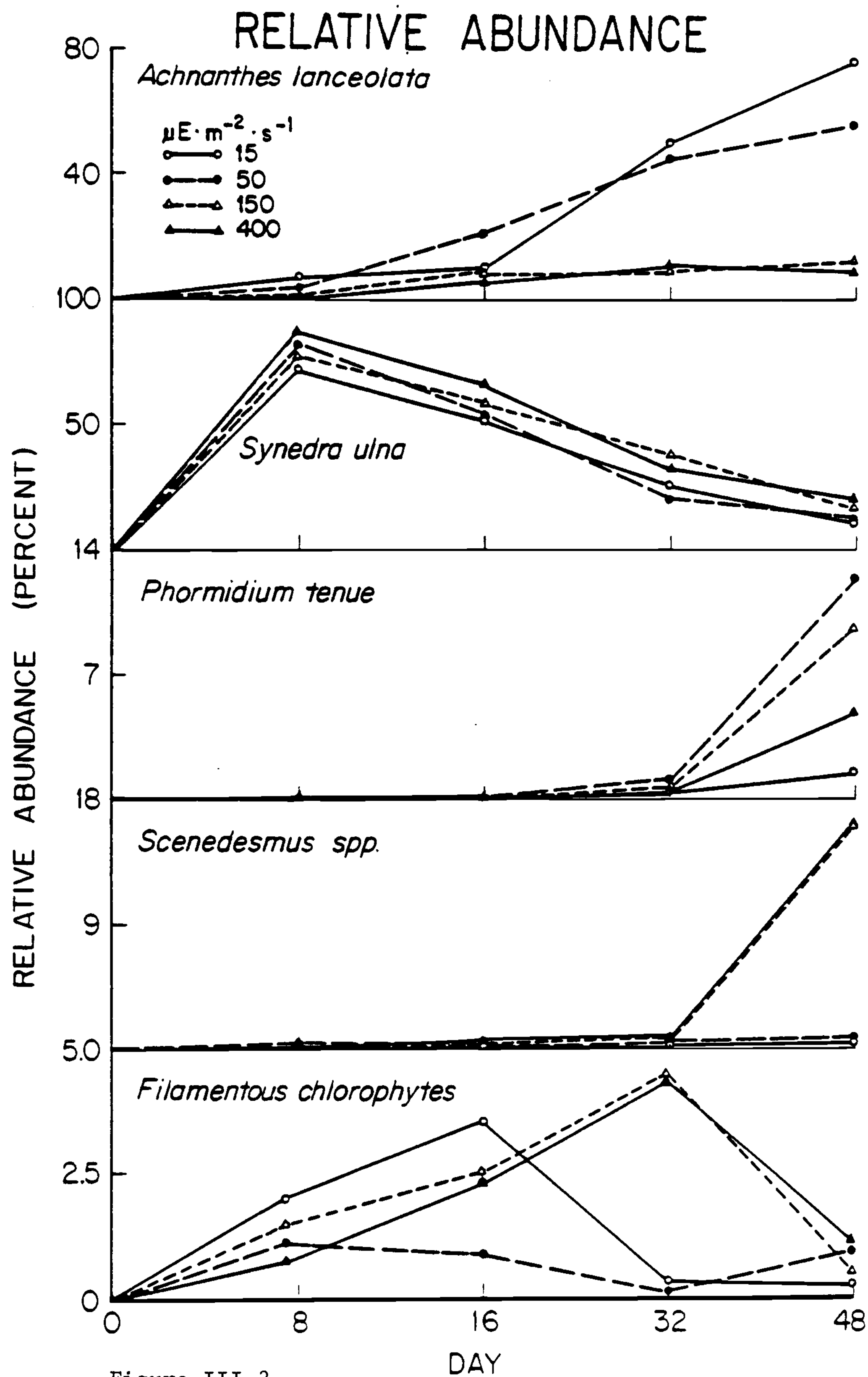


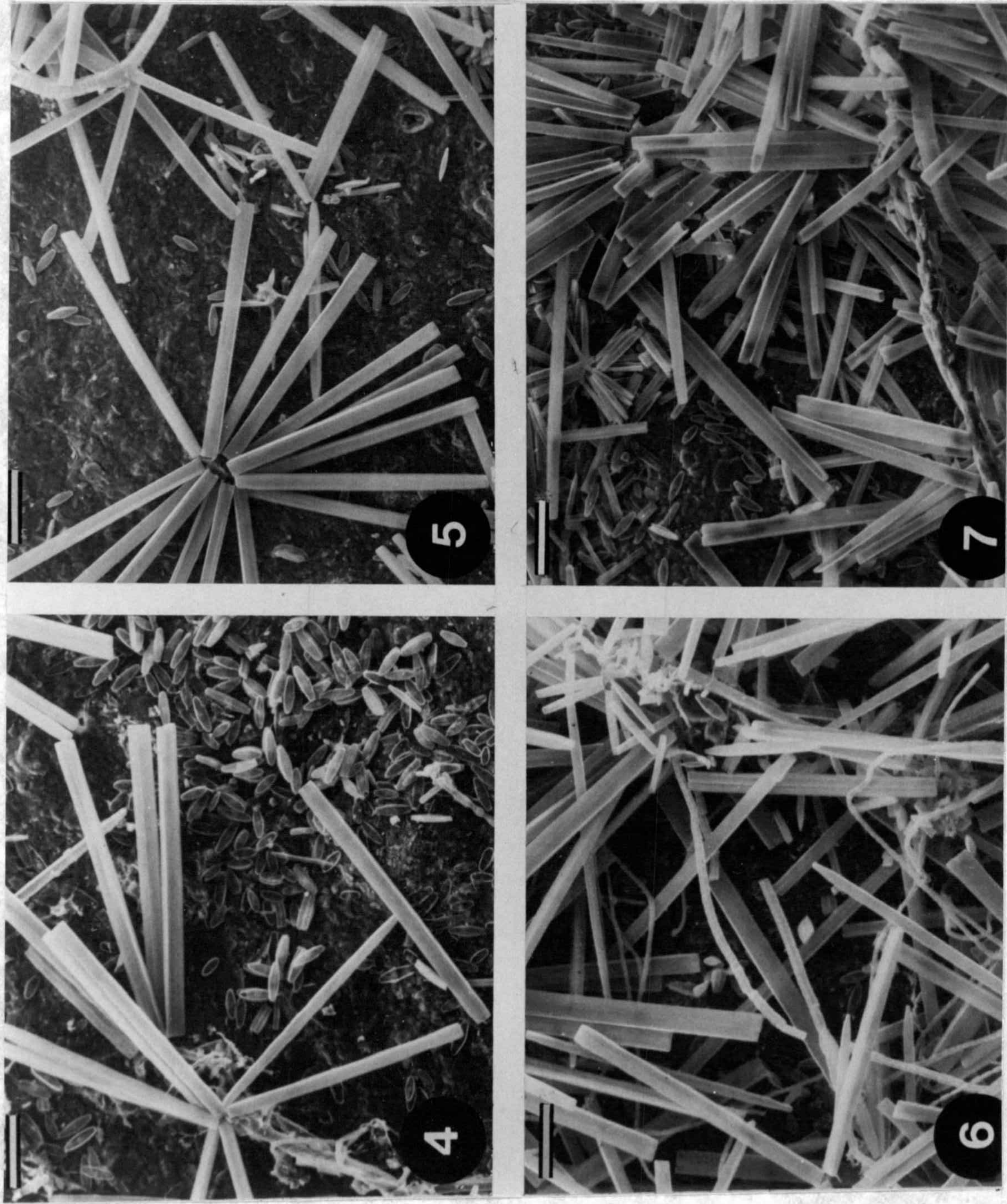
Figure III.3

Figure III.4 SEM of algal assemblage at day 8. Treatment 15 $\mu E \cdot m^{-2} \cdot s^{-1}$ (15). Note limited diatom flora consisting of Synedra ulna rosettes and adnate Achnanthes spp. Scale bar = 50 μm.

Figure III.5 SEM of algal assemblages at day 8. Treatment 50 $\mu E \cdot m^{-2} \cdot s^{-1}$ (50). Diatom assemblage similar to that in Figure III.4. Scale bar = 50 μm.

Figure III.6 SEM of algal assemblages at day 8. Treatment 150 $\mu E \cdot m^{-2} \cdot s^{-1}$ (150). Note increased accumulations of rosette- and chain-forming diatoms, with understory of Achnanthes cells.

Figure III.7 SEM of algal assemblages at day 8. Treatment 400 $\mu E \cdot m^{-2} \cdot s^{-1}$ (400). Assemblage similar to that in Figure III.6. Scale bar = 50 μm.



Figures III.4-7

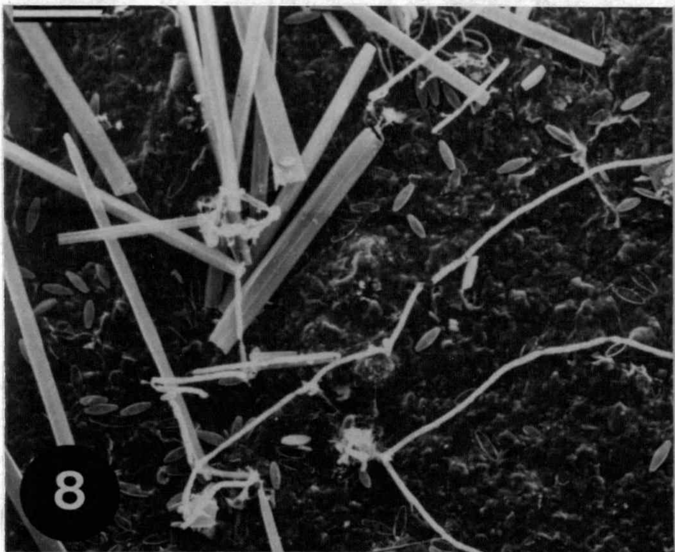
Figure III.8 SEM of algal assemblages at day 16. Treatment 15. Flora still limited, mostly diatoms present. Scale bar = 50 μm.

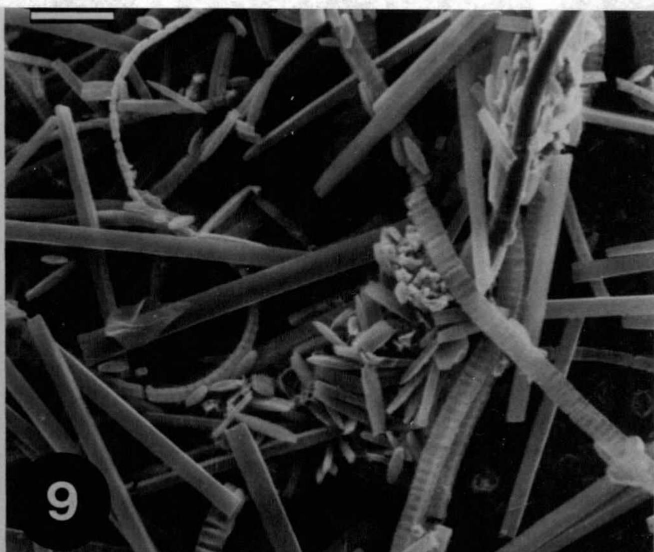
Figure III.9 SEM of algal assemblages at day 16. Treatment 50. Note denser accumulation of diatoms, with distinct chains of *Fragilaria vaucheriae*. Scale bar = 50 μm.

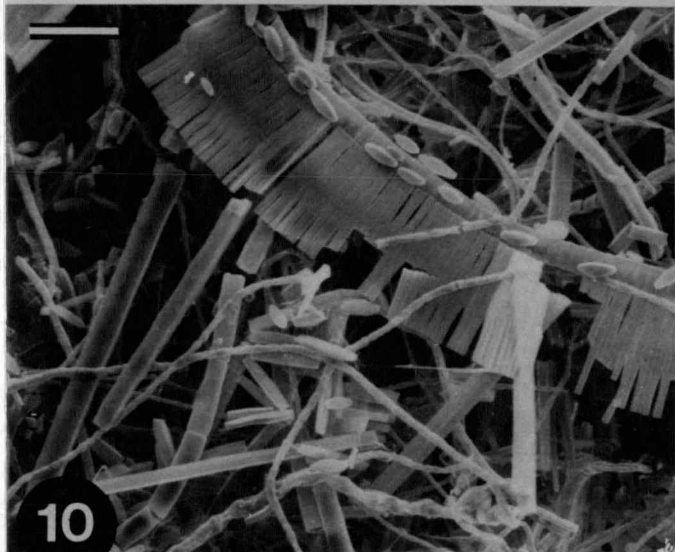
Figure III.10 SEM of algal assemblages at day 16. Treatment 150. Much denser algal accumulations with diatom chains and filamentous green algae ramifying through the assemblages. Scale bar = 50 μm.

Figure III.11 SEM of algal assemblages at day 16. Treatment 400. Assemblage similar to that in Figure III.10. Scale bar = 50 μm.

Figures III.8-11







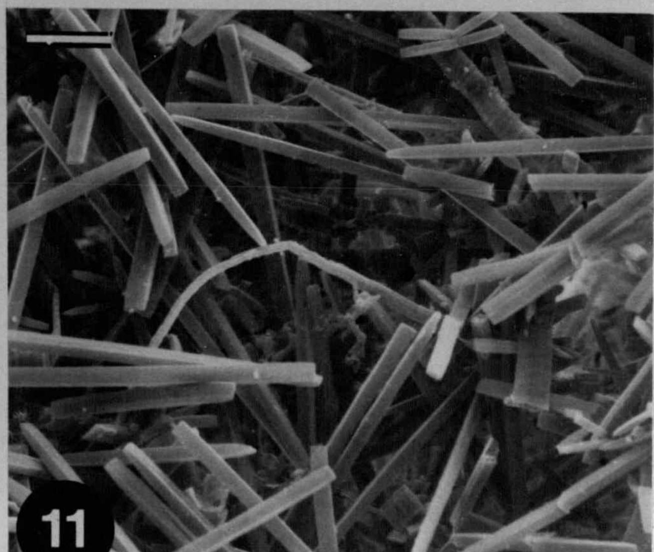


Figure III.12 SEM of algal assemblages at day 32. Treatment 15. Note dense adnate understory of mostly *Achnanthes lanceolata* with overlaying chains of *Fragilaria*. Scale bar = 50 μm.

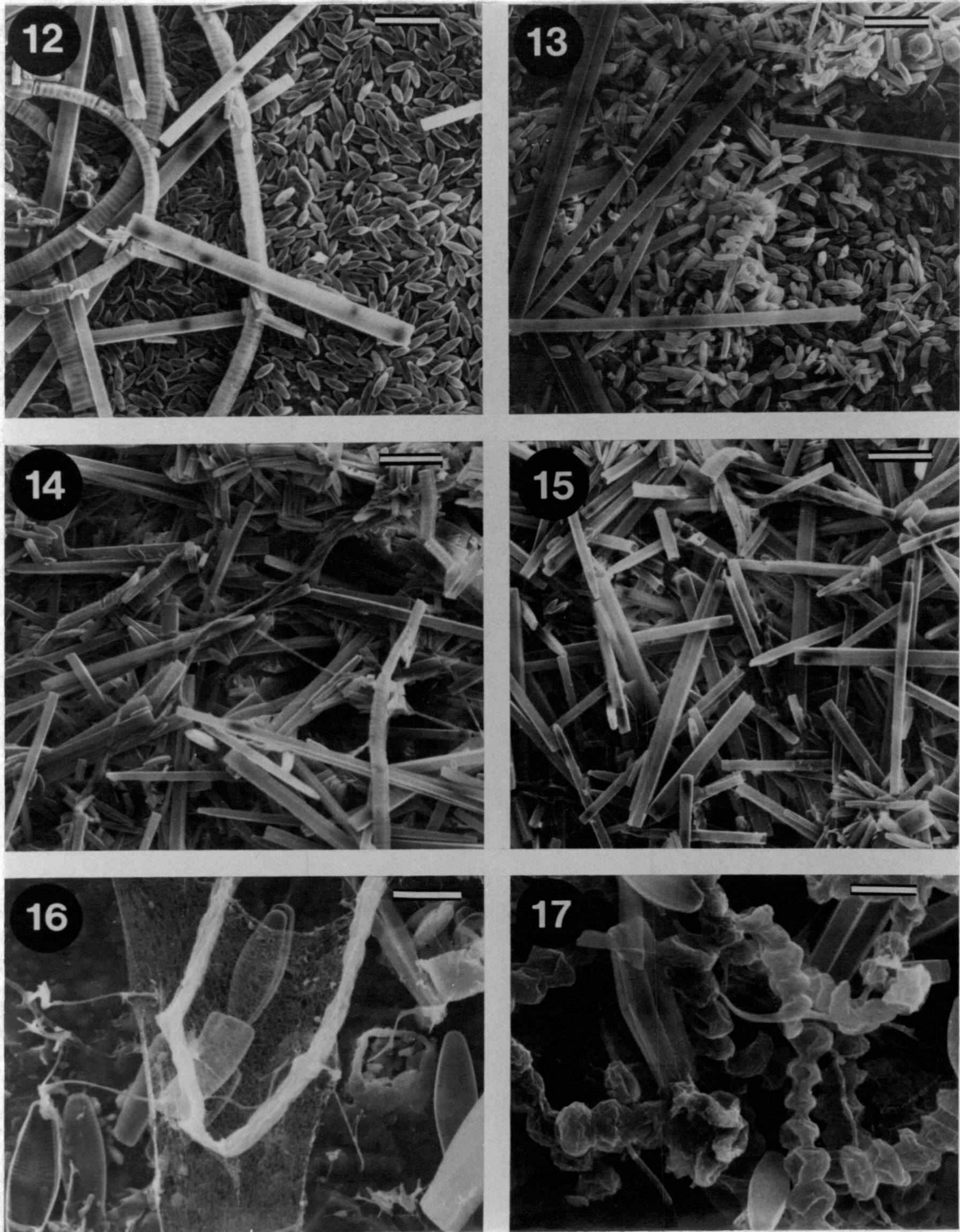
Figure III.13 SEM of algal assemblages at day 32. Treatment 50. Dense understory of *Achnanthes* "clumps" with overlaying cells of *S. ulna*. Scale bar = 50 μm.

Figure III.14 SEM of algal assemblages at day 32. Treatment 150. Dense algal accumulations in relatively unstructured assemblages. The tile surface is totally covered. Scale bar = 50 μm.

Figure III.15 SEM of algal assemblages at day 32. Treatment 400. Assemblage similar to that in Figure III.14. Scale bar = 50 μm.

Figure III.16 SEM of close-up of fine-stranded reticulum; origin unknown. Note frustules of *Rhoicosphaenia curvata* and *A. lanceolata* beneath reticulum. Scale bar = 10 μm.

Figure III.17 SEM of close-up of *Scenedesmus* coenobia. Scale bar = 10 μm.



Figures III.12-17

Figure III.18 Sample ordinations by detrended correspondence analysis showing successional trajectories of algal assemblages exposed to different irradiances. Connected points in each trajectory represent mean ordination scores for three replications of each treatment. At day 48, values for all three replications of each treatment are shown and connected by a dashed line to show variation at the final seral stage. Arrows denote temporal direction of succession: first point in trajectory represents day 8, second point day 16, third point day 32, and fourth point day 48. Treatments are indicated by open squares (15 $\mu E \cdot m^{-2} \cdot s^{-1}$), open circles (50 $\mu E \cdot m^{-2} \cdot s^{-1}$), closed circles (150 $\mu E \cdot m^{-2} \cdot s^{-1}$), and stars (400 $\mu E \cdot m^{-2} \cdot s^{-1}$).

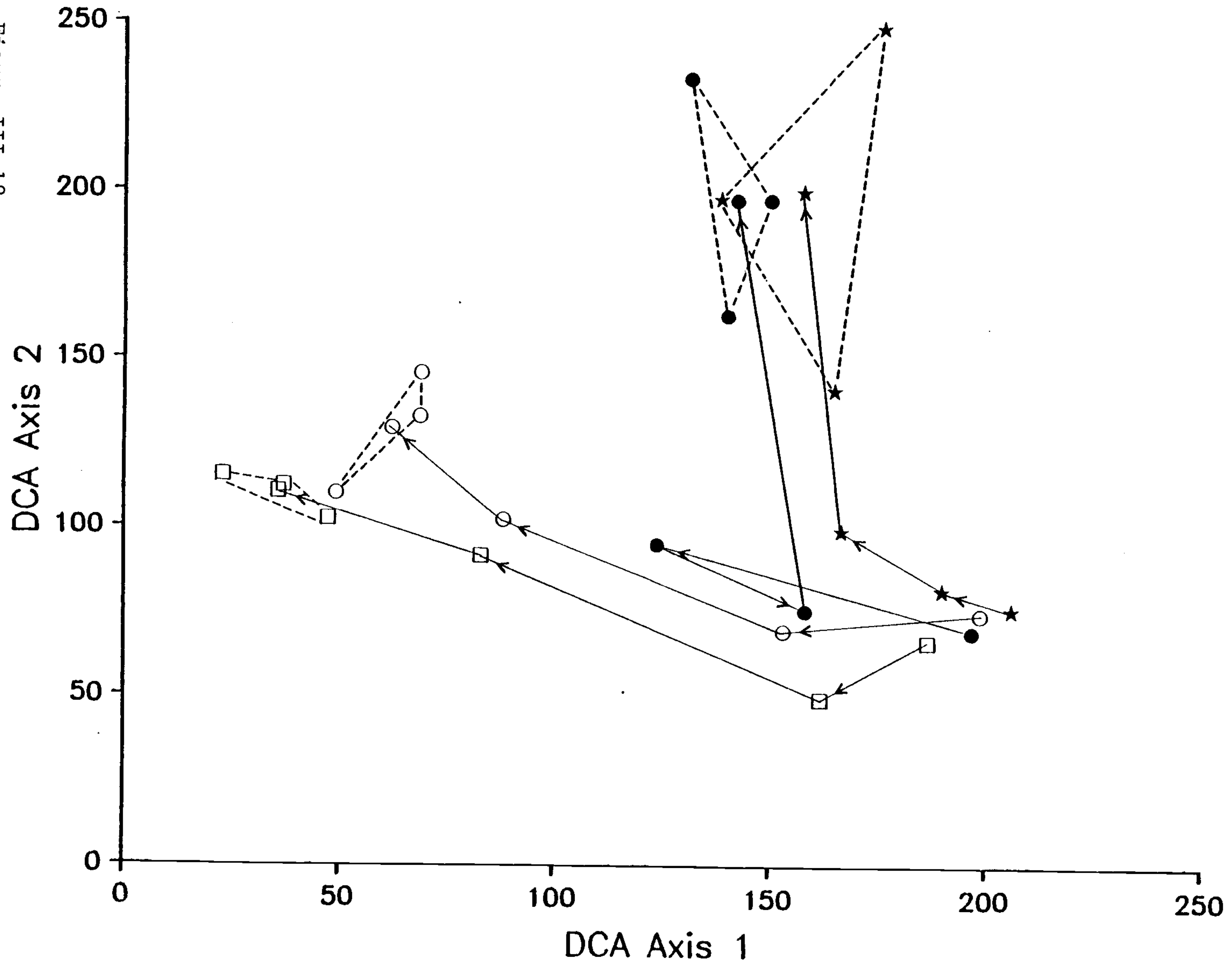


Figure III.18

IV. EFFECTS OF IRRADIANCE AND AGE ON CHEMICAL CONSTITUENTS OF ALGAL ASSEMBLAGES IN LABORATORY STREAMS

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ABSTRACT

Effects of irradiance (15, 50, 150, and 400 $\mu E \cdot m^{-2} \cdot s^{-1}$) and age (8, 15, and 31 days) on the chemical composition of algal assemblages in laboratory streams were examined. Overall, the most abundant fatty acids and amino acids were 16:0, 16:1, 18:1, and 20:5, and glutamic acid/glutamine, aspartic acid/asparagine, serine, glycine, and alanine, respectively. Day 8 assemblages exposed to low irradiances were characterized by high percentages of 16:0 and 18:3 fatty acids, glycine, and serine. Older assemblages had relatively high concentrations of 16:1, 20:5, and aspartic acid/asparagine acids. Levels of total crude lipid and combined protein also varied with light energy and age. Surprisingly little association was evident between protein level and C:N ratio. Ordinations using a reciprocal averaging algorithm revealed discontinuities between some algal assemblages based on their chemical constituents. This suggests that biochemical expressions of algal community structure in benthic ecology may be useful, especially when trophic level interactions are under consideration. In general, the data indicate that lotic algal assemblages represent food sources of high nutritional quality.

INTRODUCTION

The community structure of algal assemblages in lotic ecosystems has traditionally been described in terms of its taxonomic composition or physiognomic properties (Blum 1957; Korte & Blinn 1983; Stevenson 1984; Keithan & Lowe 1985; Sheath & Burkholder 1985; Steinman & McIntire 1986). However, chemical composition provides an additional set of criteria by which community structure can be assessed (McIntire et al. 1969; Jeffries 1970; Miyazaki 1983). Biochemical data also provide information on food quality, which can relate to patterns of herbivory by benthic aquatic invertebrates (McMahon et al. 1974; Hunter 1980; Lamberti & Moore 1984). The research described here was concerned with the analysis of the chemical composition of algal assemblages grown in laboratory streams under four different light regimes. Specifically, this study had two main objectives: (1) to determine the effects of four different irradiances on the chemical composition of lotic algal assemblages at three different stages of succession; and (2) to assess the degree to which particular taxa were associated with chemical components.

MATERIALS AND METHODS

Experimental Design and Sampling: The design of the laboratory streams was described by Steinman & McIntire (1986). Well water was exchanged in each stream at a rate of 1.5 $L \cdot min^{-1}$, and water temperature remained at 14 ± 1°C throughout the experimental period. Chemical analysis of the well water indicated that nutrient concentrations were relatively high and similar to those reported by Steinman & McIntire (1986). Light was supplied by 16 1000-Watt Metalarc lamps (Sylvania Corp.), each mounted in a symmetrical Maxigro reflector. A photoperiod of 8 h light: 16 h dark was controlled by timers. The bottom of each stream was lined with 7.5 x 7.5 cm unglazed, ceramic tiles which provided a surface for colonization and units for periodic sampling. At the start of the experiment, 12 laboratory streams were inoculated with one liter of an algal suspension obtained by scraping rocks from four local streams (Steinman & McIntire 1986). Four photon flux densities (PFD), with three replications of each treatment, were used to investigate the response of algal assemblages to the input of light energy. Treatment photon flux densities of 15, 50, 150 and 400 $\mu E \cdot m^{-2} \cdot s^{-1}$ were obtained by adjusting the height of the lamp fixtures and by placing green Chicopee screen with the appropriate mesh size over the streams. Current velocity was maintained at 10 $cm \cdot s^{-1}$ in all streams. The length of the experiment was 48 days.

For chemical analyses, a random sample of two tiles was obtained from each of eight streams on days 8, 15, and 31 (i.e.

two of the three replications of each treatment were sampled). The algae were scraped from the surface of each tile, homogenized and kept on ice until the analytical procedures were started, usually within one hour after sampling.

Methods for the microscopic analysis of taxonomic community structure were described by Steinman & McIntire (1986).

Chemical Analyses: Fifteen ml of the homogenized algal slurry were used to measure biomass as ash-free dry weight (McIntire & Phinney 1965). Another 15 ml were centrifuged and the lipids extracted from the residue according to the method of Kates (1972). Total crude lipid was determined by weighing a dried subsample from a known volume of the crude extract on a Perkin-Elmer AD-2 microbalance. Fatty acids were methylated by transesterification in 5% methanolic HCl (gas): diethyl ether (1:1, v/v) at 80°C for 90 minutes. Extraction of fatty acid methyl esters (FAME) followed the procedure of Cargill et al. (1985). FAME were analyzed by gas-liquid chromatography using the method of Hanson et al. (1983). Internal standards, comparison of retention times with external standards, and hydrogenation of methyl esters were used to identify fatty acid methyl esters.

Amino acids were determined by hydrolyzing 1 ml subsamples of the homogenized algal samples in glass ampoules in vacuo at 110°C for 22 h. This hydrolysis results in the unavoidable destruction of tryptophan, and does not distinguish glutamine from glutamic acid or asparagine from aspartic acid. Ampoules were opened and the contents dried by roto-evaporation at 35°C. Samples were then

dissolved in 1 ml of 0.2 N sodium citrate diluting buffer (pH 2.20) and Millipore-filtered. Samples were analyzed on a home-built Picomole range Amino Acid Analyzer, fitted with a single Glenco 3.0 mm glass column, packed with 25 cm of Dionex DC-4A resin. A four-step sodium elution gradient was employed using Dionex Hi-Phi sodium citrate buffers. Post-column flourescence was generated by o-phthalaldehyde (Cronin et al. 1979), and detected by a Gilson Spectra/Glo Flourescence Detector using excitation and emission frequencies of 340 and 455 nm, respectively. Protein content was calculated by summing the anhydroamino acid residues. C:N ratios were determined on a Carlo Erba CHN analyzer.

Data Analysis: The data were organized into three matrices: the fatty acid data, the amino acid data, and the species relative abundances based on biovolume. Pattern in each data matrix was examined by correspondence analysis (i.e. reciprocal averaging), a two-way averaging procedure that generated sample ordinations as weighted averages of the variable scores and concurrently produced variable ordinations as weighted averages of the sample scores (Hill 1973, 1974). The reciprocal averaging (RA) algorithm produces ordinations that maximize correspondence between the sample and variable configurations. In this study, separate sets of ordination scores were calculated from each of the three matrices which represented fatty acids, amino acids, and species, respectively. To analyze covariance among variables, the relative abundance of each species was correlated with percentage abundance of each fatty and

amino acid. The correlation analysis was performed with a Control Data Corporation CYBER 170/720 computer using SIPS (Rowe & Brenne 1982), while ordination scores were obtained with an IBM PC using DECORANA, a Cornell University ecology program.

RESULTS

The relative amounts of the fatty acid methyl esters found in the 12 different assemblages are listed in Appendix IV.1. Throughout the experimental period, palmitic acid (16:0), palmitoleic acid (16:1), oleic acid (18:1), and eicosapentaenoic acid (20:5) were the most abundant fatty acids (Fig. IV.1). On day 8, assemblages exposed to 15 and 50 $\mu E \cdot m^{-2} \cdot s^{-1}$ were characterized by high percentages of 16:0 and 18:3 fatty acids, whereas the assemblages exposed to 150 and 400 $\mu E \cdot m^{-2} \cdot s^{-1}$ had large relative amounts of 16:1 and 20:5 acids (Appendix IV.1). On day 15, the assemblages exposed to 15 $\mu E \cdot m^{-2} \cdot s^{-1}$ had much higher relative concentrations of 16:0, 18:0, and 18:3 fatty acids than the other assemblages, but lower percentages of the 16:1, 16:2 and 20:5 fatty acids. There was also a disparity in the distribution of oleic acid (18:1), with the assemblages exposed to lower PFD having greater relative concentrations than those exposed to higher PFD. By day 31, assemblages subjected to 15 and 50 $\mu E \cdot m^{-2} \cdot s^{-1}$ still had a greater proportion of 18:1 and a lower proportion of 16:1 fatty acids in comparison to those exposed to 150 and 400 $\mu E \cdot m^{-2} \cdot s^{-1}$. However, the distributions of 16:0 and 20:5 fatty acids were more uniform among treatments than on days 8 and 15 (Fig. IV.1).

Concentrations of total crude lipid were highest on day 8 in the assemblages exposed to 50 $\mu E \cdot m^{-2} \cdot s^{-1}$ (Fig. IV.2a; Appendix IV.1). On day 15, concentrations were similar in all the communities. An inverse relationship between total crude lipid

concentration and the PFD at which the assemblages were growing developed by day 31.

The amino acid profiles for 12 different assemblages are given in Table IV.1. In general, glutamic acid/glutamine, aspartic acid/asparagine, serine, glycine and alanine were most abundant in all the assemblages. The data also suggested temporal differences existed in the concentration of amino acids. On day 8, the assemblages subjected to 15 $\mu E \cdot m^{-2} \cdot s^{-1}$ had higher percentages of serine and glycine, and lower percentages of leucine, than those exposed to higher PFD. On day 15, the pattern for serine was the same as on day 8, whereas relative concentrations of glycine and leucine were similar in all assemblages. By day 31, the relative concentrations of amino acids were similar in all assemblages.

Concentrations of crude protein on days 8 and 15 were highest in algal assemblages exposed to 50 $\mu E \cdot m^{-2} \cdot s^{-1}$ (Fig. IV.2b). By day 31, more uniform concentrations were measured among the experimental assemblages. C:N ratios were similar in all assemblages (7-10:1) except those exposed to 15 $\mu E \cdot m^{-2} \cdot s^{-1}$, where the ratios were 3- to 4-fold higher on all sampling dates (Fig. IV.2).

Table IV.2 reports the relative biovolumes of the 13 most dominant taxa during the experiment. The diatom _Synedra ulna_ was by far the most abundant taxon on day 8, and remained abundant until the end of the experiment. The relative abundance of _Achnanthes lanceolata_ increased during the experiment in the assemblages exposed to 15 and 50 $\mu E \cdot m^{-2} \cdot s^{-1}$, and by day 31, it was more

abundant than S. ulna. A more detailed description of the taxonomic and physiognomic composition of these assemblages was reported by Steinman & McIntire (submitted [a]).

The RA ordinations of the 24 assemblages and 20 fatty acids are presented in Figs. IV.3 and IV.4, respectively. In Fig. IV.3, axis 1 separated out the day 8 and day 15 samples exposed to 15 $\mu E \cdot m^{-2} \cdot s^{-1}$. The majority of the other samples were clustered near the origin of axis 1, about two-fifths of the way up axis 2. The reciprocal averaging procedure generated fatty acid ordinations which exhibited maximum correspondence to the sample ordinations (Fig. IV.4). Fatty acids 22:2, 24:0, 18:0 and unknown D were positioned near the end of axis 1, which corresponded to their relative abundances in the day 8 and day 15 communities exposed to 15 $\mu E \cdot m^{-2} \cdot s^{-1}$ (Fig. IV.3). The other fatty acids formed a cluster fanning out from the origin, which in general corresponded to the position of the majority of remaining samples. This suggested that the samples were characterized by a combination of these fatty acids.

Correlations between the biovolumes of the thirteen dominant taxa (Table IV.2) and fatty acids (Table AIV.1) were calculated to assess degrees of association. Correlation coefficients that were significantly different from zero at the 5% level (i.e. >0.404) are summarized as follows: Klebsormidium fluitans: 16:0 (.501), 18:0 (.671), 18:2 (.411), 18:3 (.720), 16:1 (-.438), 16:2 (-.486) and 20:5 (-.590); Stigeoclonium tenue: unknown C (.415);

Scenedesmus bijuga: 16:1 (.653), 22:0 (.512) and 18:1 (-.638); Scenedesmus obliquus: 22:0 (.513); Phormidium tenue: 16:1 (.441); Synedra rumpens v. familiaris: 16:1 (.568) and 22:0 (.532), and Fragilaria construens v. venter: 16:1 (.462).

The RA ordinations of the 20 assemblages and 12 amino acids are presented in Figs. IV.5 and IV.6, respectively. Histidine, methionine and tyrosine were eliminated from this analysis, as these acids were present in low concentrations, and preliminary ordinations indicated that they responded as outliers. In Fig. IV.5, assemblages exposed to 15 $\mu E \cdot m^{-2} \cdot s^{-1}$ were separated out on axis 1, which loosely corresponded to the placements of lysine, glycine, and serine in Fig. IV.6. The day 15 samples exposed to 400 $\mu E \cdot m^{-2} \cdot s^{-1}$ were placed at the far end of axis 2 (Fig. IV.5), which matched the position of arginine (Fig. IV.6). The majority of the other samples formed a loose cluster near the origin of axis 1, about three-fifths of the way up axis 2 (Fig. IV.5). This configuration corresponded to the positions of leucine, isoleucine, aspartic acid/asparagine, and alanine (Fig. IV.6), all of which were found in substantial amounts in those samples.

Covariances between species biovolumes and amino acids were examined by correlation analysis to determine whether or not certain taxa were associated with particular amino acids. Correlation coefficients that were significantly different from zero at the 5% level (i.e. >0.423) are summarized as follows: Klebsormidium fluitans: serine (.443); Stigeoclonium tenue: arginine (.433); Scenedesmus bijuga: methionine (.578), alanine

(.530), tyrosine (.447), glutamic acid/glutamine (-.509) and lysine (-.502); Scenedesmus obliquus: arginine (.562) and valine (-.515); Phormidium tenue: valine (.446) and threonine (.426); Synedra ulna: lysine (.451); Synedra rumpens v. familiaris: methionine (.565), tyrosine (.505), alanine (.465), arginine (.459), threonine (.430), and lysine (-.570); Fragilaria vaucheriae: threonine (.444) and tyrosine (.436); Fragilaria construens v. venter: aspartic acid/asparagine (.451) and lysine (-.543); and Achnanthes lanceolata: aspartic acid/asparagine (.429).

DISCUSSION

Community-level biochemical analyses provided information about chemical constituents, community structure and food quality of lotic algal assemblages that had not been previously generated by examination of monospecies assemblages. However, these analyses were subject to certain limitations, namely (1) the inability to determine whether changes in the chemical composition of the assemblages were specifically related to taxonomic composition, community age (i.e. successional and/or physiological state) or irradiance; and (2) the inability to unequivocally state that certain chemicals were found in specific taxa.

Phyletic patterns have been proposed for the distribution of fatty acids among freshwater algae. For example, green algae tend to be characterized by greater abundances of 16:0, 18:1 and 18:3 fatty acids (Klenk et al. 1963; Nichols 1968; Moore 1975b; Piorreck et al. 1984), while diatoms contain relatively large amounts of 16:1 and 20 carbon chain length unsaturated fatty acids (Kates and Volcani 1966; DeMort et al. 1972; Opute 1974a). However, these trends can vary depending on physiological state and lipid class from which the fatty acids were derived (see Moore 1975b; Shifrin and Chisholm 1980). Because fatty acids were derived from total crude lipid in this study, certain patterns may have been masked. Nevertheless, *Klebsormidium fluitans* was positively correlated with some fatty acids characteristic of chlorophytes (e.g. 16:0 and 18:3), and both *Scenedesmus* spp. were positively correlated with

22:0. Synedra rumpens v. familiaris and Fragilaria construens v. venter were both positively correlated with 16:1, a characteristic fatty acid in diatoms, but no positive correlations were found between any diatom and 20:5. Therefore, the data indicated that taxonomic structure had some, but not exclusive, influence on fatty acid composition.

Age and physiological state of an algal assemblage can have an effect on fatty acid composition through the senescence of old cells (Pugh 1971) and the succession of new taxa (Morris 1984). For example, at day 8 the fatty acid 20:5, which is characteristic of diatoms (Kates & Volcani 1966; Ackman et al. 1968), was present in greater amounts in streams exposed to high PFD (Fig. IV.1). This could be attributed, at least in part, to a relatively high biomass of Synedra ulna. By day 32, an increase in the relative abundance of Achnanthes lanceolata in streams exposed to low PFD, coupled with a corresponding decrease in S. ulna, resulted in similar percentages of 20:5 in all streams.

The influence of senescence on fatty acid composition was particularly obvious in the diatoms, where deterioration of plastids was frequently observed. Pugh (1971), while working with a marine diatom in culture, found that the 16 carbon fatty acids increased in concentration with cell age, while the 18 carbon acids exhibited a concurrent decrease. In general, this pattern was consistent with our observations for the 16:0, 16:1, 18:0, and 18:1 fatty acids in the laboratory streams (Appendix IV.1). Ackman et al. (1964), in a study with another marine diatom, found increases

in 14:0 and decreases in 20:5 fatty acids over a 10-day growth period, but insignificant changes in the 16 or 18 carbon chain length groups.

The influence of environmental factors on lipids in algae is well documented (Moore 1975b; Shifrin and Chisholm 1980,1981; Harwood and Russell 1984). Nutrient levels and temperature are often cited as the most influential environmental factors, but the dynamics of these variables were kept the same in the 12 laboratory streams. In natural lotic systems, light is often considered the critical variable influencing algal abundance and taxonomic structure (McIntire 1968; Gregory 1980; Sheath and Burkholder 1985; Steinman and McIntire 1986). Opute (1974a) and Orcutt & Patterson (1974) found that diatoms grown at low light levels increased their proportion of unsaturated fatty acids. This pattern was not apparent in the laboratory stream assemblages, but taxonomic changes associated with light levels (Steinman and McIntire 1986) may have obscured photon flux density-induced changes within individuals. Even with individual taxa, it can be difficult to discriminate between the influences of environmental factors and genotypic variation (Moore 1975b). The results from this study provided indirect evidence that irradiance can influence fatty acid concentrations. At day 8, the percentages of 14:0, 16:2, and 20:5 all increased substantially at PFD of 50 $\mu E \cdot m^{-2} \cdot s^{-1}$ or greater. Conversely, the percentages of 16:0 and 18:0 decreased dramatically at PFD of 50 $\mu E \cdot m^{-2} \cdot s^{-1}$. Since the algal assemblages in all streams

were dominated by fairly uniform (and very high) relative abundances of *Synedra ulna*, it is doubtful that taxonomic composition could account for these different distribution patterns. Indeed, these trends were still evident on day 15, when all the assemblages were still dominated by *S. ulna*. By day 31, however, *S. ulna* was no longer the dominant taxon in the assemblages, and this irradiance-associated pattern was no longer evident.

The relatively high concentrations of total crude lipid (per unit biomass) in the communities exposed to 15 and 50 $\mu E \cdot m^{-2} \cdot s^{-1}$ at the end of the experiment can be attributed to the effects of either taxonomic composition or light level. These communities were dominated by diatoms, which tend to be rich in lipids (Opute 1974b). In addition, Sargent et al. (1985) found lipid formation in phytoplankton to be negatively correlated with light level, although other work (Morris and Skea 1978) indicated that carbon assimilation patterns were affected by cellular nutrient concentration, a variable not measured in this study.

The abundance of serine, glycine, alanine, glutamic acid/glutamine, and aspartic acid/asparagine in the laboratory stream assemblages did not correspond with the work of Fowden (1954). In the latter study, analyses of four species of freshwater algae, namely *Chlorella vulgaris*, *Anabaena cylindrica*, *Navicula pelliculosa* and *Tribonema aequale*, revealed that the most abundant amino acids (in order) were arginine, lysine, alanine, valine, leucine, and aspartic acid/asparagine. In contrast, only five of

the ten positive correlations between diatom taxa and amino acids in the laboratory stream assemblages corresponded to the abundant acids in the study by Fowden, and only four matched the dominant amino acids in certain marine diatoms (Cheucas & Riley 1969). Indeed, aspartic acid/asparagine and threonine were the only amino acids positively correlated with more than one diatom taxon in the laboratory stream assemblages. Lysine, a dominant acid in the freshwater diatom Navicula pelliculosa (Fowden 1954), was negatively correlated with two diatoms and positively correlated with Synedra ulna. There appears to be more consistency in amino acid dominance among green algae than diatoms, as evidenced by the similar concentrations in Chlorella (Fowden 1954) and four marine macroalgae (Munda and Gubensek 1976). However, of the six positive correlations between green algae and amino acids in our study, only one relationship corresponded to an abundant amino acid in the marine algae while three matched the prominent amino acids in Chlorella. Ironically, all three negative correlations with green algae involved amino acids which were dominant in either the marine chlorophytes or Chlorella. The positive correlation between the cyanophyte Phormidium tenue and threonine was consistent with the high amounts of that amino acid found in Anabaena cylindrica (Fowden 1954).

In general, there was little association between amino acid distributions and taxonomic structure. Two possible hypotheses that may explain this lack of correspondence are: (1) the diversity of

algae in any one community may obscure the paucity (or dominance) of a particular amino acid in one taxon; and (2) a uniformity of protein composition in algae (Fowden 1954). Although more work is needed to examine hypothesis (2), if true, one would not expect definitive associations between taxonomic and amino acid composition.

The effects of age and irradiance on amino acid composition in freshwater algae have not been well studied. Fowden (1952) found that the amino acids of Chlorella remained virtually unchanged over a 35-day period in culture. The largest changes he noted were a 1.5x increase in histidine and a one-fifth decrease in arginine levels. In the laboratory stream assemblages, histidine (and lysine) decreased in the communities over time, while arginine exhibited no consistent pattern. Whether these shifts reflected physiological changes associated with senescence or changes in taxonomic composition are unknown. Irradiance appeared to have no consistent influence on amino acid composition over the 31-day experimental period.

The relatively high amount of protein measured in the communities exposed to 50 $\mu E \cdot m^{-2} \cdot s^{-1}$ apparently was not related to taxonomic differences, as there were no consistent associations between high protein level and species composition. Studies of planktonic algae indicated that the proportion of ^{14}C-bicarbonate incorporated into the protein fraction increased with reduced irradiances (Morris et al. 1974; Morris and Skea 1978). In addition, Osborne and Raven (1986) found cell protein increased in

Scenedesmus obliquus with a decrease in light levels. Although increased synthesis of pigment protein complexes with a decrease in irradiance may account for higher amounts of cellular protein, it is unclear why the levels were not greater in the communities exposed to 15 $\mu E \cdot m^{-2} \cdot s^{-1}$.

The very high C:N ratios in the communities exposed to the lowest PFD may have been related to large amounts of mucilage or organic film on the substrate relative to biomass (Winterbourne et al. 1984). However, these products were not obvious when the tiles were viewed with scanning electron microscopy (Steinman and McIntire unpubl. data). In addition, on day 31 the C:N ratio was still >30:1 when the biomass of the living cells was relatively high. Despite their high C:N ratios, the protein content of the communities exposed to the lowest PFD was similar to that in the communities grown at higher light levels, an observation inconsistent with the suggestion that Aufwuchs with C:N ratios greater than 17:1 are protein-deficient (McMahon et al. 1974). In fact, there was surprisingly little association between C:N ratio and protein level in these communities, indicating that the concentration of total nitrogen can be a poor index of protein. If the nitrogen being measured is of a nonprotein nature, C:N ratios can actually be misleading indicators of food quality. Other researchers have also questioned the utility of C:N ratios as indicators of food quality (Harrison and Mann 1975; Horn and Neighbors 1984).

Biochemical expression of community structure in benthic ecology is a relatively unexplored area of research. The chemical composition of a benthic algal assemblage, and hence its nutritional quality, can provide important information when trophic level interactions are under consideration (Boyd and Goodyear 1971). In lotic systems, many herbivores are generalists (Gregory 1983), and therefore rarely feed in a selective manner on particular taxonomic units. Consequently, their gut contents reflect both relative abundance of food (Mecom 1972) and what their mouthpart morphologies are able to graze (Gregory 1983). Therefore, an understanding of plant-herbivore interactions may require an analysis of the chemical structure of the algal assemblage. Indeed, the fatty and amino acid ordinations revealed that some algal assemblages could be distinguished based on their chemical composition, although the differences were not large. Possibly, the importance of chemical composition (in terms of nutritional quality) will vary depending on local conditions. For example, in food-limited situations, the nutritional quality of the algae may be very important, especially if the herbivore is at a point in its life history where its dietary needs are changing and the relative abundance of a chemical is critical (Hanson et al. 1983; Cargill et al. 1985). However, where food supply is not limiting, the chemical structure of the algae may be of little significance, and the herbivore may graze those assemblages which are physically closest or best match its mouthpart morphology.

In summary, taxonomic structure, community age, and irradiance

had relatively little effect on the gross distribution of fatty and amino acids. Although protein and crude lipid levels were variable, their concentrations were consistently high. This supports the conclusion of Anderson and Cummins (1979) that lotic algal assemblages represent food sources of high nutritional quality. Indeed, the taxonomic diversity of these assemblages may enhance their nutritive quality by resulting in a more balanced diet. Future studies need to address how these chemical constituents relate to food quality, especially with respect to herbivore life history (Cargill et al. 1985), nutrient balance (Dadd 1973) and both herbivore and algal density.

ACKNOWLEDGEMENTS

We are very grateful to Linda Ashkenas and Randy Wildman for their technical assistance, Austin Cargill II and Robert Becker for their help with lipid and protein analyses, respectively, and Stan Gregory and Gary Lamberti for their advice on the experiment's design and comments on the manuscript. This study was supported by research grant No. BSR-8318386 from the National Science Foundation and by a Sigma Xi Grant-In-Aid.

Table IV.1 Quantities of combined amino acids in laboratory stream algal assemblages on days 8, 15, and 31, exposed to photon flux densities of 15, 50, 150, and 400 $\mu E \cdot m^{-2} \cdot s^{-1}$. Amino acid data are expressed as percentage of total residues. Quantities are the mean of two replications, unless otherwise noted. T denotes a trace amount (less than 0.10%).

Amino Acid	Day 8				Day 15				Day 31			
	15	50[a]	150	400[a]	15[a]	50	150[a]	400	15	50	150	400
Asp	8.42	9.86	11.61	10.70	11.18	13.06	13.08	13.56	13.44	13.50	12.71	12.39
Thr	3.81	5.07	5.63	5.95	6.95	6.38	6.24	6.26	6.30	6.59	6.68	6.47
Ser	12.44	8.30	8.08	7.31	12.26	8.06	7.11	7.37	8.92	8.34	7.62	7.42
Glu	14.03	13.90	14.05	13.76	17.60	13.69	14.13	14.69	14.18	13.53	12.74	13.00
Gly	17.09	11.17	10.71	10.41	10.94	10.42	9.86	10.70	13.06	10.99	11.46	10.99
Ala	9.80	10.14	9.54	9.86	8.43	9.45	10.02	9.89	9.45	10.44	10.97	10.52
Val	6.51	6.75	6.75	7.52	7.87	5.89	7.48	5.08	7.27	8.16	5.71	6.42
Met	0.24	0.12	T	1.57	T	0.15	0.92	0.28	T	0.32	1.48	1.75
Ile	3.67	4.79	5.34	5.44	5.06	5.33	4.93	5.04	4.69	4.87	5.26	5.09
Lue	6.26	8.77	9.22	9.14	8.07	8.50	8.21	8.53	7.45	8.90	9.45	8.73
Tyr	0.22	1.01	0.15	1.32	T	2.32	2.19	2.54	T	1.65	2.03	2.30
Phe	4.00	3.30	3.10	3.97	3.90	4.24	3.93	3.72	4.80	3.60	3.57	3.89
His	4.92	7.22	6.91	4.06	1.81	3.30	2.90	2.76	3.32	2.70	3.08	2.50
Lys	5.03	3.98	4.13	3.94	3.14	4.19	3.33	4.26	3.26	2.87	2.08	2.84
Arg	3.61	5.63	5.02	5.05	2.78	5.05	5.68	6.37	3.88	4.80	5.21	5.73

[a]Amino acid values for these treatments are based on only one replication due to the accidental destruction of samples.

Table IV.2 Relative abundance of dominant taxa in laboratory stream algal assembleges on days 8, 15, and 31, exposed to photon flux densities of 15, 50, 150, and 400 $\mu E \cdot m^{-2} \cdot s^{-1}$. Data are expressed as percentage of total community biovolume, and are the mean of two replications.

Taxon	Day 8				Day 15				Day 31			
	15	50	150	400	15	50	150	400	15	50	150	400
Chlorophyta												
Ulothrix zonata	--	--	--	--	--	--	--	4.98	--	--	--	9.06
U. tenerrima	1.03	--	--	--	0.10	--	--	--	--	--	2.64	--
Klebsormidium fluitans	9.11	0.86	5.05	0.12	22.05	1.08	8.97	0.03	2.16	0.39	14.69	0.15
Stigeoclonium tenue	2.27	6.71	1.80	2.11	0.05	0.30	5.04	8.11	0.16	0.13	0.02	0.09
Scenedesmus bijuga	0.11	0.10	0.23	0.05	0.03	0.11	0.24	0.32	--	0.47	1.15	0.76
S. obliquus	0.33	0.37	0.19	--	0.02	0.02	0.08	1.01	--	0.25	0.47	0.77
Cyanophyta												
Phormidium tenue	0.02	--	--	--	0.17	--	0.10	--	0.53	0.83	0.48	0.30
Bacillariophyta												
Synedra ulna	70.06	78.15	79.38	88.95	47.82	52.84	56.35	63.22	19.01	27.09	35.08	38.13
S. rumpens v. familiaris	1.84	2.04	2.50	1.33	3.10	6.33	6.90	5.96	3.66	6.54	11.12	15.79
Fragilaria vaucheriae	1.13	1.18	1.59	1.20	1.41	2.82	2.02	2.15	1.68	2.47	2.55	4.17
F. construens v. venter	3.02	3.85	2.26	1.21	7.34	7.84	5.32	3.84	11.89	12.20	11.04	5.72
Nitzschia oregona	1.67	1.14	1.48	1.14	3.39	2.29	1.79	2.11	2.51	4.04	2.81	4.11
Achnanthes lanceolata	7.82	3.47	3.11	2.25	11.03	25.25	8.65	6.92	54.72	42.57	9.54	13.21

Figure IV.1 Dominant fatty acids of algal assemblages (expressed as percentage of total in each sample) in laboratory streams on days 8, 15, and 31 in algal assemblages exposed to photon flux densities of 15, 50, 150, and 400 $\mu E \cdot m^{-2} \cdot s^{-1}$.

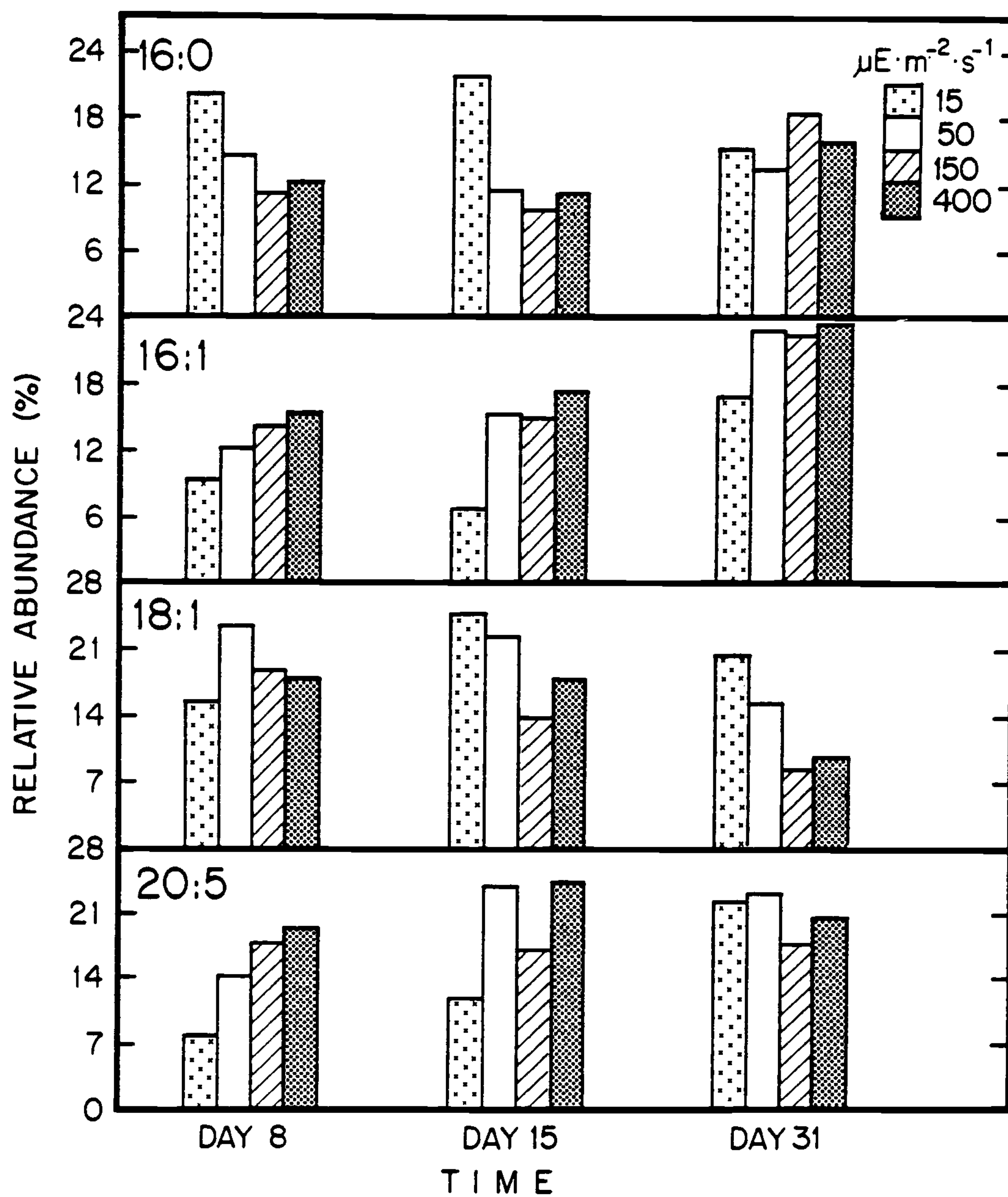

Figure IV.1

Figure IV.2 Concentrations of total crude lipid and combined protein, and C:N ratios on days 8, 15, and 31 in algal assemblages in laboratory streams exposed to photon flux densities of 15, 50, 150, and 400 $\mu E \cdot m^{-2} \cdot s^{-1}$.

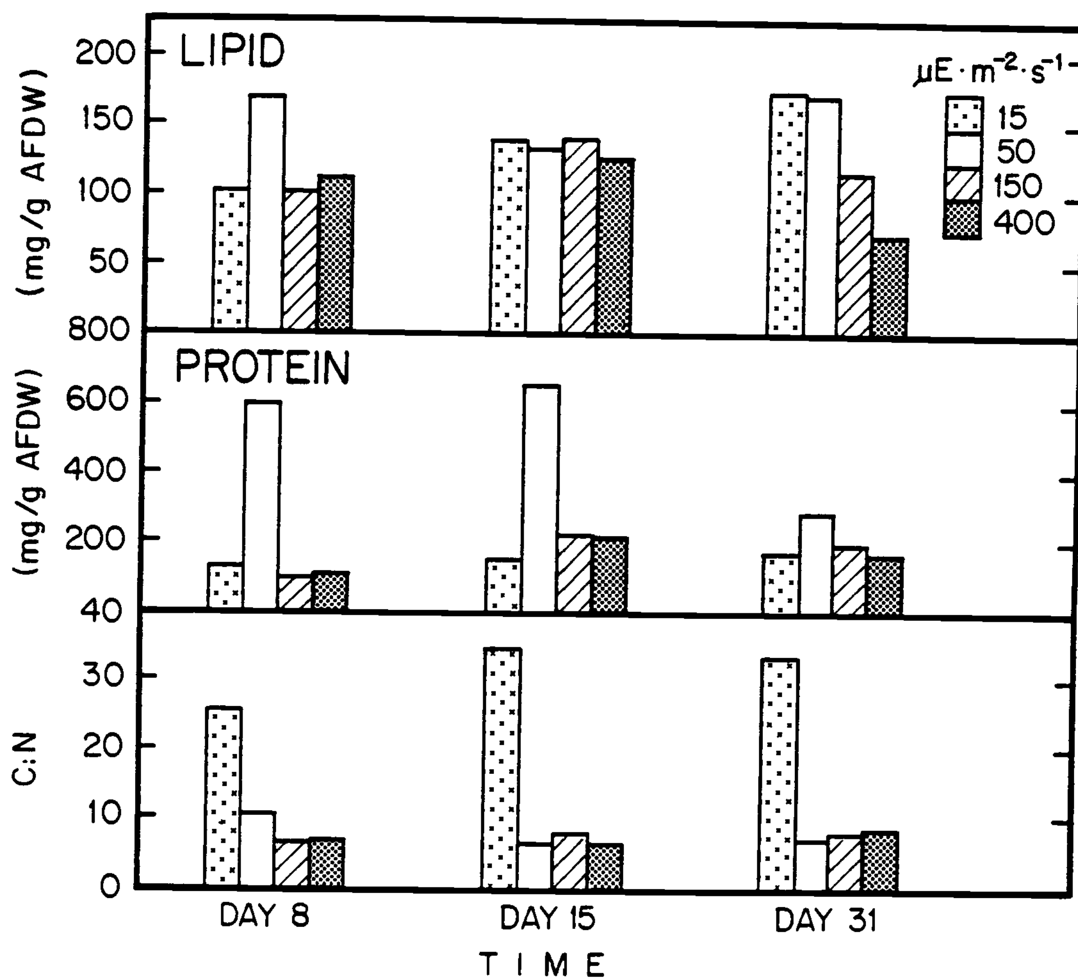

Figure IV.2

Figure IV.3 Reciprocal averaging ordination of 24 samples of algal assemblages (4 treatments x 3 dates x 2 replications). The light treatments are 15 $\mu E \cdot m^{-2} \cdot s^{-1}$ (open square), 50 $\mu E \cdot m^{-2} \cdot s^{-1}$ (open circle), 150 $\mu E \cdot m^{-2} \cdot s^{-1}$ (solid circle), and 400 $\mu E \cdot m^{-2} \cdot s^{-1}$ (star). Numbers adjacent to symbols indicate age of samples (in days). Replications are not distinguished.

Figure IV.3

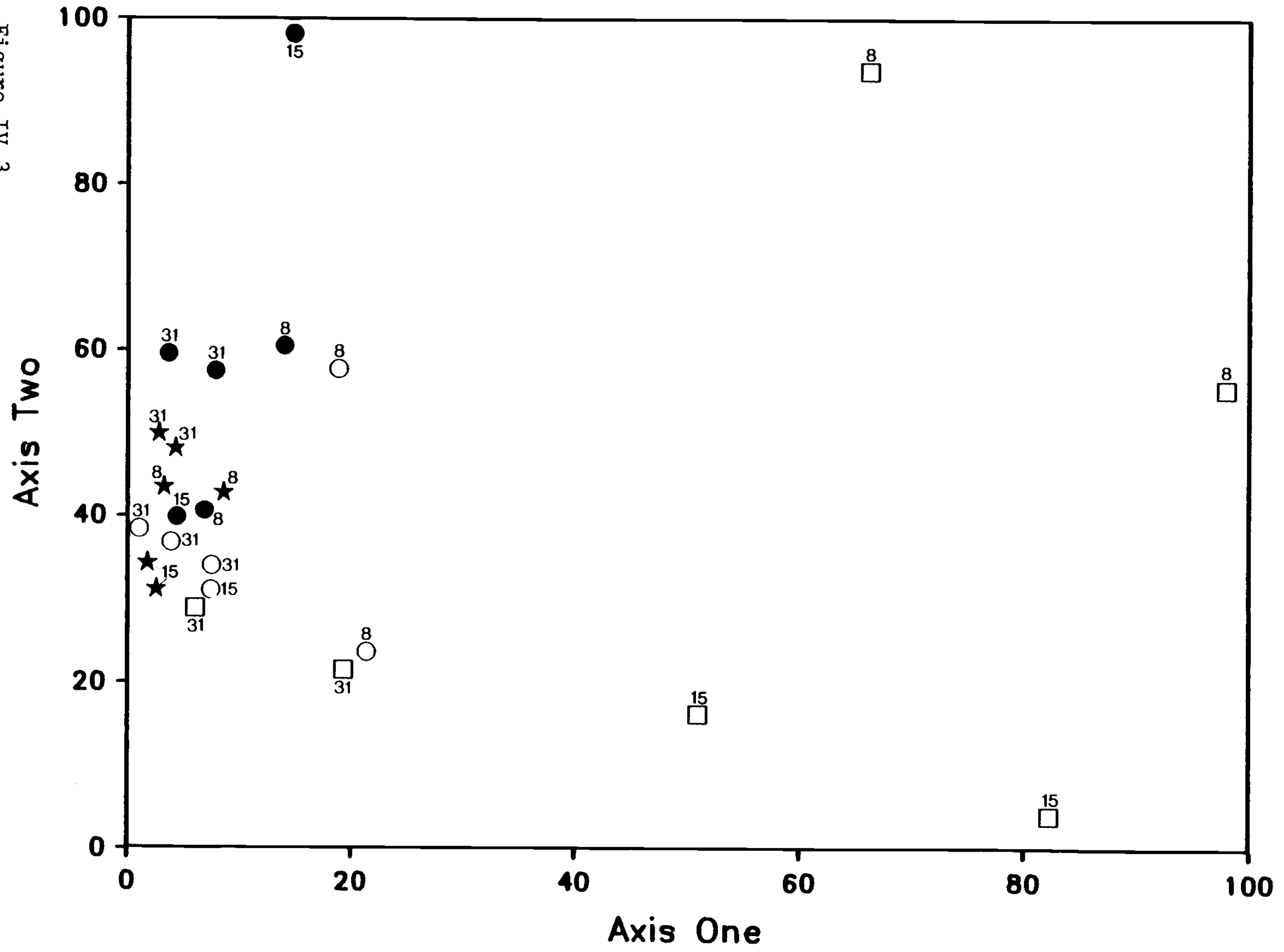

Figure IV.4 Reciprocal averaging ordination of 20 fatty acids measured in the experimental algal assemblages.

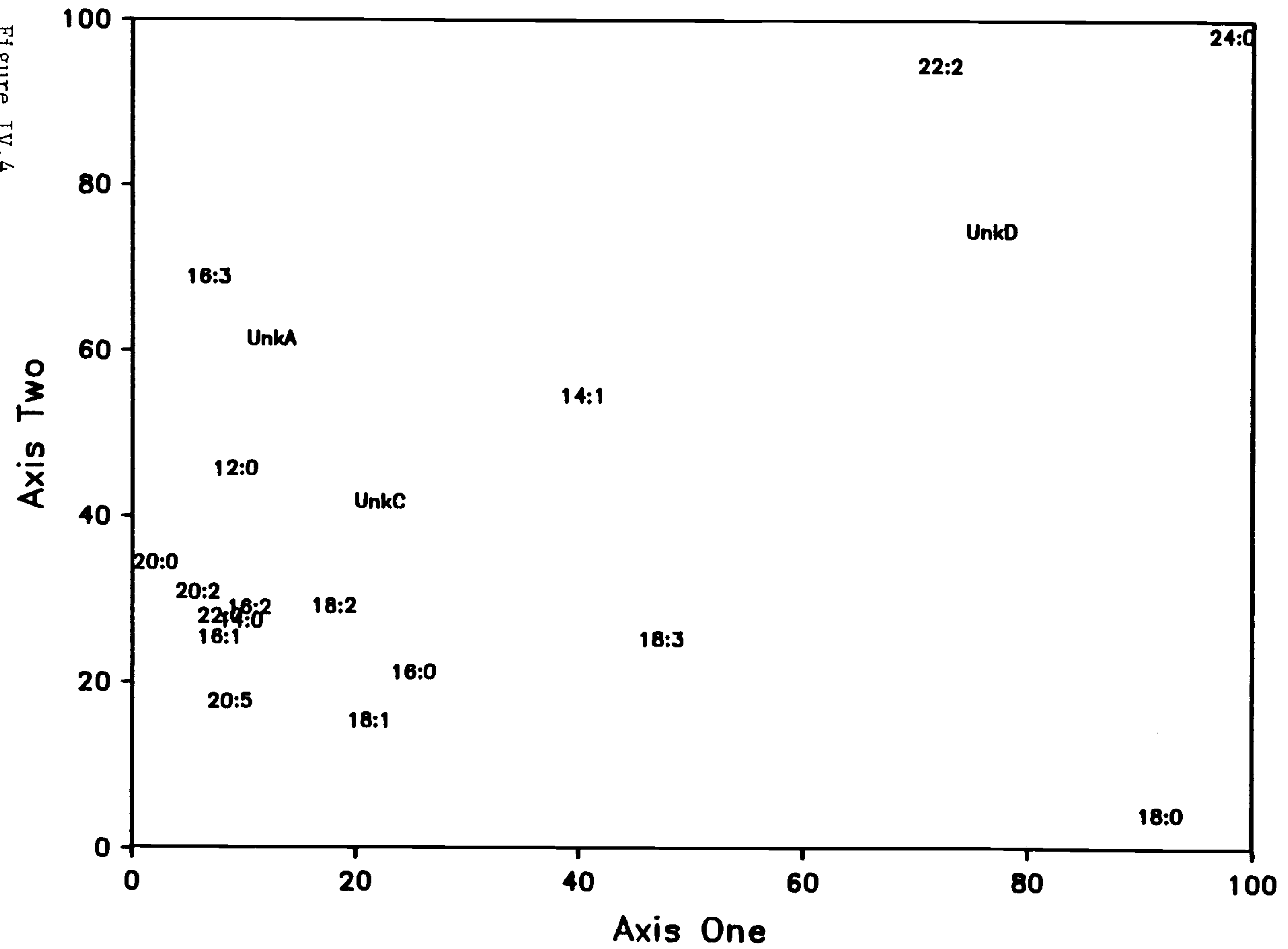

Figure IV.4

Figure IV.5 Reciprocal averaging ordination of 20 samples of algal assemblages. All symbols, numbers, and conventions as in Fig. 3.

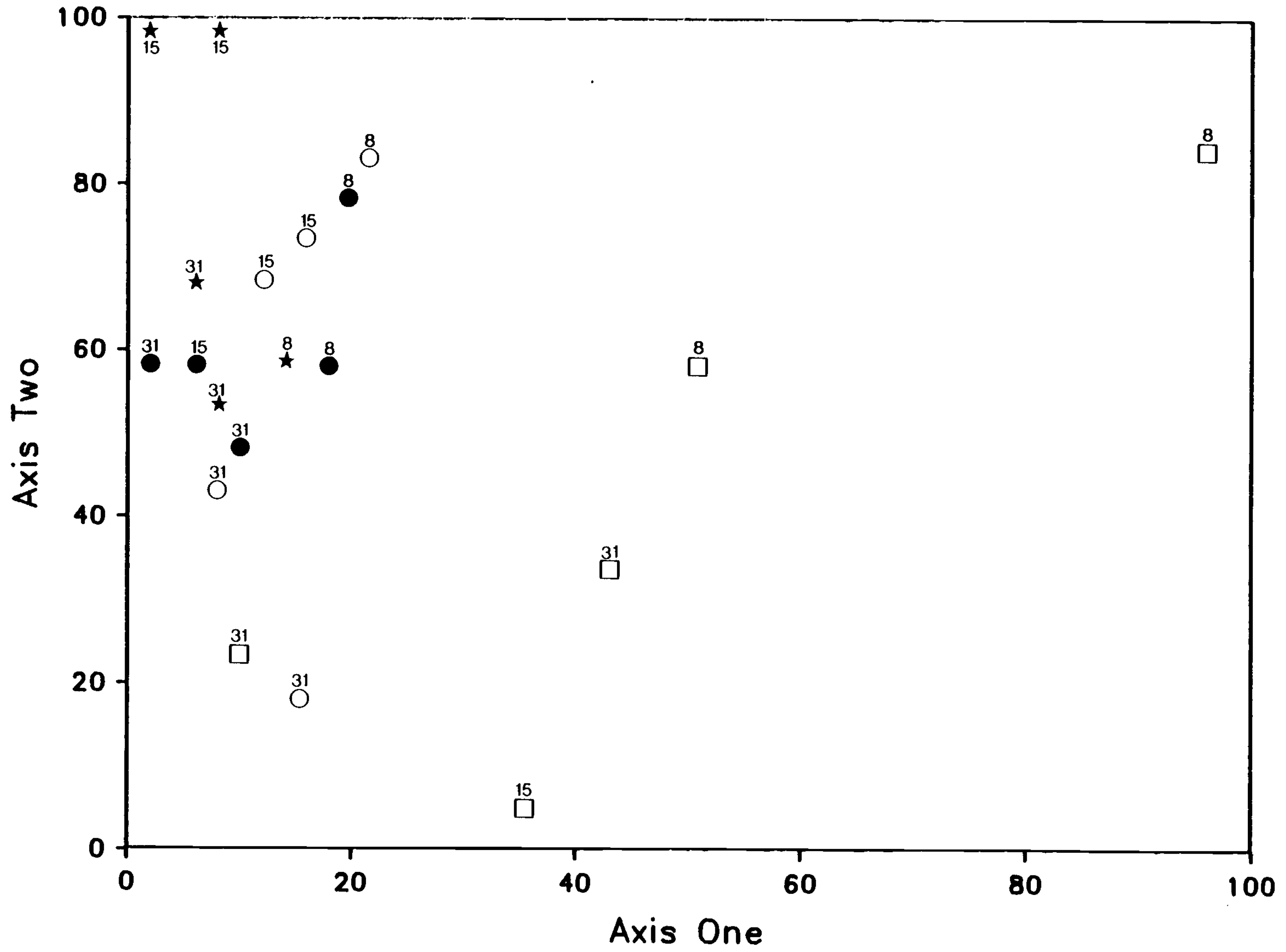

Figure IV.5

Figure IV.6 Reciprocal averaging ordination of 12 amino acids (3 amino acids omitted, see text for explanation) measured in the experimental algal assemblages.

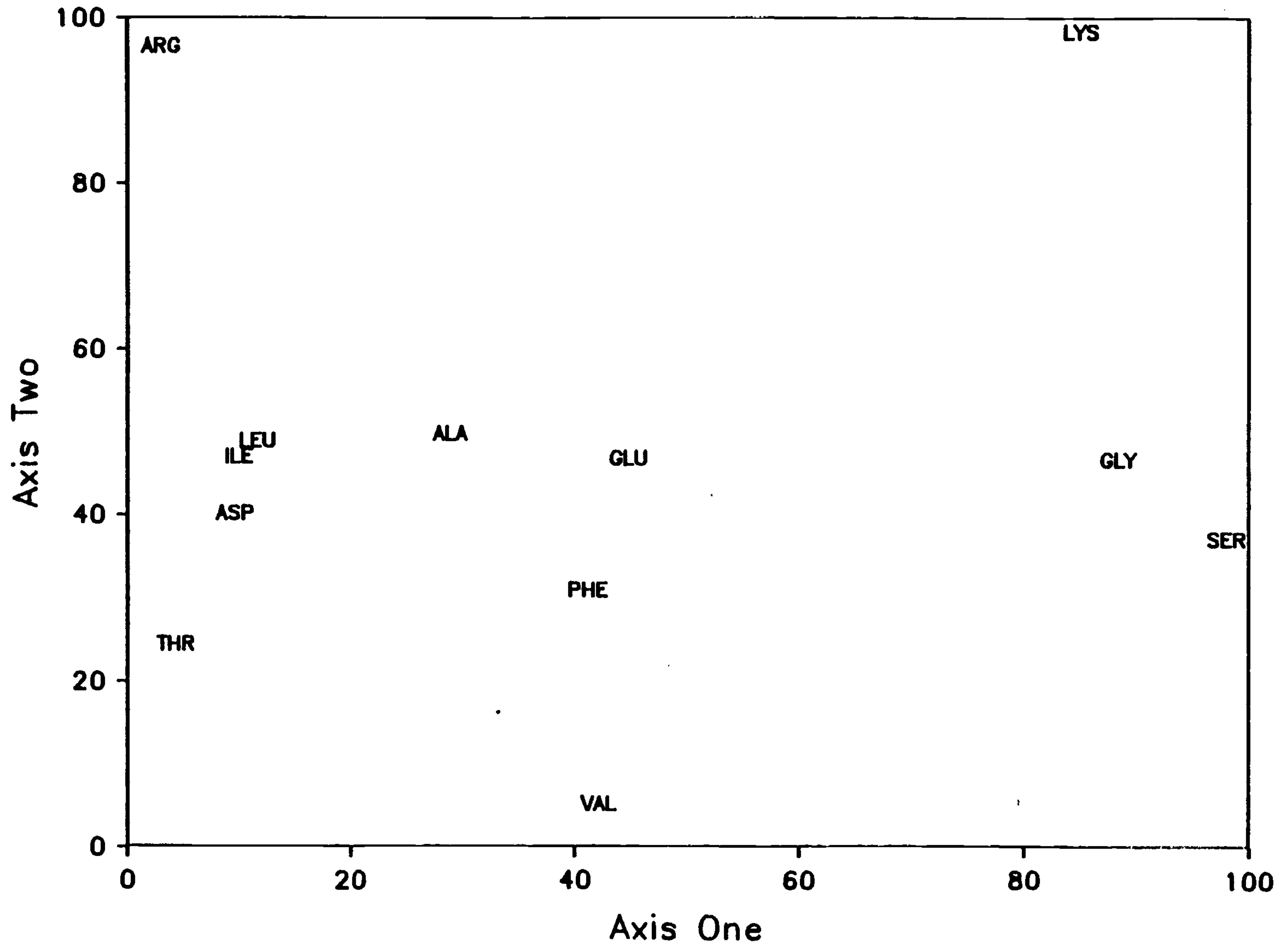

Figure IV.6

V. DENSITY-RELATED EFFECTS OF GRAZING BY A SNAIL AND A CADDISFLY ON ALGAL ASSEMBLAGES IN LABORATORY STREAMS. I. TAXONOMIC STRUCTURE AND PHYSIOGNOMY

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ABSTRACT

Four densities of a snail (*Juga silicula*) and a caddisfly (*Dicosmoecus gilvipes*) were introduced into separate laboratory streams, and their effects on algal biomass and community structure were monitored for 32 days. Tiles in an ungrazed control stream were covered by thick algal mats by day 32, and were composed primarily of *Scenedesmus* spp., *Characium*, and a variety of diatoms. Biomass and community structure of algal assemblages in the stream with the lowest density of snails were very similar to that in the control stream. In the other streams with snails, an inverse relationship developed between algal biomass and snail density after day 16. By day 32, the algal assemblage in the streams with high snail densities was dominated by adnate diatoms (*Achnanthes* spp.), and basal cells and short filaments of *Stigeoclonium tenue*. In contrast to the streams with snails, algal biomass was relatively low in all streams with caddisflies. The differences in algal biomass and structure between the streams with the lowest and highest densities of caddisflies were much smaller than those between streams with the lowest and highest densities of snails. On day 32, the taxonomic and physiognomic structure of the algal assemblages in all the streams with caddisflies resembled that in the streams with higher densities of snails. Scanning electron micrographs showed that even at the highest densities, neither snails nor caddisflies could completely remove the algal assemblage. It is concluded that algal growth form and assemblage

physiognomy can substantially influence plant-herbivore interactions in lotic ecosystems.

INTRODUCTION

Past research has shown that grazing by aquatic invertebrates in lotic ecosystems may (1) reduce the biomass of benthic algal assemblages (Bohle 1978, Eichenberger and Schlatter 1978, Gregory 1980, Sumner and McIntire 1982, Lamberti and Resh 1983, McAuliffe 1984a, Murphy 1984, Jacoby 1985); (2) stimulate primary production (Gregory 1980, Lamberti et al. 1987); (3) influence the taxonomic structure of algal assemblages (Eichenberger and Schlatter 1978, Sumner and McIntire 1982, Hart 1985, Jacoby 1985); and (4) affect nutrient recycling (Mulholland et al. 1983). However, other studies have indicated that such effects of plant-animal interactions are not always predictable, because algal assemblages are characterized by different taxonomic compositions, physiognomic properties, and chemical constituents, while herbivores have differential consumptive abilities, mouthpart morphologies, modes of feeding, and behavioral adaptations (see Gregory 1983, Lamberti and Moore 1984). The present study examines some of the mechanisms associated with the process of herbivory under controlled conditions in laboratory streams. Specifically, the objectives were: (1) to investigate the effects of grazer density on the taxonomic structure, physiognomy, and biomass of algal assemblages; and (2) to examine the effects of two types of feeding behavior (i.e., rasping and scraping) on algal community structure.

MATERIALS AND METHODS

The design of the laboratory streams was described in detail by Steinman and McIntire (1986). In brief, each stream was a 3 m x 0.6 m recirculating fiberglass channel with current provided by a motor-driven paddlewheel. Water temperature remained at 14 ± 1°C throughout the experimental period. The exchange rate and nutrient concentration of the wellwater supply was similar to that reported by Steinman and McIntire (1986). Light energy was supplied by 16 1000-Watt Metalarc lamps (Sylvania Corp.), adjusted to provide a relatively uniform photon flux density of approximately 400 $\mu E \cdot m^{-2} \cdot s^{-1}$ to all experimental streams. Timers were set to produce a daily photoperiod of 12 L: 12 D. Current velocity in all streams was maintained at 10 $cm \cdot s^{-1}$. The bottom of each stream was lined with 7.5 x 7.5 cm unglazed, ceramic tiles, which provided a surface for colonization and units for periodic sampling. One of every six tiles had an upturned end to provide heterogeneity on the stream bottom. Smaller tiles (1.2 x 1.2 cm) were spaced among the larger tiles, and served as sampling units for the investigation of assemblage physiognomy by scanning electron microscopy (SEM).

At the start of the experiment, 13 laboratory streams were inoculated with one liter of an algal suspension obtained by scraping rocks from four local streams (Steinman and McIntire 1986). Animals were collected from local streams (see Lamberti et al. 1987 for details on animals) and introduced on day 5 of the experiment. The snail <u>Juga silicula</u> (a rasper) was introduced

into four streams, each at a different density: (1) 125 snails/stream (tissue dry weight: ca. 2.5 g total); (2) 250 snails/stream (ca. 5 g); (3) 500 snails/stream (ca. 10 g); and (4) 1000 snails/stream (ca. 20 g). The caddisfly *Dicosmoecus gilvipes* (a scraper) was introduced into four other streams, each also at a different density, but at a biomass approximately equivalent to that of the snails: (1) 50 caddis/stream (tissue dry weight: ca. 3 g total); (2) 100 caddis/stream (ca. 6 g); (3) 200 caddis/stream (ca. 12 g); and (4) 400 caddis/stream (ca. 24 g). Another stream was not stocked with animals and served as an ungrazed control system. The remaining four streams were used as sources of replacement tiles (see below). The experiment lasted 32 days.

For estimates of biomass accumulation, three 7.5 x 7.5 cm tiles were randomly sampled from each of the nine experimental streams on days 8, 16, 24 and 32. Biomass was determined by the method of McIntire and Phinney (1965).

For the quantitative analysis of species composition, two 7.5 x 7.5 cm tiles were randomly selected from each experimental stream on days 4, 8, 16, and 32. Procedures for collection, fixation, microscopic examination, and counting were outlined by Steinman and McIntire (1986). For the examination of physiognomic characteristics, two 1.2 x 1.2 cm tiles were removed from each experimental stream on days 8, 16 and 32. Procedures for preparation and examination of samples by SEM were described by Steinman and McIntire (1986).

Streams that were used as sources of replacement tiles were

stocked with various densities of snails and caddisflies in order to establish a gradient of taxonomic and physiognomic structures among the algal assemblages. After a tile was removed from an experimental stream, a tile with similar biomass and community structure was selected as a replacement, thereby maintaining similar food density and type within an experimental stream.

The experiment was designed to provide a broad range of animal densities, and therefore, the separate streams represented nine different treatments without replication. Consequently, the numerical information from the experiment was treated as observational data. Species composition of the algal assemblages were compared using the SIMI measure of similarity (McIntire and Moore 1977). This measure ranges from 0 to 1, and gives greater weight to dominant taxa. A value of 0 denotes that a given pair of assemblages have no taxa in common, while a value of 1 indicates that the two assemblages have identical species compositions and proportional abundances. SIMI values were based on biovolumes, and analyses were performed with a Cyber 170/720 computer.

RESULTS

Streams with Juga: Algal biomass accumulation varied with snail density over the 32-day experimental period (Fig. V.1). There was little difference in biomass between the stream with no snails and that with the lowest density (125 snails). The other three streams showed little biomass accumulation through day 16, after which snail density was negatively associated with algal biomass.

Grazing by *Juga* affected the relative abundance of several taxa in the Chlorophyta (Fig. V.2). In general, the relative abundance of the filamentous alga, *Stigeoclonium tenue*, was low in each stream through day 16. On day 32, this taxon comprised almost 25% of the total algal biovolume in the stream with 1000 snails, although its growth form consisted primarily of prostrate basal cells and short filaments. The unicellular *Characium* was abundant before the introduction of snails (Fig. V.2). Although the relative abundance of *Characium* decreased during the experiment in each stream, the decline was greater in the streams with 250, 500 and 1000 snails than in the channels with 0 and 125 snails. Coenobic *Scenedesmus* spp. (*S. obliquus*, *S. bijuga*, *S. bijuga* v. *major*, *S.quadricauda*, and *S. incrassatulus*) were abundant on days 4, 8, and 16 in the control stream and in most channels with *Juga*. On day 32, these taxa were dominant in the streams with 0 and 125 snails, but exhibited very low relative abundances in the streams with $>$ 125 snails.

The filamentous cyanophyte *Phormidium uncinatum* comprised

between 10 and 20% of the algal biovolume in the streams on day 4 (Fig. V.3). By day 32, however, the relative abundance of this taxon was less than 5% in all streams. The relative abundance of the diatom Synedra ulna increased between days 4 and 16 in the control and 125-snail streams, but decreased by day 32 (Fig. V.3). Its contribution to assemblage biovolume remained relatively low in the other streams on days 8, 16 and 32. Although the adnate diatom Achnanthes lanceolata was initially a minor component of the algal assemblage, its relative abundance increased rapidly in the streams with 250, 500 and 1000 snails after the animals were introduced (Fig. V.3).

SIMI values for streams with Juga indicated that patterns of algal succession were similar in the control and 125-snail streams (Table V.1). Change in taxonomic structure was relatively small in both of these streams between days 4 and 16, and somewhat greater between days 16 and 32. The stream stocked with 250 snails had a distinct change in species composition between days 4 and 8, after which the taxonomic structure remained relatively constant. In the streams with 500 and 1000 snails, there was a moderate change in structure between days 4 and 8 (somewhat greater in the stream with 1000 snails), a small change between days 8 and 16, and a large transition between days 16 and 32. On day 32, the taxonomic structures in streams with 0 and 125 snails were very similar (SIMI = 0.958), but dissimilar to the streams with 250, 500 and 1000 snails (SIMI < 0.3).

Streams with Dicosmoecus: Caddisflies greatly reduced algal

biomass at all stocking densities (Fig. V.4). On days 24 and 32 there was a negative relationship between caddisfly density and algal biomass.

Stigeoclonium tenue was a minor component of the algal assemblages through day 16 (Fig. V.5). However, by day 32, its relative abundance had increased in the control stream, as well as in the streams with 200 and 400 caddisflies. In the latter two streams, its growth form was primarily basal cells and very short filaments (see Fig. V.26). Characium accounted for more than 25% of assemblage biovolume in all streams through day 8, after which its relative abundance declined. Scenedesmus spp. increased in percentage biovolume in all streams between days 4 and 8, after which their relative abundance declined in all streams with caddisflies, but continued to increase in the control stream.

Phormidium uncinatum comprised between 10 and 20% of the assemblage biovolume in streams with caddisflies on day 4, but its relative abundance decreased sharply after that date (Fig. V.6). By day 32, it was observed only in the control stream. Through day 16, the relative abundance of Synedra ulna fluctuated in all streams, but by day 32 it was less than 10% of the total biovolume in each stream. The relative abundance of Achnanthes lanceolata increased rapidly after day 8, and by day 16 it comprised ca. 60% and 80% of the assemblage biovolume in the 200 and 400-caddisfly streams, respectively. Although these percentages declined by day 32, the relative abundance of this taxon remained much greater in streams

with caddisflies than in the control stream.

SIMI values for streams with *Dicosmoecus* indicated that the streams stocked with 50 and 100 caddisflies exhibited gradual changes in taxonomic structure throughout the experiment (Table V.2). The streams with 200 and 400 caddisflies had a small change in structure between days 4 and 8, followed by a large transition between days 8 and 16. The assemblage in the 200-caddisfly stream exhibited a gradual change through day 32, but that in the 400-caddisfly stream showed little change between days 16 and 32. On day 32, algal taxonomic structure in the caddisfly streams exhibited two distinct patterns. Grazing at densities of 50 and 100 caddisflies resulted in a taxonomic structure similar to each other (SIMI = .949) and relatively dissimilar to that in the control stream (SIMI < .5). Grazing at densities of 200 and 400 caddisflies also resulted in assemblages structurally similar to each other (SIMI = .944), but very dissimilar to that observed in the control channel (SIMI < .2).

Physiognomic characteristics: On day 8, three days after the animals were introduced, SEM analysis revealed that the flora in the control stream was dominated by rosettes of *Synedra ulna* and aggregates of *Characium* (Figs. V.7 and V.8). A tile surface from the stream stocked with 250 snails appeared barren (Fig. V.9), but a few isolated diatoms (primarily *A. lanceolata*) could be detected at higher magnification (Fig. V.10). Similar patterns were observed on tiles from the streams with 1000 snails (Fig. V.11) and 400 caddisflies (Fig. V.12) on day 8, although the latter tile appeared

to have a denser diatom flora.

By day 16, a thick algal assemblage had developed on the tiles in the control stream (Fig. V.13). Again, Characium aggregates and S. ulna rosettes dominated the flora. In the stream exposed to 250 snails (Fig. V.15), a dense monolayer of adnate diatoms covered the tile surface. A close-up of this tile surface (Fig. V.16) revealed an assemblage of Achnanthes lanceolata, Cocconeis sp. (probably C. placentula v. euglypta), and Navicula minima. The diatom flora was much sparser, however, on tiles from the streams with 1000 snails (Figs. V.17 and V.18) and 400 caddisflies (Fig. V.14).

On day 32, a thick mat was still evident on the tiles of the control stream (Fig. V.19). Micrographs taken at higher magnification (Fig. V.20) indicated that this assemblage consisted of a mosaic of relatively discrete populations. For example, in Figure V.20A, a Scenedesmus-populated area (left side) is shown adjacent to a population of Achnanthes (right side). In a different region, approximately 750 µm from the location in Figure V.20A, the algal assemblage was dominated by a Nitzschia population (Fig. V.20B). By day 32, a dense algal mat had developed in the stream with 250 snails (Fig. V.21). This assemblage consisted of a network of filamentous algae with an understory of unicellular diatoms (Fig. V.22). At the end of the experiment, the tiles in the stream containing 1000 snails supported a dense monolayer of diatoms (Fig. V.23). Observations at higher magnification revealed that this assemblage was composed of mostly Cocconeis and Achnanthes species

(Fig. V.24). At low magnification, the tile surface from the stream stocked with 400 caddisflies appeared to support a sparse assemblage of diatoms (Fig. V.25), but higher magnification revealed a distinct layer of *Stigeoclonium* basal cells underneath the diatoms and mucilage (Fig. V.26).

DISCUSSION

Grazing activity by different densities of the snail Juga silicula and the caddisfly Dicosmoecus gilvipes had obvious effects on algal biomass, taxonomic composition and physiognomic properties in the laboratory streams. Other studies in aquatic systems have shown similar density-related effects by herbivores (Dickman 1968, Gregory 1980, Hunter and Russell-Hunter 1983, McAuliffe 1984a, Jacoby 1985). In this study, the lowest snail density of 125/stream (= 66/m^2) was apparently too low to markedly affect algal development. Thus, community structure changed at a rate only slightly faster in the stream with 125 snails than in the control stream (Table V.1). In addition, the taxonomic structure in these two streams was quite similar, even at day 32 (SIMI = .958). As grazing pressure increased at greater snail densities, there was less algal biomass accumulation. Algal standing crops were uniformly low until day 16 in the streams with 250, 500, and 1000 snails. The subsequent increase in algal biomass was attributable, at least in part, to the fact that snail ingestion rates on day 32 had declined to 5-10% of the original values measured on days 8 and 16 (unpubl. data).

Juga grazed in small, discrete areas (pers. obs.) amd moved at rates of less than 0.2 cm·min^{-1} (Judy Li, pers. comm). At low snail densities, spatial patchiness in feeding may have allowed some plants, such as Stigeoclonium, to reach a size that was less vulnerable to grazing. For example, a patchy distribution of large

and small Stigeoclonium individuals was observed on days 8 and 16 in the stream with 250 snails. This pattern may be analogous to plant-herbivore interactions in marine intertidal systems, where some macroalgae are able to attain a size-escape from their consumers (Dayton 1975, Lubchenco 1980, Duggins and Dethier 1985). The absence of Stigeoclonium in the streams with low snail densities on days 8 and 16 suggests that grazing may enhance the growth of this alga, perhaps by removing overstory species that shade the basal cells. The streams with 500 and 1000 snails apparently contained sufficiently high herbivore densities to prevent any plants from reaching a size large enough to escape consumption. As a result, the assemblages were dominated by sheet-like thalli of Phormidium (day 16), adnate diatoms (Achnanthes spp.), and basal cells and short filaments of Stigeoclonium. The removal of large filamentous algae, and subsequent development of diatom assemblages at high snail densities also has been documented by Gregory (1980) and Jacoby (1985). However, they did not report the coexistence of basal cells (or holdfasts) from the filaments.

Three reasons may have accounted for the lowest density of Dicosmoecus removing substantially more biomass than the lowest density of Juga. First, Dicosmoecus traveled at much faster rates than Juga (Judy Li, pers. comm.) and hence, could graze a larger surface area per unit time. Second, the caddisflies had substantially higher ingestion rates than the snails throughout the experiment (unpubl. data). Third, the sweeping movement of the tarsal claws of Dicosmoecus was particularly effective in removing

filamentous algae. It is unlikely that differences in biomass between *Juga* and *Dicosmoecus* could have accounted for differences in algal biomass since the tissue dry weights of the 125 snails and 50 caddisflies were very similar.

The effects of grazing by *Dicosmoecus* at all densities and by *Juga* at high densities on algal community structure were surprisingly similar given the fact that they have different mouthpart morphologies. It was hypothesized that the radulae of *Juga* could rasp the tile surface, and hence, either remove algal cells completely or maintain a monolayer of cells in regions where grazing took place. The mandibles of *Dicosmoecus*, which move horizontally, were anticipated to be less efficient at removing adnate algae. However, observations from this study suggested that grazing by *Juga* and *Dicosmoecus* did not result in very different types of algal community structure, at least with respect to assemblages grown on flat, relatively smooth surfaces.

The relationship between algal physiognomy and the process of herbivory in lotic ecosystems largely has been unexplored, despite claims that physiognomic characteristics may be closely related to food consumption (Gregory 1983). Results from this study suggested that assemblage physiognomy was an important factor influencing plant-herbivore interactions. For example, the dense, aggregated morphology of *Characium* populations (Figs. V.7 and V.8) apparently made this taxon particularly vulnerable to grazing, as evidenced by its decrease in relative abundance between days 8 and 16 in all

streams with animals. Although *Characium* is commonly found as an epiphyte, it can form dense stands on submerged substrates (Smith 1933).

The dominance of *Achnanthes lanceolata* and *S. tenue* basal cells in streams subjected to heavy grazing pressure by *Juga* and in all streams with *Dicosmoecus* was also related to the interaction between grazing and algal growth form, i.e., the ability to maintain an adnate layer of actively growing cells, even under intense grazing pressure. Previous studies have indicated that herbivores reduce the relative abundance of large, overstory taxa, which allows a subsequent increase in the proportion of small, adnate species (Gregory 1980, Kesler 1981, Sumner and McIntire 1982, Hunter and Russell-Hunter 1983). Data from the present study suggested that the heterotrichous growth form of *Stigeoclonium* had adaptive significance. The prostrate basal cells are small enough to avoid being grazed, and when grazing pressure subsides and physical conditions are appropriate, these cells can generate a branched, erect filamentous growth form. The adaptive significance of heterotrichy has been investigated in marine intertidal regions (Littler 1980, Littler and Littler 1980, Lubchenco and Cubit 1980, Littler and Kauker 1984), but rarely has been noted in freshwater systems. The removal of overstory populations by herbivory in the laboratory streams presumably resulted in relatively high levels of incident light reaching the understory algae. High biomasses of filamentous green algae, and *Stigeoclonium* in particular, have been reported in streams exposed to high photon flux densities (Lyford

and Gregory 1975, Shortreed and Stockner 1983, Steinman and McIntire 1986, submitted [a]). Therefore, the high relative abundance of S. tenue on day 32 may have been attributable to both its ability to resist herbivory and its physiological response to an increase in available light energy. On the other hand, the dominance of A. lanceolata appeared to be related strictly to growth form, because its relative abundance has been shown to decrease as photon flux density increases (Steinman and McIntire 1986, submitted[a]).

Plant succession in lotic systems and the influence of herbivory on that process are not well understood (Fisher 1983). Short generation times of algal species, the strong influence of seasonal changes (Busch 1978), and the persistence of algal propagules on substrates (Wehr 1981) complicate the traditional use of taxonomic units to monitor succession in streams. Physiognomic properties provide an alternative approach to examining succession in lotic algal assemblages (e.g. Hoagland et al. 1982). From a physiognomic viewpoint, an early seral stage can be characterized by either a monolayer of adnate cells that have persisted through a disturbance or new colonizers that have high immigration rates and/or attach well to substrates (Oemke and Burton 1986, Steinman and McIntire 1986). As succession continues, stalked diatoms and short filamentous algae may appear, and toward later seral stages, long filamentous algae may become abundant, assuming that sufficient nutrients and light are available (Hoagland et al. 1982,

Steinman and McIntire 1986). Therefore, if a herbivore grazes a mature algal assemblage, thereby removing long filaments and leaving adherent cells, the grazing process can return the assemblage to an early seral stage, or alter its trajectory to a different sere, in terms of physiognomy. Alternatively, if a herbivore grazes a young algal assemblage, where adherent cells are the prominent growth form, grazing can maintain the assemblage in an early (physiognomic) seral stage. This is analogous to terrestrial systems, where grazing has been shown to set back succession (Watt 1981, Brown 1985).

The results of this study are based on algal assemblages exposed to a single herbivore species and a relatively uniform, flat substrate. In natural systems, the co-existence of a variety of herbivores, each with different feeding modes and nutritional requirements, should increase the susceptibility of all parts of the algal assemblage to grazing (Gaines 1985). In addition, interspecific competition among herbivores (McAuliffe 1984b), predator-prey interactions (Peckarsky 1984), and substrate complexity, which can provide refugia for both plants and animals (Flecker and Allan 1984), all complicate the nature of plant-herbivore interactions in natural streams. Results from this study indicate that in streams where grazing occurs, herbivore density and feeding behavior may help explain changes in the spatial heterogeneity, standing crop, and taxonomic composition of the benthic algal assemblage. Moreover, the relative success or failure of a herbivore may, in part, be a function of how well its

mouthpart morphology is suited for the physiognomic characteristics of an algal assemblage (Gregory 1983). Conversely, species composition, metabolic characteristics, and successional stage of an algal assemblage may reflect how susceptible its physiognomy is to the grazing behavior of local herbivores. If the algal assemblage is vulnerable to grazing, then high grazer densities may change the structure of the assemblage from a mosaic of algal patches in various successional stages (Fisher 1983) to a relatively uniform algal community with a physiognomy characteristic of early seral stages of succession.

ACKNOWLEDGEMENTS

We are very grateful to Randy Wildman and Al Soeldner for their excellent technical assistance, and Judy Li for her help in collecting and maintaining the animals. This study was supported by research grant No. BSR-8318386 from the National Science Foundation and a Sigma Xi Grant-In-Aid.

Table V.1 Matrices of similarity values (SIMI) of laboratory stream algal assemblages exposed to five densities of snails (0, 125, 250, 500, and 1000/stream) pooled by sampling date. Also included is matrix of similarity values of assemblages from above streams on day 32.

Control (0 snails)

	4	8	16	32
4	1.000			
8	.913	1.000		
16	.800	.880	1.000	
32	.659	.546	.798	1.000

125 snails

	4	8	16	32
4	1.000			
8	.916	1.000		
16	.730	.872	1.000	
32	.491	.664	.710	1.000

250 snails

	4	8	16	32
4	1.000			
8	.217	1.000		
16	.268	.972	1.000	
32	.218	.970	.937	1.000

500 snails

	4	8	16	32
4	1.000			
8	.829	1.000		
16	.651	.921	1.000	
32	.162	.384	.384	1.000

Table V.1 continued.

	1000 snails			
	4	8	16	32
4	1.000			
8	.626	1.000		
16	.509	.756	1.000	
32	.113	.360	.567	1.000

	Day 32				
	0	125	250	500	1000
0	1.000				
125	.958	1.000			
250	.290	.236	1.000		
500	.103	.116	.911	1.000	
1000	.182	.160	.721	.770	1.000

Table V.2 Matrices of similarity values (SIMI) of laboratory stream algal assemblages exposed to five densities of caddisflies (0, 50, 100, 200, and 400/stream) pooled by sampling date. Also included is matrix of similarity values of assemblages from above streams on day 32.

	Control (0 caddisflies)			
	4	8	16	32
4	1.000			
8	.913	1.000		
16	.800	.880	1.000	
32	.659	.546	.798	1.000

	50 caddisflies			
	4	8	16	32
4	1.000			
8	.885	1.000		
16	.471	.574	1.000	
32	.289	.423	.800	1.000

	100 caddisflies			
	4	8	16	32
4	1.000			
8	.785	1.000		
16	.576	.421	1.000	
32	.237	.325	.711	1.000

	200 caddisflies			
	4	8	16	32
4	1.000			
8	.762	1.000		
16	.278	.329	1.000	
32	.091	.215	.792	1.000

Table V.2 continued.

	400 caddisflies			
	4	8	16	32
4	1.000			
8	.644	1.000		
16	.107	.206	1.000	
32	.112	.178	.887	1.000

	Day 32				
	0	50	100	200	400
0	1.000				
50	.452	1.000			
100	.424	.949	1.000		
200	.186	.747	.802	1.000	
400	.195	.716	.814	.944	1.000

Figure V.1 Biomass accumulation of algal assemblages (expressed as ash-free dry weight) in laboratory streams stocked with 0, 125, 250, 500, and 1000 snails during the 32-day experimental period. All streams were exposed to a photon flux density of ca. 400 $\mu E \cdot m^{-2} \cdot s^{-1}$ and a current velocity of 10 $cm \cdot s^{-1}$.

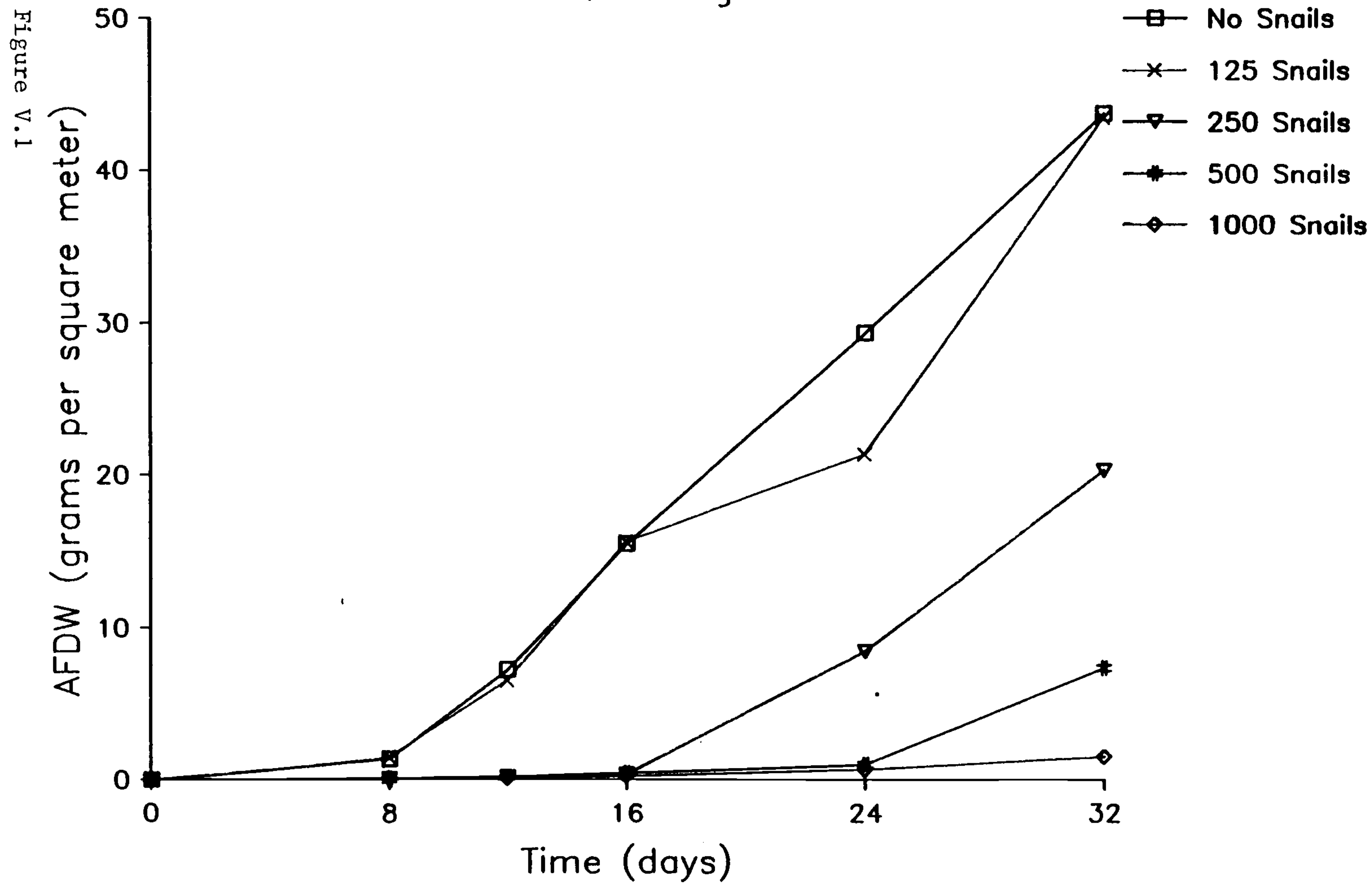


Figure V.1

Figure V.2 Relative abundance (expressed as percentage of total community biovolume) of dominant chlorophytes in laboratory streams stocked with 0, 125, 250, 500, and 1000 snails on days 4, 8, 16, and 32.

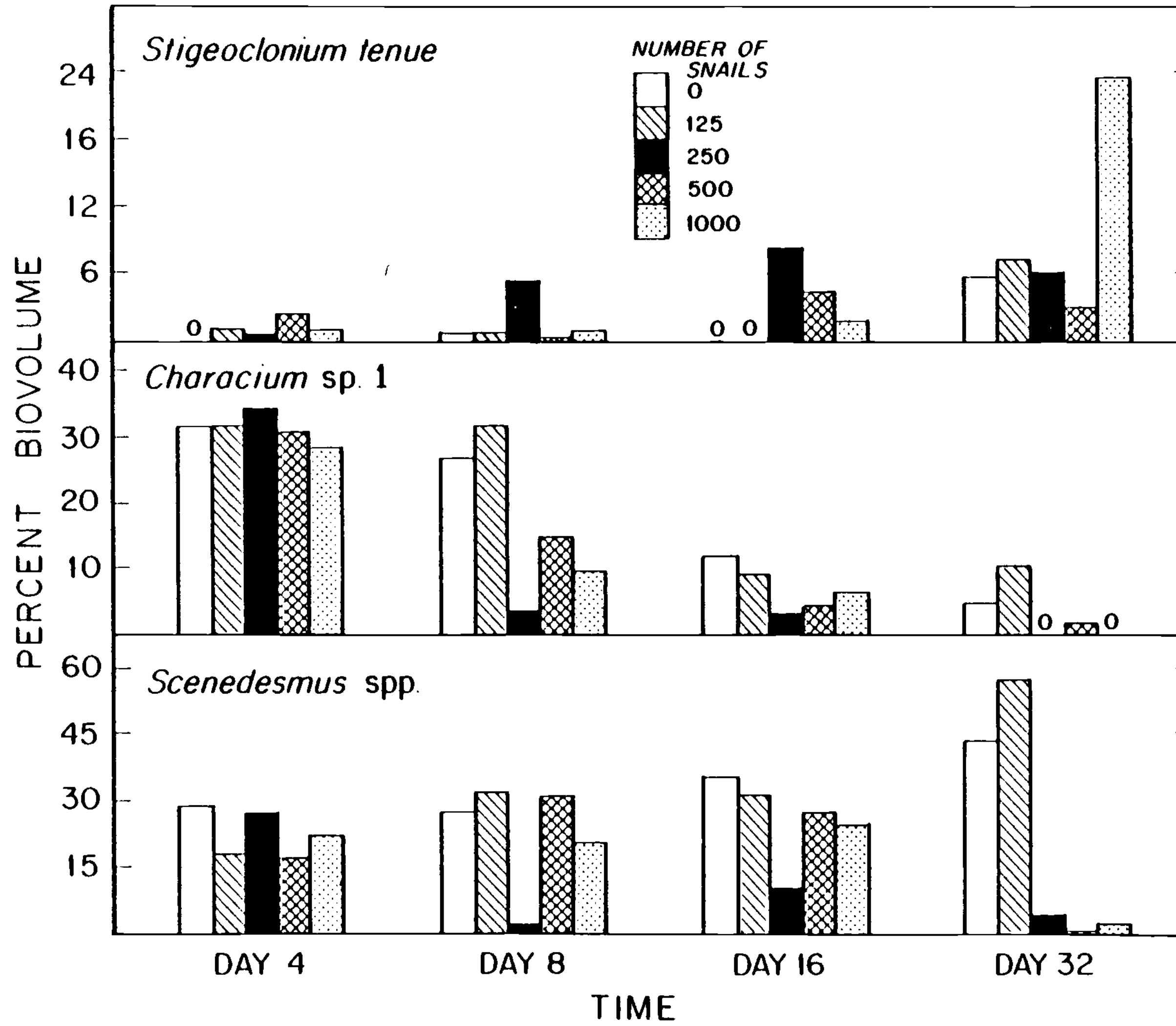


Figure V.2

Figure V.3 Relative abundance (expressed as percentage of total community biovolume) of dominant cyanophyte and diatoms in laboratory streams stocked with 0, 125, 250, 500, and 1000 snails on days 4, 8, 6, and 32.

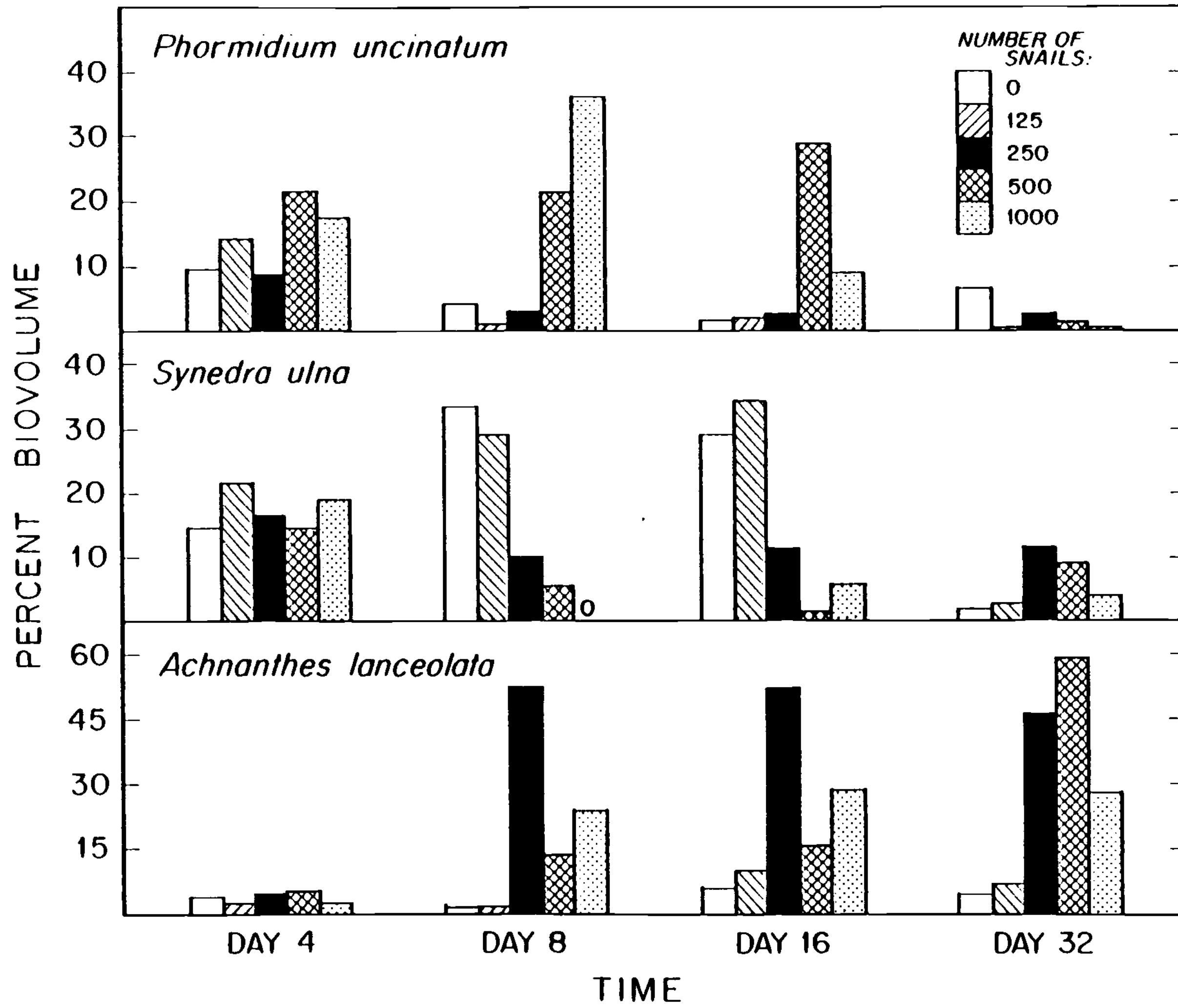


Figure V.3

Figure V.4 Biomass accumulation of algal assemblages (expressed as ash-free dry weight) in laboratory streams stocked with 0, 50, 100, 200, and 400 caddisflies during the 32-day experimental period. Biomasses in the control stream are the same as in Fig. 1.

Figure V.4

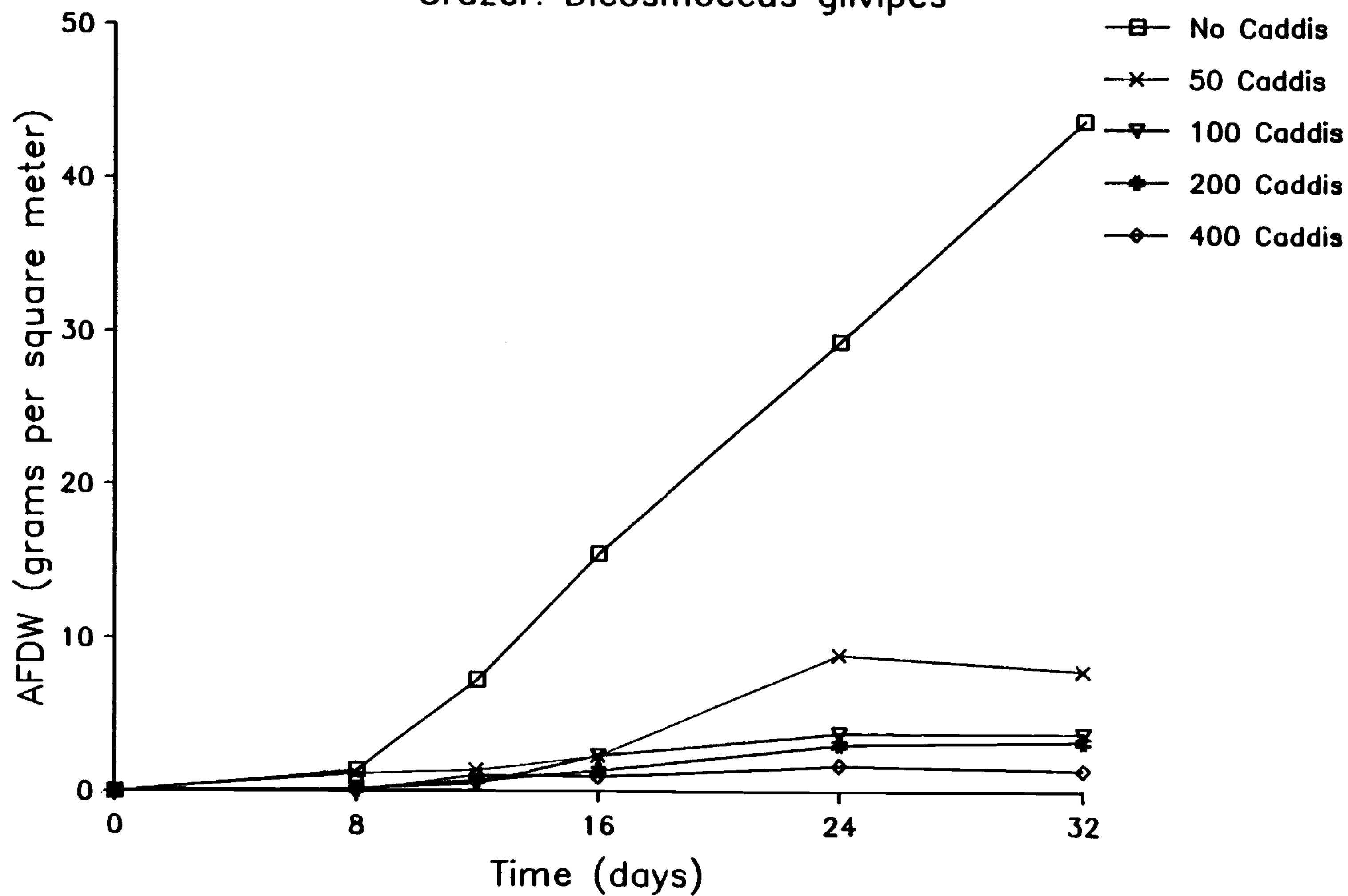


Figure V.5 Relative abundance (expressed as percent of total community biovolume) of dominant chlorophytes in laboratory streams stocked with 0, 50, 100, 200, and 400 caddisflies on days 4, 8, 16, and 32.

Figure V.5

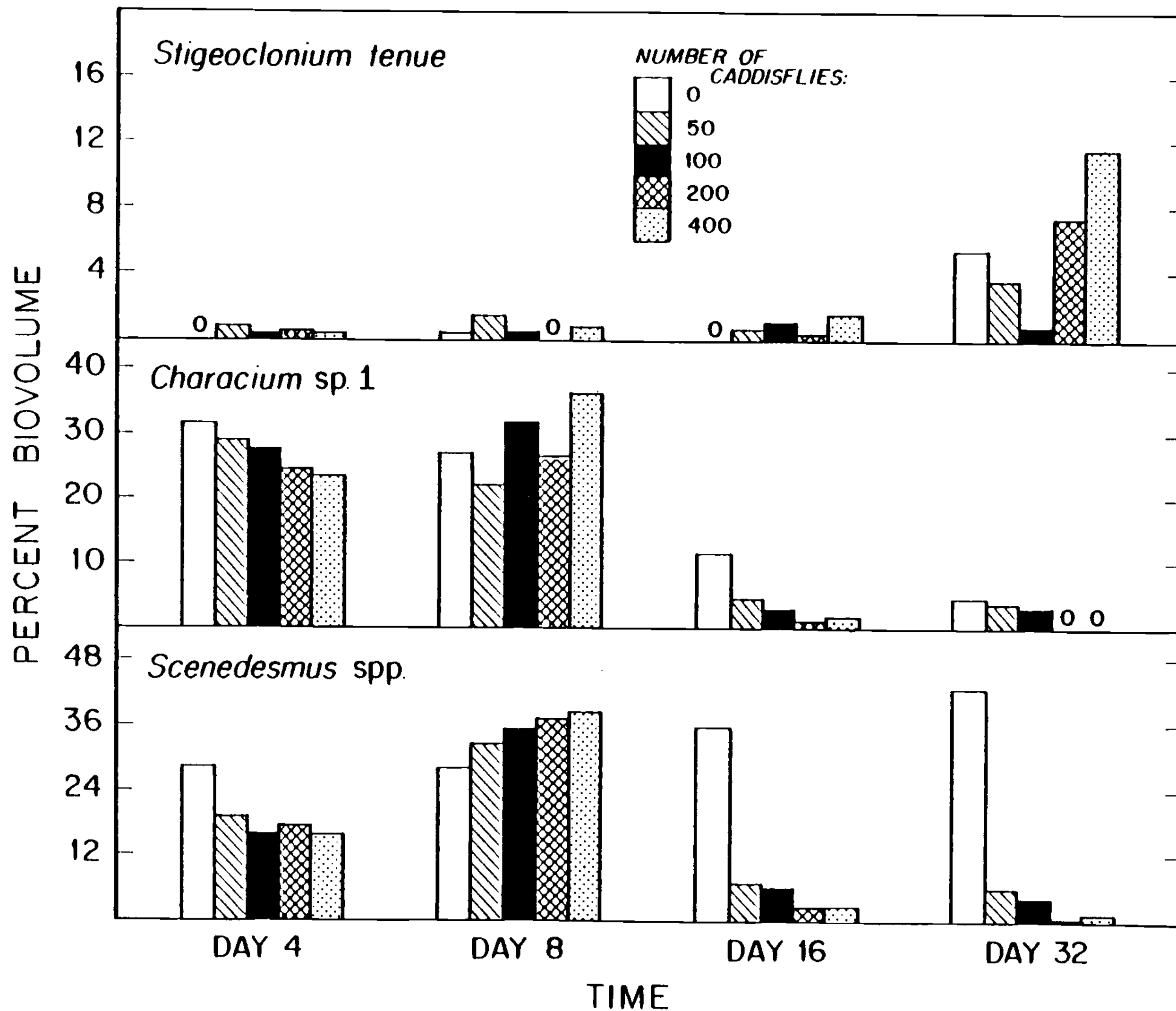


Figure V.6 Relative abundance (expressed as percent of total community biovolume) of dominant cyanophyte and diatoms in laboratory streams stocked with 0, 50, 100, 200, and 400 caddisflies on days 4, 8, 16, and 32.

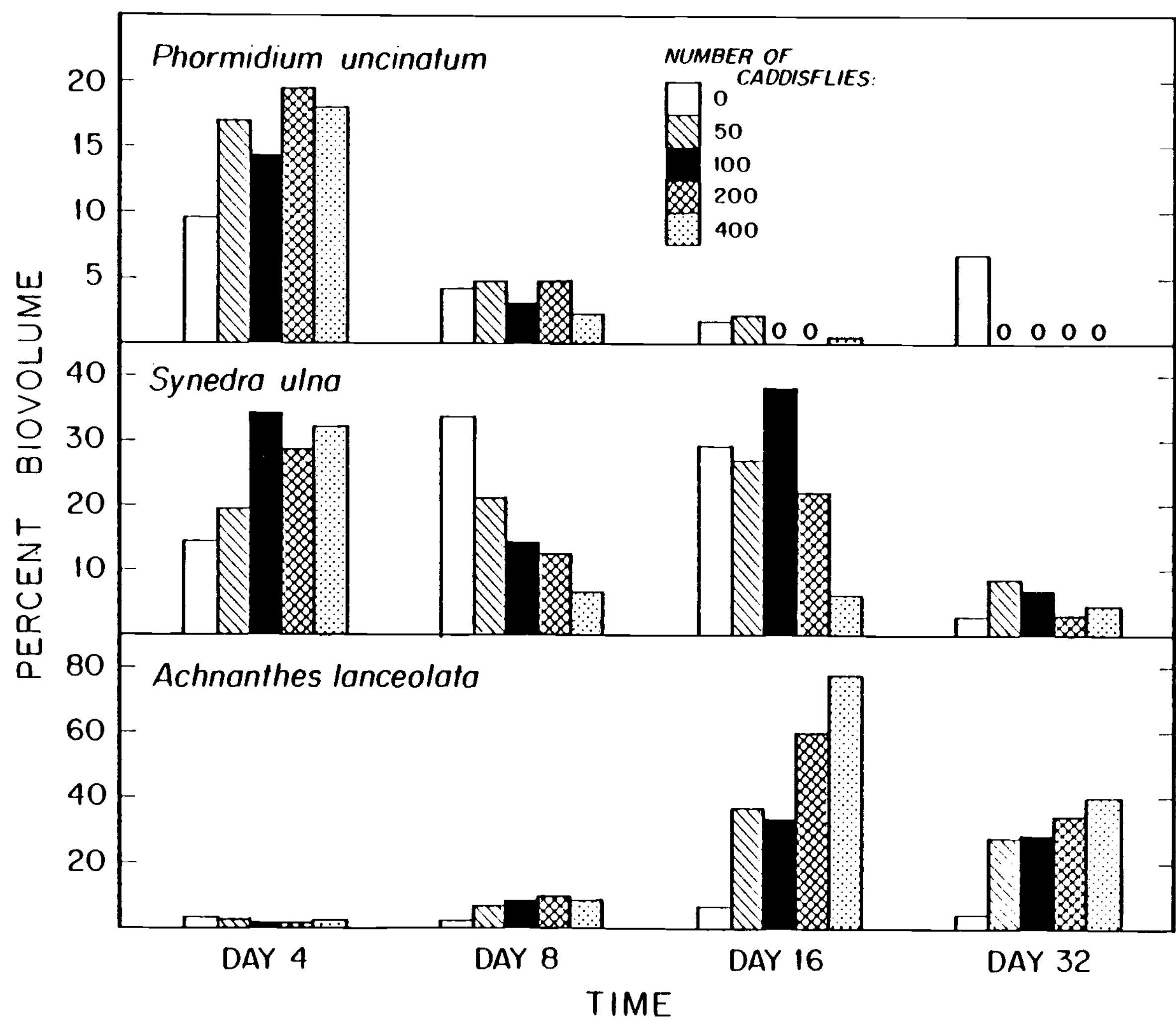


Figure V.6

Figure V.7 SEM of algal assemblage on day 8. Control stream. Clumps of Characium, rosettes and scattered cells of Synedra ulna and curved filament of Fragilaria dominate the tile surface. Scale = 300 µm.

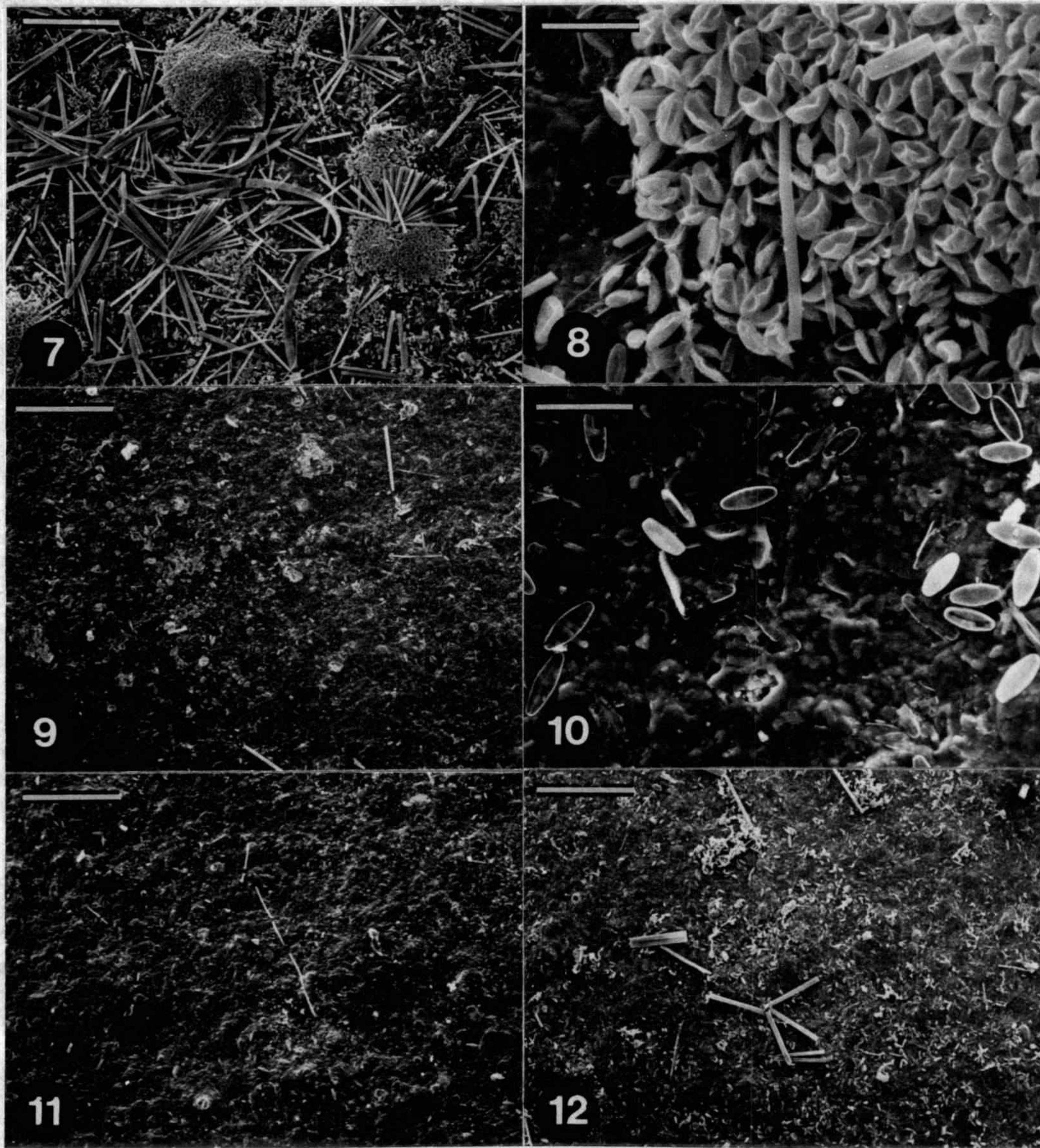
Figure V.8 SEM of Characium aggregate. Tile surface is to the left of the clump. Scale = 30 µm.

Figure V.9 SEM of algal assemblage on day 8. Relatively barren tile surface. 250-snail stream. Scale = 300 µm.

Figure V.10 SEM of algal assemblage on day 8. Close-up of tile from Fig. 9. Note scattered frustules of Achnanthes lanceolata. 250-snail stream. Scale = 30 µm.

Figure V.11 SEM of algal assemblage on day 8. Tile surface is populated by sparse cover of diatoms. 1000-snail stream. Scale = 300 µm.

Figure V.12 SEM of algal assemblage on day 8. Note similarity to Figure V.11. 400-caddisfly stream. Scale = 300 µm.



Figures V.7-12

Figure V.13 SEM of algal assemblage on day 15. Thick algal mat consisting of *Characium* aggregates and dense accumulations of diatoms. Control stream. Scale = 300 μm.

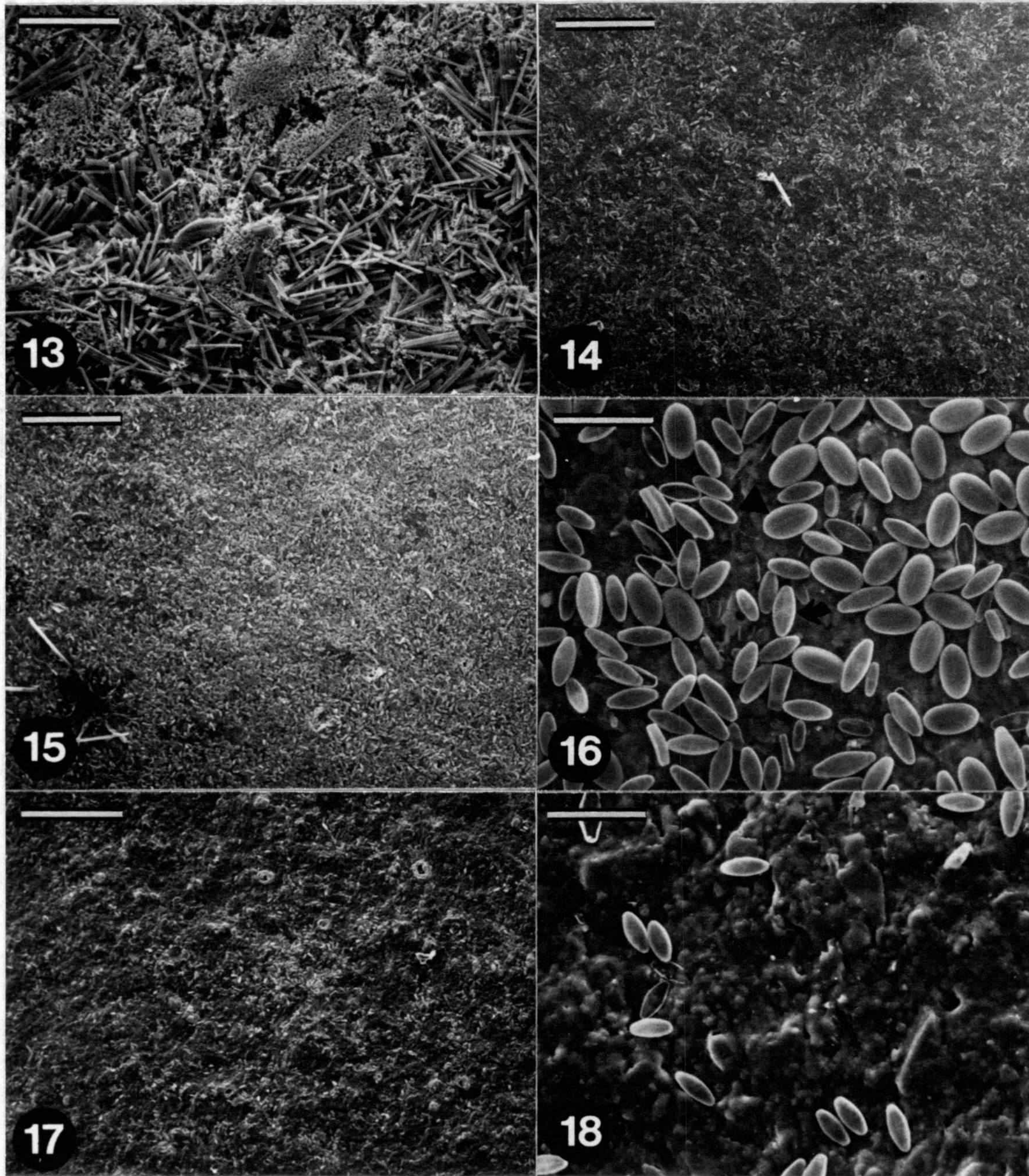
Figure V.14 SEM of algal assemblage on day 15. Unicellular diatoms dot the tile surface. 400-caddisfly stream. Scale = 300 μm.

Figure V.15 SEM of algal assemblage on day 15. Tile surface covered by dense monolayer of diatoms. 250-snail stream. Scale = 300 μm.

Figure V.16 SEM of algal assemblage on day 15. Close-up of diatom layer in Fig. 15. Most conspicuous taxa are *Achnanthes lanceolata* (arrow) and *Cocconeis* (arrowhead). Scale = 30 μm.

Figure V.17 SEM of algal assemblage on day 15. Tile surface shows scattered assemblage of diatoms. 1000-snail stream. Scale = 30 μm.

Figure V.18 SEM of algal assemblage on day 15. Close-up of tile from Fig. 17 showing a sparse distribution of diatoms (*A. lanceolata*). Scale = 300 μm.



Figures V.13-18

Figure V.19 SEM of algal assemblage on day 31. Thick algal mat covers tile surface. Note branching filament of Stigeoclonium in lower left corner. Control stream. Scale = 300 µm.

Figure V.20a SEM of algal assemblage on day 31. Close-up of Fig. 19. Left side of micrograph depicts Scenedesmus coenobia that intergrade with dense accumulation of diatoms on right side. Scale = 30 µm.

Figure V.20b SEM of algal assemblage on day 31. Close-up of Fig. 19 showing population of Nitzschia cells. Assemblages depicted in Figs. 20a and 20b were ca. 750 µm apart. Scale = 30 µm.

Figure V.21 SEM of algal assemblage on day 31. Algal mat overlaid by filamentous network covers tile surface. 250-snail stream. Scale = 300 µm.

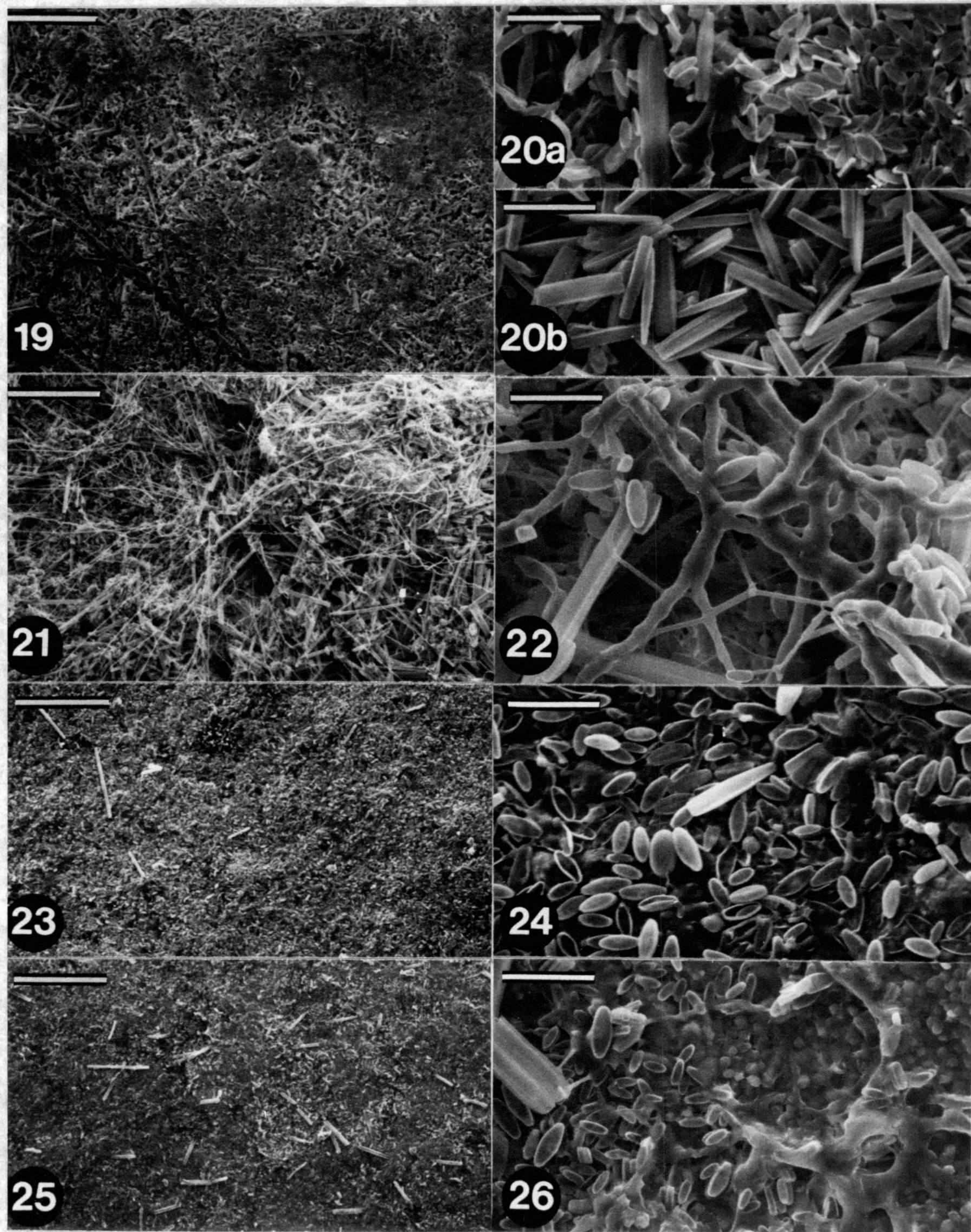
Figure V.22 SEM of algal assemblage on day 31. Close-up of filaments from Fig. 21 showing complex reticulum. Scale = 30 µm.

Figure V.23 SEM of algal assemblage on day 31. Tile surface covered by monolayer of diatoms. 1000-snails stream. Scale = 300 µm.

Figure V.24 SEM of algal assemblage on day 31. Close-up of tile from Fig. 23. Note monolayer dominated by A. lanceolata. Scale = 30 µm.

Figure V.25 SEM of algal assemblage on day 31. "Apparently" barren tile surface. 400-caddisfly stream. Scale = 300 µm.

Figure V.26 SEM of algal assemblage on day 31. Note thin layer of diatoms and mucilage, and in middle and upper-right portion of micrograph, an understory of Stigeoclonium basal cells. Scale = 30 µm.



Figures V.19-26

VI. DENSITY-RELATED EFFECTS OF GRAZING BY A SNAIL AND A CADDISFLY ON ALGAL ASSEMBLAGES IN LABORATORY STREAMS. II. ALGAL CHEMICAL COMPOSITION

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ABSTRACT

Effects of grazing by a snail (*Juga silicula*) and a caddisfly (*Dicosmoecus gilvipes*) on the chemical composition of algal assemblages were monitored in laboratory streams for 32 days. Three days after the herbivores were introduced, the fatty acid and amino acid profiles were similar among algal assemblages. However, after four weeks, substantial differences were noted, especially with respect to the 16:0, 16:1, 16:3, 18:3, and 20:5 fatty acids. Algal assemblages subjected to low grazing pressure were characterized by high levels of glycine, serine, and the 16:3 and 18:3 fatty acids. Assemblages exposed to high grazing pressure were characterized by relatively high concentrations of alanine, and the 16:0, 16:1, and 20:5 fatty acids.

INTRODUCTION

Grazing activity by aquatic invertebrates in lotic ecosystems can influence the biomass and community structure of benthic algal assemblages (Eichenberger and Schlatter 1978, Gregory 1980, Hart 1985, Jacoby 1985, Sumner and McIntire 1982). If different algal taxa have characteristic chemical constituents, then the process of herbivory may also lead to identifiable changes in the chemical structure of these assemblages. These changes may have important implications with respect to food quality. Steinman et al. (submitted[c]), using ordination procedures, were able to reveal that chemical differences existed in algal assemblages with different taxonomic structures. In the study reported here, we examined the hypothesis that grazer-induced changes in algal taxonomic structure generate corresponding changes in chemical structure. Algal assemblages were subjected to grazing by different densities of the snail *Juga silicula* and the caddisfly *Dicosmoecus gilvipes* in laboratory streams, and fatty acid and amino acid profiles, total crude lipid and protein concentrations, and carbon:nitrogen ratios were monitored during community development. A companion paper describes the effects of grazing on algal biomass, species composition, and physiognomy (Steinman et al. submitted [b]).

MATERIALS AND METHODS

The design of the laboratory streams was described by Steinman and McIntire (1986). Water temperature remained at 14 ± 1°C throughout the experimental period. The exchange rate and nutrient concentration of the wellwater supply was similar to that reported by Steinman and McIntire (1986). Light energy was supplied by 16 1000-Watt Metalarc lamps (Sylvania Corp.), adjusted to provide a uniform photon flux density of approximately 400 $\mu E \cdot m^{-2} \cdot s^{-1}$ to all experimental streams. Timers were set to produce a daily photoperiod of 12 L: 12 D. Current velocity in all streams was maintained at 10 $cm \cdot s^{-1}$. The bottom of each stream was lined with 7.5 x 7.5 cm unglazed ceramic tiles, which provided a surface for colonization and units for periodic sampling. One of every six tiles had an upturned end to provide heterogeneity on the stream bottom.

The procedure for inoculation of the laboratory streams with algae was described by Steinman and McIntire (1986). Animals were collected from local streams and introduced five days after algal inoculation. Animals were introduced into eight streams, each at a different density (see Steinman et al. submitted [b]), and one stream was not stocked with animals and served as an ungrazed control system. Chemical analyses were performed on algae from five of these streams: (1) 125 snails/stream (tissue dry weight: ca. 2.5 g total), (2) 500 snails/stream (ca. 10 g), (3) 50 caddis/stream (tissue dry weight: ca. 3 g total), (4) 200 caddis/stream (ca. 12

g), and (5) the control stream. The experiment lasted for 32 days.

Methods for microscopic analysis of species composition were described by Steinman and McIntire (1986). Sampling for taxonomic composition was conducted on days 4, 8, 16, and 32. For chemical analysis, a random sample of two tiles was obtained from the streams on days 8 and 32. Two of the five streams were not sampled for chemical composition on day 8 because of insufficient biomass. The algae were scraped from the tile surface, homogenized, and kept on ice until the analytical procedures were started, usually within one hour.

Lipid extractions were performed according to the method of Kates (1972). Total crude lipid was determined by weighing a dried subsample from a known volume of the crude extract on a Perkin-Elmer AD-2 microbalance. Fatty acids were methylated by transesterification in 5% methanolic HCl (gas): diethyl ether (1:1, v/v) at 80°C for 90 minutes. Extraction of fatty acid methyl esters (FAME) followed the procedure of Cargill et al. (1985). FAME were analyzed by gas-liquid chromatography using the method of Hanson et al. (1983). Internal standards, comparison of retention times with external standards, and hydrogenation of methyl esters were used to identify fatty acid methyl esters.

Amino acids were determined by hydrolyzing 1 ml subsamples of the homogenized algal samples in glass ampoules in vacuo at 110°C for 22 h. This hydrolysis results in the unavoidable destruction of tryptophan and does not distinguish glutamine from glutamic acid or asparagine from aspartic acid. Ampoules were opened and the

contents dried by roto-evaporation at 35 C. Samples were then dissolved in 1 ml of 0.2 N citrate diluting buffer (pH 2.20) and Millipore-filtered. Samples were analyzed on a home-built Picomole range Amino Acid Analyzer, fitted with a single Glenco 3.0 mm glass column, packed with 25 cm of Dionex DC-4A resin. A four-step sodium elution gradient was employed using Dionex Hi-Phi sodium citrate buffers. Post-column flourescence was generated by o-phthalaldehyde (Cronin et al. 1979), and detected by a Gilson Spectra/Glo Flourescence Detector using excitation and emission frequencies of 340 and 455 nm, respectively. Protein content was calculated by summing the anhydroamino acid residues. C:N ratios were determined on a Carlo Erba CHN analyzer.

The data were organized into three matrices: the fatty acid data, the amino acid data, and the species relative abundances based on biovolume. To analyze covariance among variables, the relative abundance of each species was correlated with percentage abundance of each fatty acid and amino acid. Chemical composition of the algal assemblages was compared using the SIMI measure of similarity (McIntire and Moore 1977). This measure ranges from 0 to 1, and gives greater weight to dominant variables. A value of 0 denotes that a given pair of assemblages have none of the variables under consideration in common, while a value of 1 indicates that the two assemblages have identical proportional values for the variables. In this case, the variables for the calculation of SIMI values were fatty acid and amino acid percentages. The statistical

analyses were performed with a Control Data Corporation CYBER 170/720 computer using SIPS (Rowe and Brenne 1982), and the program AIDN.

RESULTS

On day 8, the fatty acid distributions of the algal assemblages from each stream were similar (Table VI.1). The most abundant fatty acids were 16:0, 16:1, 16:3, 18:1, 18:3, and 20:5. The percentages in the control and 125-snail stream were very similar, while the stream with 50 caddisflies had higher relative abundances of 16:0, 16:1, and 18:1, and lower relative amounts of 16:3 and 18:3 fatty acids than the control stream. SIMI values in Table 2 also reflected these patterns, as the indices revealed very high similarity between the control and 125-snail streams (SIMI = .996), and slightly less similarity between the control and 50-caddisfly streams (SIMI = .967).

On day 32, distinct differences were evident among algal assemblages (Table VI.1). The control and 125-snail streams still had very similar fatty acid distributions (Tables VI.1 and VI.2) and contained high relative amounts of 16:0, 16:1, 18:1, and 18:3 acids. However, the stream with 500 snails had percentages of 16:1, 16:3, 18:3, and 20:5 fatty acids that were intermediate between the control stream and the streams with caddisflies, observations that were consistent with the corresponding SIMI values (Table VI.2). The algal assemblages in the 50- and 200-caddisfly streams had higher percentages of 16:0, 16:1, and 20:5 fatty acids, and lower relative concentrations of 16:3 and 18:3 acids than the assemblages in the other streams. The SIMI values also showed distinct dissimilarities between the assemblages in these streams and those

in the control and 125-snail streams.

Concentrations of total crude lipid were similar in the control and 125-snail streams on day 8 (Table VI.1), but were approximately one-half those concentrations in the stream with 50 caddisflies. On day 32, the lipid concentrations were again similar in the control and 125-snail streams, although at greater levels than on day 8. The algal assemblages in streams with caddisflies also had lipid concentrations similar to those measured in the control stream assemblages, but the stream with 500 snails had lower levels than the other streams.

Amino acid percentages were similar among algal assemblages in all streams on day 8 (Table VI.3). The dominant amino acids were glutamic acid/glutamine, aspartic acid/asparagine, glycine, serine, and alanine. SIMI values gave further indication that these assemblages had similar amino acid compositions (Table VI.4). On day 32, the algal assemblages still had very similar amino acid distributions and percentages (Tables VI.3 and VI.4). Although relative concentrations of serine and glycine decreased slightly, and the percentage of alanine increased during the experiment, the dominant amino acids remained the same.

On day 8, the protein concentration in the control stream was approximately one-half that in the stream with 125 snails, but almost double that in the stream with 50 caddisflies (Table VI.3). By day 32, protein concentration had decreased in both the control and 125-snail streams, resulting in relatively uniform levels. Assemblages in the streams with 500 snails and 50 caddisflies had

slightly greater concentrations than that in the control stream, while the assemblages in the stream with 200 caddisflies had the lowest protein concentration.

C:N ratios were all greater than 25 in the stream assemblages on day 8 (Table VI.3), with the assemblages exposed to 50 caddisflies having the highest ratio. By day 32, C:N levels had decreased 3- to 4-fold and were quite similar in all the assemblages except those in the stream with 200 caddisflies, where the ratio was almost double that in the control stream algae.

The analysis of chemical constituents on a community level precluded the direct association of taxa with specific chemicals. However, correlations between 10 algal taxa and a select group of dominant fatty and amino acids were calculated to assess relative degrees of association (Table VI.5). In general, diatoms were positively associated, and chlorophytes negatively correlated, with the fatty acids 16:0, 16:1, and 20:5, and the amino acid alanine. On the other hand, the 16:3 and 18:3 fatty acids, glycine, and serine were negatively associated with diatoms and positively correlated with the green algae. The fatty acid correlations with *Synedra ulna* more closely resembled those for chlorophytes than for other diatoms, while correlations with *Stigeoclonium* were similar to those for diatoms. The correlations between the fatty acids and *Phormidium uncinatum* resembled those for chlorophytes (and *S. ulna*), while those for *Phormidum tenue* were similar to those for the diatoms (and *Stigeoclonium*).

DISCUSSION

The results of this study indicated that herbivore-induced changes in the taxonomic structure of algal assemblages can influence their chemical composition. By day 8, after the algae had been exposed to the herbivores for only three days, there were relatively few differences in the chemical compositions of the assemblages among streams. However, differences in algal biomass among the three streams were also small (Steinman et al. submitted[b]), indicating that the overall impact of the herbivores at this time was negligible.

The distinct differences in the relative abundances of the fatty acids among the five streams on day 32 were associated with the degree of grazing pressure exerted on the algal assemblages, and its subsequent effect on algal taxonomic structure. For example, the assemblages in the 125-snail and control streams, which were subjected to very little or no grazing pressure, respectively, had similar fatty acid profiles. Both assemblages were characterized by high relative abundances of 16:3 and 18:3 fatty acids. These acids are abundant in chlorophytes (Moore 1975b, Nichols 1968, Piorreck et al. 1984), and indeed, the assemblages in the control and 125-snail streams had high relative abundances of chlorophyte taxa (Steinman et al. submitted[b]). However, those assemblages subjected to high grazing pressure had lower relative abundances of 16:3 and 18:3, and higher relative abundances of 16:0, 16:1, and 20:5 fatty acids than the assemblages exposed to

low densities of grazers. Assemblages in the 500-snail, 50-caddisfly, and 200-caddsifly streams were characterized by high relative abundances of diatoms (Steinman et al. submitted[b]), algae that have been shown to contain high levels of 16:0, 16:1, and 20:5 fatty acids (Demort et al. 1972, Kates and Volcani 1966, McIntire et al. 1969, Nichols et al. 1986, Opute 1974a).

The increase in levels of total crude lipid from days 8 to 32 can be attributed to either senescence or changes in taxonomic composition. Microscopic examination of assemblages in the control and 125-snail streams indicated the deterioration of plastids on day 32, which was suggestive of senescence. Shifrin and Chisholm (1981) observed lipid accumulation in freshwater diatoms and chlorophytes in response to nutrient depletion and senescence. The assemblages in the 500-snail, 50-caddisfly, and 200-caddisfly streams were grazed to a much greater degree and algal senescence was not as apparent. However, the algae did exhibit a shift in taxonomic structure from chlorophyte to diatom domination. Opute (1974b) and Shifrin and Chisholm (1981) noted that diatoms tend to be rich in lipids relative to other algal classes, which may have accounted for the increase in lipid concentration in these assemblages.

Despite grazer-induced changes in taxonomic structure, the relative concentrations of amino acids remained similar among streams during the experiment. Fowden (1954) suggested that algal proteins are not subject to wide variation among species, a conclusion these data tend to confirm. However, the dominant amino

acids in the algal assemblages in this study were different from those in the freshwater algae that Fowden (1954) studied. The positive correlation of alanine and negative correlation of glycine with diatoms (Table VI.5) indicated that these amino acids may have certain taxonomic affinities.

It is unclear why protein levels were so disparate among the stream assemblages on day 8. The similar taxonomic compositions should have resulted in more similar protein concentrations. The high C:N ratios in the assemblages on day 8 may have reflected large amounts of organic mucilage on the tiles relative to algal biomass (Winterbourne et al. 1984), although examination by scanning electron microscopy failed to reveal noticeable amounts of mucilage. Protein concentrations were more uniform on day 32 than on day 8. The lower concentrations in the assemblages from the control and 125-snail streams may have been related to the presence of senescent cells in the thick mats (Millie 1986, Shifrin and Chisholm 1981). In contrast, grazing by Dicosmoecus and Juga resulted in a thin layer of actively growing cells (based on chlorophyll-specific primary production data, S. V. Gregory. pers. comm.). Thus, cells in assemblages exposed to 500 snails and 50 caddisflies on day 32 presumably incorporated a larger proportion of cell carbon into protein than the senescent cells (Millie 1986, Morris 1981). The low protein concentrations in the 200-caddisfly assemblage on day 32 may have been due to its taxonomic composition. In terms of relative abundance based on biovolumes,

this assemblage had 3.5x more Stigeoclonium tenue, 25x more Phormidium tenue, and one-third less Nitzschia lancettula than the 500-snail or 50-caddisfly assemblages (Steinman and McIntire submitted [b], unpubl. data). Low C:N ratios in periphyton have been suggested to be indicative of relatively high protein levels (McMahon et al. 1974), and hence, of high food quality. However, there was very little association between C:N ratio and protein concentration in the algal assemblages from this study.

One of the limitations of community level biochemical analyses is the inability to unequivocally determine whether certain chemicals are found in specific taxa. It is possible that a relationship may be masked due to the dominance of other taxa. For example, Stigeoclonium tenue was negatively correlated with 16:3 and 18:3 fatty acids, despite the high reported abundance of these acids in chlorophytes (Moore 1975b, Piorreck et al. 1984). However, unlike the chlorococcalean taxa, which constituted a majority of the assemblage when they were dominant (and thus had an overwhelming influence on assemblage chemical structure), Stigeoclonium was often found in streams where diatoms dominated the assemblage. This was a function of the taxon's heterotrichous growth form, whereby its prostrate stage with basal cells and short, finely cropped filaments coexisted with adnate diatoms in heavily grazed assemblages. As a consequence, the chemical composition of the assemblages primarily reflected that of diatoms even though the chemistry of S. tenue may have been quite different.

Herbivory-induced changes in the chemical composition of lotic algal assemblages may have important relationships with herbivore growth. The results from this study indicated that the most distinct changes occurred in the fatty acid distributions. Hanson et al. (1983) and Cargill et al. (1985) both found that specific fatty acids were critical dietary components in a detritivorous caddisfly. The inability of most insects to synthesize polyunsaturated fatty acids (Downer 1978, Ziegler 1984) and sterols (Dadd 1983, Robbins et al. 1971) indicates that these lipids may play crucial roles in insect nutrition. More detailed studies are needed to elucidate the role of algal lipids and other chemicals in terms of food quality. Specific topics of consideration for future research may include: (1) the dynamics of these chemicals in commonly grazed algal taxa under different physical conditions; (2) how lipids are "edited" (sensu Prahl et al. 1984) in herbivores after ingestion; and (3) the effects that these lipids have on growth and reproductive capacity of lotic herbivores.

ACKNOWLEDGEMENTS

We are very grateful to Linda Ashkenas and Randy Wildman for their technical assistance, Austin Cargill II and Robert Becker for their help with lipid and protein analyses, respectively, and Stan Gregory and Gary Lamberti for their advice on experimental design. This study was supported by research grant No. BSR-8318386 from the National Science Foundation and by a Sigma Xi Grant-In-Aid.

Table VI.1. Amounts of fatty acids and total crude lipid in laboratory stream algal assemblages on days 8 and 32, exposed to different densities of either Juga silicula or Dicosmoecus gilvipes. Fatty acid data are expressed as percentage of total in each sample. Total crude lipid is expressed as mg lipid/g AFDW. T denotes a trace amount (less than 0.2%). All streams were exposed to the same physical conditions (see Materials and Methods).

Fatty Acid	Day 8 Control	Day 8 125 Juga	Day 8 50 Dico	Day 32 Control	Day 32 125 Juga	Day 32 500 Juga	Day 32 50 Dico	Day 32 200 Dico
12:0	5.82	5.13	3.57	4.76	5.81	2.79	2.91	2.39
14:0	6.32	6.13	4.61	3.65	3.49	3.47	4.32	5.91
14:1	1.28	0.53	0.79	0.73	T	T	0.72	0.27
Unk A[a]	1.65	1.06	1.19	1.52	0.62	0.31	0.88	0.30
16:0	12.21	10.65	14.73	12.96	13.47	16.34	16.47	18.55
16:1	6.41	8.20	10.75	11.55	10.91	20.77	26.61	25.09
16:2	1.55	1.85	1.64	1.70	1.18	3.57	3.18	2.12
16:3	14.25	13.64	10.88	9.99	10.05	6.03	2.90	3.70
18:0	0.34	0.39	1.79	T	T	T	T	0.37
18:1[b]	8.75	10.40	12.24	10.65	10.22	9.77	10.74	9.38
18:2	2.39	2.38	3.29	5.83	5.74	2.02	1.53	2.31
18:3	27.26	26.72	21.97	19.20	19.96	13.51	4.92	7.58
20:0	0.39	0.45	T	0.42	0.45	0.81	0.85	1.18
20:2	3.13	3.12	2.59	3.86	4.08	1.61	1.64	1.33
20:5	6.69	7.53	6.86	9.20	10.02	13.28	14.95	13.41
22:0	0.76	0.90	1.07	2.33	3.35	5.52	6.20	5.64
22:2	--	--	--	--	--	--	T	--
24:0	--	T	T	T	--	--	--	--
Total Lipid	98.2	92.9	51.2	146.0	146.3	118.0	162.7	134.5

[a] Relative retention time of Unknown A was 0.61, with 18:0 = 1.00
[b] This fatty acid apparently was comprised of two unresolvable isomers.

Table VI.2. Matrix of similarity values (SIMI) based on fatty acid percentages of experimental algal assemblages on days 8 and 32.

Day 8

	Control	125 Juga	50 Dico
Control	1.000		
125 Juga	.996	1.000	
50 Dico	.967	.976	1.000

Day 32

	Control	125 Juga	500 Juga	50 Dico	200 Dico
Control	1.000				
125 Juga	.998	1.000			
500 Juga	.917	.912	1.000		
50 Dico	.780	.769	.956	1.000	
200 Dico	.824	.816	.974	.992	1.000

Table VI.3. Amounts of amino acids, protein, and C:N ratios in laboratory stream algal assemblages on days 8 and 32, exposed to different densities of either Juga silicula or Dicosmoecus gilvipes. Amino acid data are expressed as percentage of total sample residues. Protein data are expressed as mg protein/g AFDW. T denotes a trace amount (less than 0.1%). All streams were exposed to the same physical conditions.

Amino Acid	Day 8			Day 32				
	Control	125 Juga	50 Dico	Control	125 Juga	500 Juga	50 Dico	200 Dico
Asp	14.89	9.07	12.38	12.14	10.15	12.83	12.32	12.79
Thr	6.83	7.48	6.91	6.80	5.77	7.04	6.38	7.03
Ser	11.07	10.65	12.38	8.40	6.88	9.85	8.75	8.01
Glu	13.18	12.34	16.81	12.86	11.60	13.88	13.37	14.71
Gly	10.29	11.03	13.24	10.24	10.26	9.40	9.20	9.10
Ala	10.95	10.00	9.07	11.02	12.91	12.48	13.28	12.35
Val	7.86	7.60	8.54	7.65	8.47	8.18	7.21	9.25
Met	0.78	0.45	T	2.43	1.99	1.09	0.91	0.90
Ile	3.77	4.71	2.98	4.47	4.28	3.56	2.93	2.70
Leu	7.91	9.07	7.01	8.61	10.00	7.85	7.95	8.04
Tyr	0.63	1.85	T	1.63	1.90	0.86	0.58	T
Phe	3.50	3.77	1.32	3.85	4.07	4.72	4.04	4.29
His	1.97	2.93	3.02	1.61	1.98	1.62	2.65	1.71
Lys	3.06	4.31	2.50	3.37	4.06	3.14	6.53	2.88
Arg	3.31	4.73	3.84	4.93	5.70	3.50	3.89	4.57
Protein	154.9	324.0	83.5	64.9	75.3	131.3	108.2	47.0
C:N	25.7	28.6	37.3	6.8	7.0	8.0	8.7	13.4

Table VI.4. Matrix of similarity values (SIMI) based on amino acid percentages of experimental algal assemblages on days 8 and 32.

Day 8

	Control	125 Juga	50 Dico
Control	1.000		
125 Juga	.977	1.000	
50 Dico	.980	.973	1.000

Day 32

	Control	125 Juga	500 Juga	50 Dico	200 Dico
Control	1.000				
125 Juga	.990	1.000			
500 Juga	.993	.980	1.000		
50 Dico	.986	.982	.991	1.000	
200 Dico	.990	.981	.996	.988	1.000

Table VI.5. Correlation coefficients of selected algal taxa with prominent fatty acids and amino acids.

Taxon	16:0	16:1	16:3	18:3	20:5	Asp	Glu	Gly	Ser	Ala	Leu
Chlorophyta											
Scenedesmus obliquus	-.686	-.732	.627	.610	-.601	-.454	-.466	.404	-.214	-.237	.661
Characium sp. 1	-.774	-.789	.856	.844	-.851	-.177	-.004	.671	.691	-.750	-.001
Stigeoclonium tenue	.473	.418	-.517	-.515	.512	-.119	-.254	-.541	-.903	.621	.457
Cyanophyta											
Phormidium uncinatum	-.322	-.490	.435	.428	-.551	.419	.280	.450	.386	-.568	-.355
P. tenue	.768	.651	-.622	-.588	.578	.236	.292	-.510	-.303	.370	-.199
Bacillariophyta											
Synedra ulna	-.603	-.605	.718	.710	-.684	.117	.098	.478	.818	-.653	-.257
Nitzschia lancettula	.244	.465	-.519	-.582	.489	-.058	-.169	-.301	-.470	.461	.083
N. linearis	.345	.437	-.516	-.560	.450	.020	-.129	-.424	-.664	.387	.147
Navicula minima	.888	.975	-.934	-.929	.927	.249	.206	-.691	-.357	.674	-.289
Acnanthes lanceolata	.752	.767	-.741	-.686	.783	.255	.219	-.553	-.171	.551	-.312

VII. EFFECTS OF IRRADIANCE AND GRAZING ON ALGAL ASSEMBLAGES IN LABORATORY STREAMS

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ABSTRACT

Effects of grazing and irradiance on algal assemblages were monitored in laboratory streams over 75 days. As hypothesized, algal biomass was positively associated with irradiance, but grazing by moderate densities of the snail *Juga silicula* (500/stream) influenced this pattern. Algal biomass levels were similar between grazed and ungrazed streams after day 27 at high (400 $\mu E \cdot m^{-2} \cdot s^{-1}$) and intermediate irradiances (100 $\mu E \cdot m^{-2} \cdot s^{-1}$), indicating that the productive capacity of the algae was sufficient to meet the nutritional demands of *Juga* without exhibiting a noticeable decrease in standing crop. At the low irradiance (15 $\mu E \cdot m^{-2} \cdot s^{-1}$), biomass levels were also similar between the streams with and without snails (through day 43), but in this case the pattern was related to light-limited growth in ungrazed streams and grazer activity in streams with *Juga*. Effects of grazing on taxonomic structure were primarily a function of algal growth form. Adnate cells exhibited large relative abundances under grazed conditions, although the individual taxa varied depending upon light level. Large, overstory cells were vulnerable to grazing and decreased in relative abundance in streams with snails. Grazed assemblages were characterized by lower diversities than ungrazed assemblages, regardless of irradiance level, assemblage age, or type of dominant growth form. It is concluded that in natural streams, where light levels and grazer densities and types vary over time, a continuum of algal assemblage responses will be exhibited, which contributes

to the heterogeneity of stream benthos.

INTRODUCTION

Grazing and light energy have been identified as major determinants of algal community structure in lotic ecosystems (Whitton 1975, Gregory 1983). Previous studies have shown that both light quantity (McIntire 1968, Lyford and Gregory 1975, Shortreed and Stockner 1983, Lowe et al. 1986, Steinman and McIntire 1986) and quality (Antoine and Benson-Evans 1983) have an impact on community structure and accumulation of algal biomass in streams. Grazing also can reduce algal biomass (Bohle 1978, Gregory 1980, Lamberti and Resh 1983, McAuliffe 1984a, Lamberti et al. 1987) and change the species composition of a periphyton assemblage (Eichenberger and Schlatter 1978, Sumner and McIntire 1982, Hart 1985, Jacoby 1985). However, it is still unclear how the process of grazing influences irradiance-induced changes in the productive capacity of lotic algal assemblages.

The present study examined effects of grazing on benthic algal assemblages at different levels of light energy in laboratory streams, where irradiance and grazing pressures could be manipulated and controlled. Data from prior experiments were used to choose irradiance levels that ranged from severely light-limiting to photosynthetically-saturating (Steinman and McIntire submitted [a]), and a density of grazing animals that resulted in moderate levels of algal biomass reduction (Steinman et al. submitted [b]). The following hypotheses were examined: (1) at the highest irradiance level, algal productive capacity exceeds the

nutritional demands of the grazing animals and therefore little difference exists in algal biomass between grazed and ungrazed streams, although differences in community structure may be evident on a localized scale; (2) at an intermediate light level, algal growth is partially limited by irradiance so grazing activity maintains assemblages at a relatively early successional stage, and therefore differences in biomass and structure are detectable between grazed and ungrazed streams; and (3) at the lowest light level, the productive capacity of the algae is light-limited so biomass levels are low in channels with and without grazing, and differences in community structure are evident if animals graze in a selective manner.

MATERIALS AND METHODS

The design of the laboratory streams was described by Steinman and McIntire (1986). Water temperature remained at 13 $\pm$ 1 C throughout the experimental period. The exchange rate and nutrient concentration of the well water supply was similar to that reported by Steinman and McIntire (1986). Light energy was supplied by 16 1000-Watt Metalarc lamps (Sylvania Corp.), each mounted in a symmetrical Maxigro reflector. Three photon flux densities (PFD), with four replications of each PFD, were used to investigate the response of algal assemblages to light. Treatment PFD of approximately 15, 100, and 400 $\mu E \cdot m^{-2} \cdot s^{-1}$ were obtained by adjusting the height of the lamp fixtures and by placing green Chicopee screen with an appropriate mesh size over the streams. Timers were set to produce a daily photoperiod of 10:14 L:D. Rotating paddle wheels connected to a variable speed motor were used to maintain a current velocity of 10 $cm \cdot s^{-1}$ in all streams. The bottom of each stream was lined with 7.5 x 7.5 cm unglazed, ceramic tiles that provided a surface for colonization and units for periodic sampling. One of every six tiles had an upturned end to provide heterogeneity on the stream bottom.

Sixteen laboratory streams were used in this study. Experimental results were obtained from 12 of the 16 channels, and the remaining four were used as sources of replacement tiles (see below). At the start of the experiment, all laboratory streams were inoculated with one liter of an algal suspension obtained by

scraping rocks from four local streams (Steinman and McIntire 1986). The snail *Juga silicula* was collected from local streams, and 11 days after algal inoculation, snails were introduced into nine of the twelve experimental streams (i.e. of the four replicate streams at each PFD, three received snails). Therefore, one stream was kept free of snails at each PFD. Snails were introduced at the same density in each stream (500 snails per stream; total tissue dry weight of ca. 10 g). The experiment was terminated after 75 days.

For estimates of biomass accumulation, random samples of three 7.5 x 7.5 cm tiles were obtained from each of the 12 experimental streams on days 19, 27, 43, and 75. In addition, three tiles were randomly selected from one of the four streams exposed to each PFD on day 11 (before the snails were introduced). Biomass was determined by the method of McIntire and Phinney (1965).

For the quantitative analysis of species composition, two 7.5 x 7.5 cm tiles were randomly selected from each experimental stream on days 19, 27, 43, and 75. On day 11, two tiles were also taken from the same three streams sampled for biomass. Procedures for collection, fixation, microscopic examination, and counting were outlined by Steinman and McIntire (1986).

Streams that were used as sources of replacement tiles were exposed to a combination of irradiances and grazing pressures. This procedure generated a gradient of taxonomic structures among the algal assemblages. After a tile was removed from an experimental stream, a tile with similar biomass and community structure (judged

by macroscopic appearance) was selected as a replacement, thereby maintaining similar food density and type within an experimental stream.

Species composition of the algal assemblages was compared using the SIMI measure of similarity (McIntire and Moore 1977). This measure ranges from 0 to 1, and gives greater weight to dominant taxa. A value of 0 denotes that a given pair of assemblages have no taxa in common, while a value of 1 indicates that the two assemblages have identical species compositions and proportional abundances. SIMI values are reported for both biovolumes and cell numbers. Statistical analyses were performed with a Cyber 170/720 computer and an IBM PC using the program AIDN and the MGLH module of Systat (Systat, Inc. 1984), respectively.

RESULTS

Response of biomass to light and herbivory:

Algal biomass increased in all streams over the first 43 days of the experiment (Fig. VII.1). While streams exposed to 15 or 100 $\mu E \cdot m^{-2} \cdot s^{-1}$ continued to show an increase in biomass through day 75, biomass decreased between days 43 and 75 in the streams exposed to 400 $\mu E \cdot m^{-2} \cdot s^{-1}$. There was a positive association between irradiance and biomass level in all streams through day 43, regardless of whether or not snails were present. Comparisons between grazed and non-grazed streams revealed that herbivory by snails resulted in lower biomasses at each irradiance level on days 19 and 27. On days 43 and 75, however, biomass levels were quite similar in grazed and ungrazed streams exposed to 100 and 400 $\mu E \cdot m^{-2} \cdot s^{-1}$.

Response of algal taxa to light and herbivory:

Stigeoclonium tenue is a heterotrichous alga whose two growth stages (erect filaments and prostrate basal cells) are found in differing amounts depending upon local conditions. In this study, the relative abundances of both growth forms were generally greater in snail-present than snail-absent streams (Fig. VII.2). At 400 $\mu E \cdot m^{-2} \cdot s^{-1}$, this effect was less pronounced, especially with respect to basal cells. There was also a distinct difference in filament size among treatments. In streams with snails, the filaments were usually very short (5 to 20 cells long) and often were observed attached to the prostrate growth stage, while filaments from non-grazed streams were much longer (> 100 cells) and their point of

attachment to the prostrate portion was rarely seen. Both filament types were grouped together in Figure VII.2.

In most samples the relative abundance of Scenedesmus obliquus was greater in streams without grazers than in streams with snails (Fig. VII.2). This was particularly evident at intermediate and high irradiances. No general pattern was apparent in the relative amounts of the cyanophyte Phormidium tenue, although it was very abundant on day 75 in the low-light, snail-present streams.

The percentage abundance of Nitzschia linearis was generally greater in streams without snails than in streams with them, particularly on days 43 and 75 (Fig. VII.3). The relative amounts of Synedra ulna were also greater in snail-absent than snail-present channels, but this pattern was more pronounced on days 19 and 43 (Fig. VII.3). On day 75, irradiance level appeared to have a greater effect on the relative abundance of this taxon than the presence of snails. Streams treated with low light and the presence of snails exhibited substantially greater relative abundances of Cocconeis placentula v. euglypta relative to the other treatments (Fig. VII.3). The relative biovolume of Achnanthes lanceolata was larger in snail-present than snail-absent streams on day 19 at all irradiance levels (Fig. VII.3). However, this pattern was not observed on days 43 and 75, as the relative abundance of A. lanceolata decreased in all streams except the low-light, snail-absent channel.

Grazing by snails tended to enhance the relative abundance of adnate taxa such as Cocconeis placentula v. euglypta, Achnanthes

lanceolata, and the basal cells of Stigeoclonium tenue (Table VII.1). The relative abundance of the filamentous form of S. tenue also increased in grazed treatments, as grazing resulted in dense growths of short, cropped filaments. Conversely, cells that were characterized by large biovolumes and that did not have adnate growth forms, such as Synedra ulna, Nitzschia linearis, Fragilaria vaucheriae, and Scenedesmus obliquus, exhibited low relative abundances in the presence of snails.

Measurements of community response to light and herbivory:

Analysis by Time: On day 19, taxonomic structure was similar in all non-grazed assemblages, regardless of irradiance (Table VII.2, 15N vs 400N: SIMI = .842). In the streams with snails, different irradiance regimes resulted in moderate dissimilarities in community structure (15G vs 400G: SIMI = .575). On day 43, taxonomic structure was more dissimilar with respect to irradiance in the non-grazed streams (Table VII.3, 15N vs 400N: SIMI = .254) than in the grazed channels (15G vs 400G: SIMI = .424). SIMI values for day 75 were lower among the non-grazed (Table VII.4, 15N vs 400N: SIMI = .193) than the grazed communities (15G vs 400G: SIMI = .509) with respect to irradiance. However, structural similarity increased between days 43 and 75 among the intermediate and high light treatments in both sets of streams (Tables VII.4 and VII.5).

Comparisons of grazed vs. non-grazed assemblages exposed to the same irradiance revealed that on day 19 the greatest dissimilarities occurred at 400 $\mu E \cdot m^{-2} \cdot s^{-1}$ (400G vs 400N: SIMI =

.270), on day 43 the greatest difference was at 100 $\mu E \cdot m^{-2} \cdot s^{-1}$ (100G vs 100N: SIMI = .303), and on day 75 the largest dissimilarity occurred at 15 $\mu E \cdot m^{-2} \cdot s^{-1}$ (15G vs 15N: SIMI = .305).

Analysis by Irradiance: At the lowest irradiance, the structure of the non-grazed assemblage was dissimilar between days 19 and 43, but quite similar thereafter (Table VII.5; SIMI = .408 to .990). Conversely, the grazed assemblages exhibited a high degree of similarity between days 19 and 43 but high dissimilarity between days 43 and 75 (SIMI = .884 to .316). At 100 $\mu E \cdot m^{-2} \cdot s^{-1}$ (Table VII.6), both the non-grazed and grazed assemblages exhibited trends similar to those observed at 15 $\mu E \cdot m^{-2} \cdot s^{-1}$. At 400 $\mu E \cdot m^{-2} \cdot s^{-1}$ (Table VII.7), the non-grazed communities were moderately similar between days 19 and 43, and very similar between days 43 and 75 (SIMI = .602 to .903). The grazed assemblages, on the other hand, were characterized by similar taxonomic structures on days 19, 43, and 75 at this irradiance (SIMI = .914 to .868).

The effects of grazing on algal species diversity varied, depending upon whether the index was based on biovolume or cell count data (Table VII.8). When cell counts were used, diversity was generally lower in grazed relative to ungrazed assemblages. When diversity was based on biovolumes, diversity was generally higher in grazed than ungrazed streams through day 43, but lower by day 75. Non-grazed assemblages exposed to 15 $\mu E \cdot m^{-2} \cdot s^{-1}$ exhibited a gradual decrease in diversity values during the experiment, while those exposed to 100 and 400$\cdot \mu E ^{-2} \cdot s^{-1}$ displayed decreases between days 19 to 43, but increases between days 43 to 75. These trends

held for both biovolume and cell count data. Among grazed assemblages, diversity values decreased between days 19 to 43, regardless of irradiance or basis of diversity calculation. However, between days 43 to 75, diversity based on biovolume increased in the assemblages exposed to 15 $\mu E \cdot m^{-2} \cdot s^{-1}$ (but decreased when based on cell counts), and decreased in the assemblages exposed to 100 and 400 $\mu E \cdot m^{-2} \cdot s^{-1}$ (but increased when based on cell counts).

DISCUSSION

The results from this study indicated that irradiance and grazing strongly influence algal biomass in laboratory streams. Increased irradiance generally resulted in greater algal biomass, a finding which is in agreement with many prior field and laboratory studies (McIntire 1968, Lyford & Gregory 1975, Gregory 1980, Shortreed & Stockner 1983, Steinman & McIntire 1986). The decrease in biomass levels from days 43 to 75 in streams exposed to 400 $\mu E \cdot m^{-2} \cdot s^{-1}$ was attributable to sloughing of mature communities, as indicated by the high export rates of particulate organic matter in these channels (Gary Lamberti, pers. comm.).

Grazing by herbivores in streams has been shown to reduce algal biomass (Sumner & McIntire 1982, Lamberti & Resh 1983, McAuliffe 1984a, Lamberti et al. 1987) and the data in this study for days 19 and 27 support that finding. On days 43 and 75, however, there was very little difference in biomass between intermediate and high irradiance-streams with *Juga* and the corresponding streams without *Juga*. Other studies have failed to detect decreases in algal standing crop in the presence of grazers, and the investigators have attributed the lack of response to low grazing intensity (Kehde & Wilhm 1972, Gregory 1980). In general, the specific amount of biomass in a stream will depend upon many factors, including physical and chemical variables, growth rates of algal species, and the feeding behavior, mouthpart morphology and densities of the grazers present. Samples obtained on days 43 and

75 in this study indicated that under intermediate or high irradiance and moderate densities of snails, the productive capacity of the algae was sufficient to meet or exceed the nutritional demands of the animals and not exhibit a noticeable decrease in the biomass of the food resource.

Three explanations may account for the fact that biomass in grazed and ungrazed streams were similar on days 43 and 75: (1) both grazed and ungrazed assemblages exhibited equal productive capacities, but biomass loss from export in streams without snails was equivalent to the combined biomass lost by grazing and export in streams with snails; (2) the productive capacity of the grazed assemblages was greater than that of ungrazed ones, but ingestion by snails and/or higher export rates (due to disruption of mats by animal movement) in streams with snails reduced biomass amounts to levels found in ungrazed streams; or (3) ingestion rates decreased over time as snails became satiated, thereby obviating any grazing effects on biomass levels. The data indicate that on day 43, grazed assemblages had higher chlorophyll a-specific primary production (CSPP) rates than ungrazed assemblages, although rates were much more equivalent on day 75 (Stan Gregory, pers. comm.). Export rates of particulate matter (> 10 μm) were higher in the ungrazed than grazed streams at intermediate irradiances on days 43 and 75, but were similar on day 43 and higher on day 75 in grazed than ungrazed streams exposed to high light levels (Gary Lamberti, pers. comm.). Ingestion rates remained relatively constant throughout the experiment in streams exposed to intermediate irradiances and

increased slightly in streams subjected to high light levels (Gary Lamberti, pers. comm.). Therefore, different mechanisms appear to be operating at different times and in streams with different treatments through the experiment. On day 43, explanation (2) appears to best fit the data, as CSPP was greater in grazed then ungrazed streams, but high ingestion (and not export) rates reduced biomass levels. At day 75, however, explanation (1) best fits the data for streams exposed to intermediate irradiances, since CSPP rates were similar in grazed and ungrazed streams, and export rates were much greater in ungrazed than grazed streams. Explanation (2) may better fit the data for channels exposed to high irradiances on this day, since grazed assemblages had slightly higher CSPP rates and significantly larger export rates than ungrazed assemblages.

Regardless of which explanations account for the similar biomass levels in grazed and ungrazed streams, previous studies have shown that at a higher density than used in this experiment (1000 snails/stream), Juga was able to substantially reduce algal biomass, even at high irradiances (Steinman et al. submitted [b]). Therefore, it is proposed that algal biomass dynamics in natural systems may be explained, at least partially, by the interaction between herbivore grazing intensity (related to density and type) and algal productive capacity (related in large part to irradiance).

Irradiance and grazing also have a strong influence on algal taxonomic structure (Lyford and Gregory 1975, Sumner and McIntire

1982, Gregory 1983). In the present study, relatively high light levels were associated with greater abundances of *Stigeoclonium tenue* and *Scenedesmus obliquus*. This pattern is consistent with work previously conducted in laboratory channels (McIntire 1968, Steinman & McIntire 1986, submitted [a]) and natural streams (Lyford & Gregory 1975, Stockner & Shortreed 1983, Lowe et al. 1986), where greater abundances of filamentous chlorophytes were observed under conditions of high irradiance. It is unknown what mechanism accounts for the increased growth of these taxa under high light, but higher maximum rates of photosynthesis (Steinman and McIntire submitted [a]) and a requirement for light of a certain quality (Lowe et al. 1986) have been proposed as putative causes. Other taxa, such as *Achnanthes lanceolata* and *Cocconeis placentula* v. *euglypta*, exhibited greater abundances in streams exposed to low rather than high light levels in this study. High abundances of *Achnanthes* and *Cocconeis* have been observed at low irradiances in other studies (McIntire & Wulff 1969, Hudon & Bourget 1983, Goldsborough & Robinson 1986, Steinman & McIntire 1986). A prostrate growth form is susceptible to shading by overstory species, so tolerance to low irradiance may represent an adaptive strategy (Moss 1977). The greater abundance of *C. placentula* in grazed relative to non-grazed streams also suggests that competition for space with *Achnanthes lanceolata* may have occurred. *A. lanceolata* has been shown to form a monolayer on the tile substrate (Steinman & McIntire submitted [a]) and may prevent attachment and growth of *Cocconeis* by monopolizing space. Grazing

by Juga may have removed Achnanthes populations on a local basis, allowing Cocconeis cells to colonize and grow.

The effect of grazing on algal taxonomic structure was primarily a function of a taxon's growth form. Under grazed conditions, adnate taxa exhibited large relative abundances, while non-adnate forms generally were found in low relative amounts. Moore (1975a) proposed that the close physical attachment of adnate forms to the substrate made such taxa less vulnerable to consumption, which explained their high relative abundances under grazed conditions. The data from this study are consistent with this hypothesis, but they also indicate that a taxon's response to light level influences its relative abundance. For example, although the adnate growth form of Cocconeis placentula made it difficult for grazers to harvest this taxon, it only exhibited large relative abundances under low irradiance levels.

The association of grazing with a reduction in overstory or large, non-adnate attached taxa (e.g. Synedra ulna rosettes) was in agreement with the observations of Sumner & McIntire (1982). These growth forms decrease rapidly in relative abundance when harvested by Juga (Steinman et al. submitted [b]). The apparent increase of Stigeoclonium tenue filaments under grazed conditions was associated with a change in growth form. Examination of tile surfaces by scanning electron microscopy indicated that snails were rarely able to completely remove the algal material from the tile substrate (unpubl. data), and hence, when Stigeoclonium was

present, grazing activity resulted in a dense blanket of short, finely cropped filaments. These short filaments were morphologically distinct from the long, irregularly branched filaments observed in non-grazed treatments. Therefore, grazing actually led to a reduction in filamentous biomass, although it was not readily apparent from Figure VII.2 because both filamentous growth forms were lumped together in the "erect" catagory.

As hypothesized, the biomass and community structure of grazed and ungrazed assemblages were much more similar, at least initially, at the low than at the intermediate irradiance. A distinct difference in the taxonomic composition between grazed and ungrazed assemblages at low irradiance had developed by day 75, despite the fact that adnate growth forms were dominant in both. The dominance of Cocconeis placentula and Phormidium tenue in grazed assemblages, and A. lanceolata in ungrazed assemblages, suggested that snails may be selectively feeding among the taxa available at low irradiances. While some studies have suggested snails are selective feeders (Bovbjerg 1965, Calow and Calow 1975), others have found little evidence for this (see Gregory 1983). In the present study, the ungrazed assemblage was not replicated, so the data must be viewed cautiously. It may be that snails graze in a non-selective manner when food is scarce, such as at the beginning of this experiment, but graze selectively when food resources are more plentiful, such as at day 75.

Dissimilarity in community structure between grazed and ungrazed assemblages persisted longer at the intermediate

irradiance than at the high light level, validating in part the hypothesis that grazer-induced differences in community structure would be more detectable at intermediate than at high irradiances. However, grazer activity was unable to maintain algal assemblages in an early successional stage at the intermediate irradiance, and similar taxonomic structures developed between grazed and ungrazed assemblages by day 75. This suggests that an irradiance of 100 $\mu E \cdot m^{-2} \cdot s^{-1}$ was sufficient to allow vigorous algal growth.

Diversity values derived from cell counts almost always were lower in grazed than ungrazed assemblage pairs. This occurred regardless of irradiance, age of assemblage, or type of dominant algal growth form. The diversity values were particularly high for ungrazed assemblages exposed to an intermediate irradiance. This may have been a result of more algal species being able to grow at this light level than at either a high or low irradiance. Sumner and McIntire (1982) suggested that grazing should lead to a decrease in diversity when assemblages were dominated by adnate species, but not when dominated by large, overstory taxa. The fact that the streams in the present study were only seeded once, thereby precluding additional recruitment of new species, probably contributed to low diversity values in grazed assemblages.

The effects of irradiance and grazing on the relative abundance of different algal growth forms are summarized in a series of hypothetical growth curves (Fig. VII.4). In all ungrazed streams, the relative abundances of cells with large growth forms

(e.g. rosettes, long filaments) increased quickly. Other studies have found that the vertical community structure of periphyton assemblages starts out low, and proceeds to a high physical stature (Hoagland et al. 1982; Korte and Blinn 1983). However, the early colonization of Synedra ulna in this study (and others: Oemke and Burton 1986; Steinman and McIntire 1986) resulted in an assemblage with a high vertical structure at an early seral stage. At high irradiances, the large growth forms continued to dominate, as filamentous algae replaced Synedra. At low irradiances, however, the decline in Synedra relative abundance resulted in a shift from large to small growth forms.

The patterns were distinctly different in grazed streams compared to the ungrazed channels. In grazed streams, the cells with large growth forms were quickly reduced in relative abundance at all irradiances, presumably because of their vulnerable physiognomy. The relative abundances of cells with small growth forms increased over time at all irradiances, and remained very high at the lowest irradiance. At the intermediate irradiance, their relative levels declined slightly over time, while at the highest light level, they decreased somewhat more noticeably. Concurrent with decline of small cells was an increase in the relative abundance of cells with large growth forms. These increases were the result of two interrelated factors: (1) a reduction in grazer activity, presumably due to satiation; and (2) stimulation of filament growth at high irradiances.

The present research showed that by varying light levels and

grazer densities, it was possible to produce a continuum of algal responses. Therefore, it is proposed that in natural streams, the changing levels of irradiance and grazer density on both fine and gross spatial and temporal scales significantly contribute to the heterogeneity of benthic algal assemblages observed in lotic ecosystems.

ACKNOWLEDGEMENTS

We are very grateful to Linda Ashkenas for her technical assistance, Judy Li for her help in collecting and maintaining the animals, and Dean DeNicola for his help with sample collection. Stan Gregory and Gary Lamberti kindly provided the biomass data and collaborated with the authors on the design of the experiment. This study was supported by research grant No. BSR-8318386 from the National Science Foundation and a Sigma Xi Grant-In-Aid.

Table VII.1 Relative abundances of common algal taxa (based on cell numbers and biovolumes) pooled into the grazed and ungrazed groups of samples. Values for ungrazed treatments are the mean of 12 observations and values for grazed treatments are the mean of 36 observations.

Taxon	Biovolume Not Grazed	Biovolume Grazed	Numbers Not Grazed	Numbers Grazed
Chlorophyta				
Stigeoclonium tenue (erect)	9.98	27.15	6.51	14.31
S. tenue (basal cells)	0.64	4.00	3.53	11.31
Scenedesmus obliquus	9.45	1.13	13.91	1.11
Characium sp.1	1.67	0.31	1.39	0.18
Cyanophyta				
Phormidium tenue	1.28	4.99	19.37	37.01
Bacillariophyta				
Synedra ulna	24.18	5.22	2.44	0.33
Nitzschia linearis	9.46	2.10	1.54	0.23
N. oregona	2.61	0.70	4.64	1.12
N. lancettula	1.71	0.53	2.76	0.65
Fragilaria vaucheriae	3.39	1.96	6.53	2.97
Gomphonema parvulum	4.12	2.19	2.89	1.21
Navicula minima	5.37	6.18	15.85	11.59
Cocconeis placentula v. euglypta	0.34	4.29	0.07	0.44
Achnanthes lanceolata	18.16	32.61	7.13	12.06
Total	92.36	93.36	88.56	94.52

Table VII.2 Matrix of similarity values (SIMI) on day 19 of laboratory stream algal assemblages exposed to different irradiance levels. 15, 100, and 400 refer to irradiance levels (see methods); G = grazed treatment and N = non-grazed treatment. SIMI values are based on % biovolume.

	15G	100G	400G	15N	100N	400N
15G	1.000					
100G	.961	1.000				
400G	.575	.643	1.000			
15N	.475	.302	.238	1.000		
100N	.387	.276	.296	.931	1.000	
400N	.305	.189	.270	.842	.936	1.000

Table VII.3 Matrix of similarity values (SIMI) on day 43 of laboratory stream algal assemblages exposed to different irradiance levels. 15, 100, and 400 refer to irradiance levels (see methods); G = grazed treatment and N = non-grazed treatment. SIMI values are based on % biovolume.

	15G	100G	400G	15N	100N	400N
15G	1.000					
100G	.905	1.000				
400G	.424	.374	1.000			
15N	.871	.932	.132	1.000		
100N	.156	.303	.118	.116	1.000	
400N	.320	.304	.821	.254	.243	1.000

Table VII.4 Matrix of similarity values (SIMI) on day 75 of laboratory stream algal assemblages exposed to different irradiance levels. 15, 100, and 400 refer to irradiance levels (see methods); G = grazed treatment and N = non-grazed treatment. SIMI values are based on % biovolume.

	15G	100G	400G	15N	100N	400N
15G	1.000					
100G	.516	1.000				
400G	.509	.887	1.000			
15N	.305	.270	.355	1.000		
100N	.361	.708	.732	.271	1.000	
400N	.296	.642	.812	.193	.833	1.000

Table VII.5 Matrix of similarity values (SIMI) of laboratory stream algal assemblages exposed to 15 $\mu E \cdot m^{-2} \cdot s^{-1}$. 19, 43, and 75 refer to sampling dates. G = grazed treatment and N = non-grazed treatment. SIMI values are based on % bivolume.

	19G	43G	75G	19N	43N	75N
19G	1.000					
43G	.884	1.000				
75G	.316	.575	1.000			
19N	.475	.239	.111	1.000		
43N	.949	.871	.294	.408	1.000	
75N	.936	.887	.305	.307	.990	1.000

Table VII.6 Matrix of similarity values (SIMI) of laboratory stream algal assemblages exposed to 100 $\mu E \cdot m^{-2} \cdot s^{-1}$. 19, 43, and 75 refer to sampling dates. G = grazed treatment and N = non-grazed treatment. SIMI values are based on % biovolume.

	19G	43G	75G	19N	43N	75N
19G	1.000					
43G	.932	1.000				
75G	.377	.439	1.000			
19N	.276	.350	.295	1.000		
43N	.192	.303	.354	.330	1.000	
75N	.298	.399	.708	.438	.656	1.000

Table VII.7 Matrix of similarity values (SIMI) of laboratory stream algal assemblages exposed to 400 $\mu E \cdot m^{-2} \cdot s^{-1}$. 19, 43, and 75 refer to sampling dates. G = grazed treatment and N = non-grazed treatment. SIMI values are based on % biovolume.

	19G	43G	75G	19N	43N	75N
19G	1.000					
43G	.914	1.000				
75G	.868	.883	1.000			
19N	.270	.271	.605	1.000		
43N	.741	.821	.879	.602	1.000	
75N	.554	.594	.812	.697	.903	1.000

Table VII.8 Diversity indexes (Shannon common information index) for grazed (G) and non-grazed (N) assemblages on days 19, 43, and 75. Measures for grazed assemblages are a mean of three values, and indexes for non-grazed assemblages are based on a single observation. 15, 100, and 400 refer to irradiance level.

Assemblage	Biovolume	Cell Counts
Day 19:		
15G	2.36	2.63
15N	2.31	2.61
100G	2.60	2.08
100N	1.91	2.62
400G	2.12	2.16
400N	2.00	2.37
Day 43:		
15G	1.60	1.29
15N	1.70	1.34
100G	1.84	1.17
100N	1.64	1.85
400G	1.87	1.57
400N	1.17	1.97
Day 75:		
15G	1.84	0.49
15N	1.50	1.25
100G	1.15	1.36
100N	2.45	2.02
400G	1.80	1.76
400N	2.10	2.19

Figure VII.1 Biomass accumulation of algal assemblages (expressed as ash-free dry weight) in laboratory streams with and without snails and exposed to 15, 100, or 400 $\mu E \cdot m^{-2} \cdot s^{-1}$.

Figure VII.1

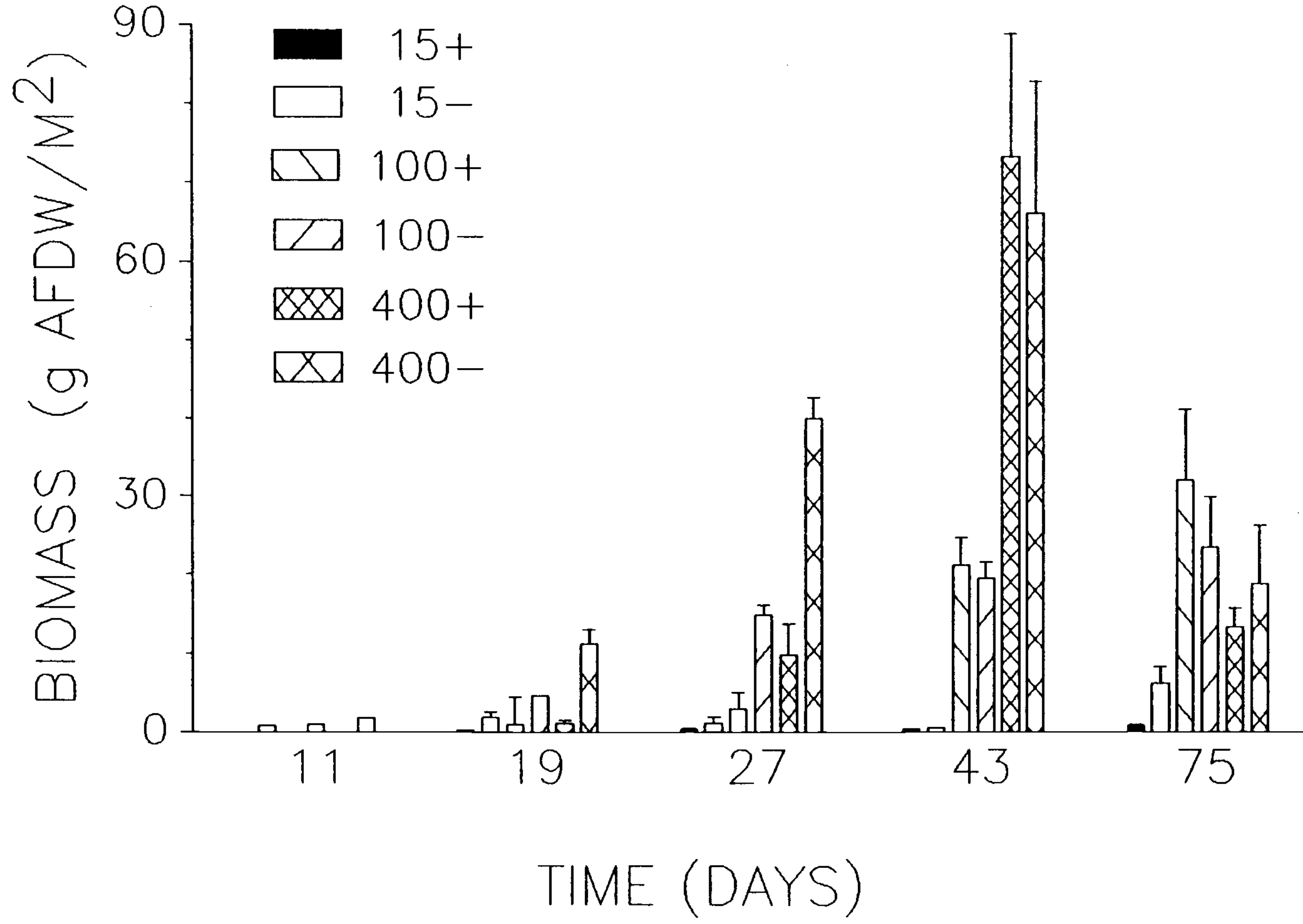

Figure VII.2 Relative abundance of dominant chlorophytes and cyanophyte in laboratory streams with and without snails and exposed to 15, 100, or 400 $\mu E \cdot m^{-2} \cdot s^{-1}$.

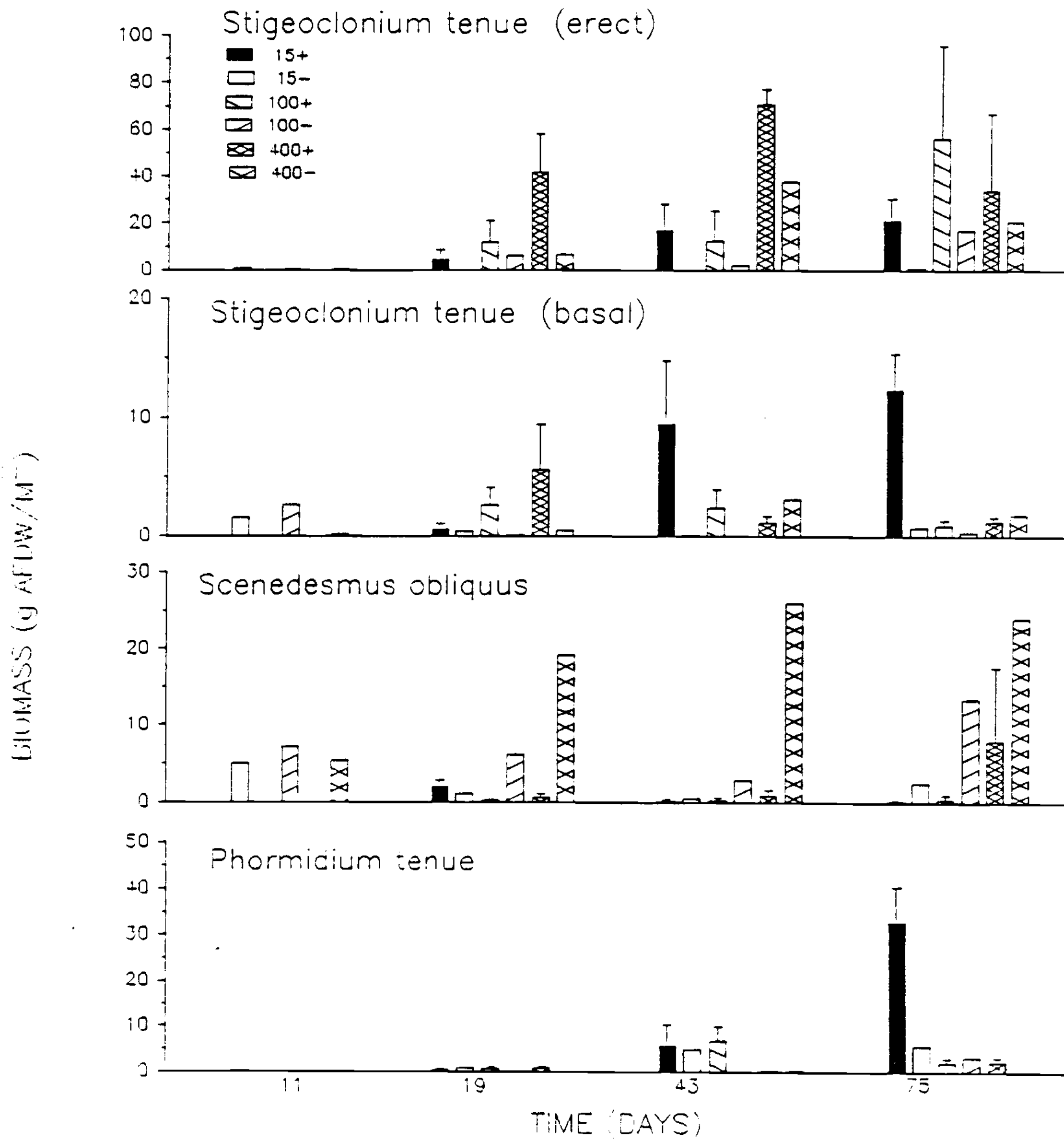

Figure VII.2

Figure VII.3 Relative abundance of dominant diatoms in laboratory streams with and without snails and exposed to 15, 100, or 400 $\mu E \cdot m^{-2} \cdot s^{-1}$.

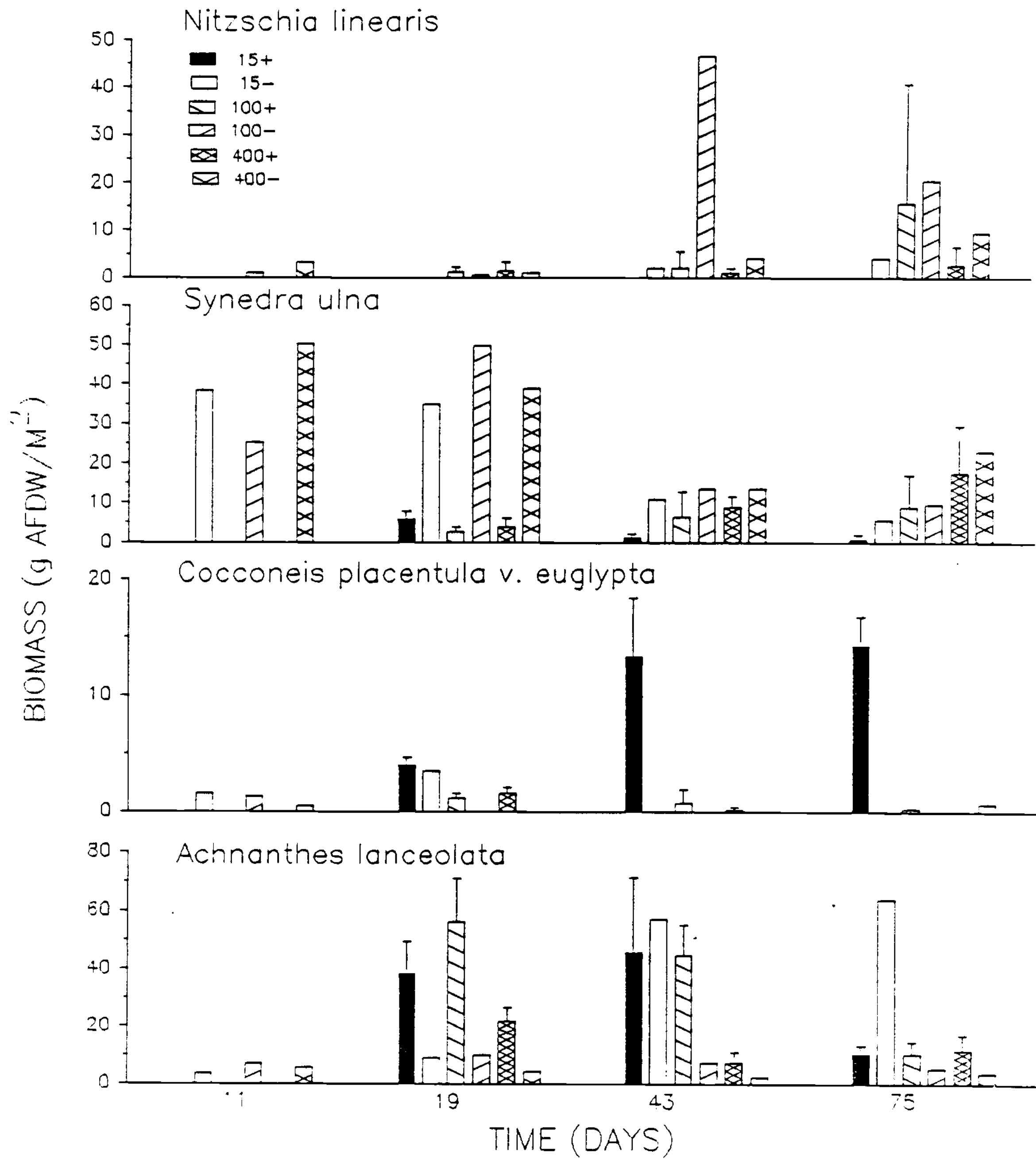

Figure VII.3

Figure VII.4 Proposed relative abundances for algae with different growth forms grown in laboratory streams with and without snails, and exposed to low (15), intermediate (100), or high (400 $\mu E \cdot m^{-2} \cdot s^{-1}$) irradiances. Open circles refer to large growth forms (e.g. filaments, chains, rosettes, solitary large cells); closed circles refer to small or adherent growth forms (e.g. adnate cells, basal cells, adherent filaments or crusts).

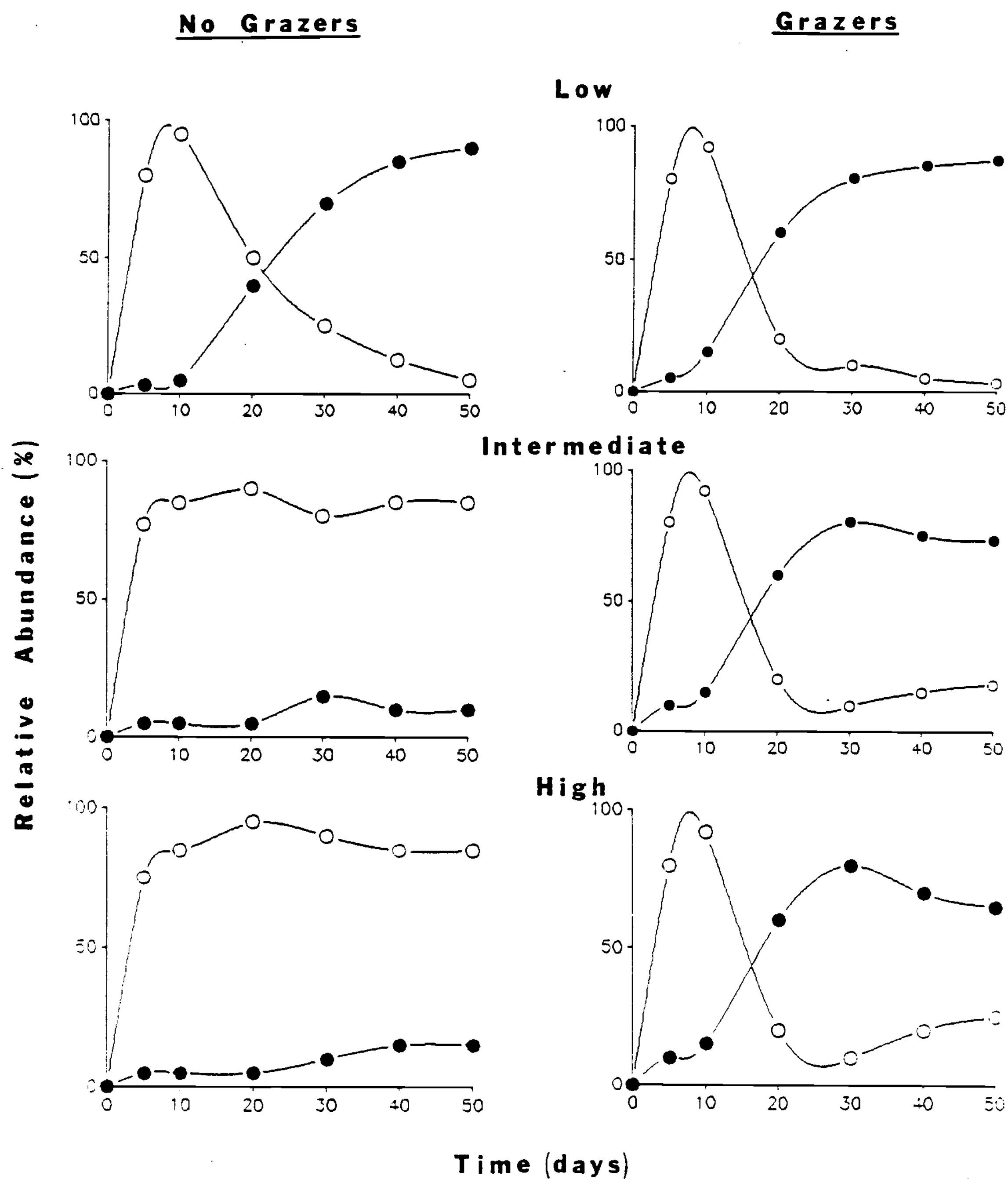

Figure VII.4

VIII. SYNTHESIS

It is a common paradigm among stream ecologists that most lotic ecosystems are heterotrophic in nature, with an energy base derived primarily from allochthonous sources (Hynes 1975, Vannote et al. 1980). As a consequence, primary producers have received relatively little attention by stream ecologists. However, several factors suggest that these organisms, and the algal assemblages in particular, may play an important role in stream ecosystems. For example, recent research has revealed that autotrophic production provides the overwhelming majority of fixed carbon in certain stream systems (e.g. thermal streams [Naiman 1976] and desert streams [Cushing and Wolf 1984]). Indeed, even in streams commonly considered heterotrophic, primary production may play an important role (Minshall 1978, Gregory 1980). The relatively low biomasses at which benthic algae usually are found may have contributed to the perception that these organisms play a minor role in streams. However, both modeling (McIntire 1973) and empirical studies (Gregory 1980, Sumner and McIntire 1982) have shown that despite low standing crops, lotic algal assemblages can support grazer biomasses ca. 10-20 times greater than their own because of high algal turnover rates. In addition, the nutritive quality of algae tends to be higher than that of allochthonous material (Anderson and Cummins 1979, Fuller and Mackay 1981), so a small amount of algae may be nutritionally or energetically equivalent to a large quantity of allochthonously-derived particulate matter. Macroalgal

assemblages also may provide structurally complex substrates to which fauna can attach, seek refuge, or graze (Scheffer et al. 1984, Dudley et al. 1986).

The study of benthic algal assemblages in lotic environments need not be justified solely on the role of algae in trophic level interactions. Short generation times of algal species, the strong influence of seasonal changes on community structure (Busch 1978), the persistence of algal propagules on benthic substrates (Wehr 1981, Sheath et al. 1986a), and the need for these assemblages to adapt to a high frequency of perturbation and constant, unidirectional flow combine to produce plant assemblages with unique attributes. Thus, research on benthic algae will not only strengthen the knowledge of trophic level dynamics in stream ecosystems, but also may provide insights into plant community ecology at different temporal and spatial scales than those normally associated with terrestrial vegetation.

For this disseration, experiments were conducted in laboratory streams to determine the role of two physical factors (current velocity and irradiance) and one biological factor (grazing) in regulating the dynamics of benthic algal assemblages. Although these factors act in concert with each other to influence the dynamics of algal assemblages, the effects of each one first will be reviewed separately, in an attempt to understand how they operate apart from each other. The interactive effects of these factors will then be examined in a final synthesis section.

<u>Current Velocity</u>: Current velocity may influence stream algal

communities in at least three different ways: (1) enhance colonization of primary substrate by algae in low flow regimes (McIntire 1966, Reisen and Spencer 1970, Stevenson 1983); (2) stimulate growth of established algal communities at relatively high current velocities (Whitford and Schumacher 1964, McIntire 1966, Horner and Welch 1981); and (3) remove attached algae from substrate at high current velocities because of increased shear stress (Douglas 1958, Horner and Welch 1981). Current may also result in a change of algal assemblage physiognomy. For example, Keithan and Lowe (1985) observed primarily adnate cells in fast flow areas of a Tennessee stream, while more structurally complex physiognomies were found in areas with slow currents. The results from this study are consistent with the first effect: algal colonization was faster at a lower current velocity (5 $cm \cdot s^{-1}$) than at a higher current velocity (15 $cm \cdot s^{-1}$) through day 4, regardless of irradiance level. The reduced turbulance and shear stress associated with the lower current velocity presumably resulted in higher immigration rates than those in the faster flow regime. After day 4, however, the effect of irradiance on algal growth became apparent, and the influence of current velocity alone could no longer be discerned. In terms of biomass accumulation, there was a positive interaction between irradiance and current velocity. This provided indirect evidence for effect (2): high flow may enhance algal growth by allowing a rapid exchange of nutrients and dissolved gasses to occur between algal cells and the aquatic

medium.

Recent research has indicated that differences in taxonomic composition and morphology of algal mats may not be attributable to current velocity (Reiter and Carlson 1986). These investigators, using laboratory flumes, showed that algal mats modify local current velocities to produce increasingly similar local velocities, regardless of the free-water velocity (i.e. velocity away from the mat). Reiter and Carlson's (1986) results are difficult to reconcile with observed metabolic increases under high current velocities (Whitford and Schumacher 1964, McIntire 1966, point (2) above), although the results obtained by Reiter and Carlson may have been influenced by their flume design and the algal growth forms used in their study (see Lock and John 1979).

Irradiance: Irradiance is the primary source of energy for algal assemblages in lotic ecosystems. Changes in light regime can influence taxonomic composition (McIntire 1968, Lyford and Gregory 1975, Antoine and Benson-Evans 1983, Shortreed and Stockner 1983, Sheath and Burkholder 1985), biomass (McIntire 1968, Lyford and Gregory 1975, Murphy and Hall 1981, Shortreed and Stockner 1983), and primary production (Gregory 1980, Duncan and Brusven 1985, Jasper and Bothwell 1986). Results from this dissertation are consistent with irradiance levels influencing algal community structure and biomass. Specifically, relatively high levels of irradiance generated a greater relative abundance of filamentous green algae, a lower relative abundance of adnate diatoms, and higher overall biomass than low irradiance levels.

Despite the similarity of algal responses to light in this and other studies, some interesting questions regarding the role of light in lotic ecosystems still need to be resolved. For example, (1) are the taxonomic changes a result solely of light quantity, or does light quality also play a role; and (2) are light-induced changes in the relative abundances of certain taxa a result of competitive interactions among algal species, or are they simply different autecological responses by different taxa?

The increased abundance of filamentous chlorophytes under high light levels may be a response to absorption of light from the blue and red portions of the visible light spectrum. The primary pigment of light absorption in both riparian vegetation and green algae is chlorophyll a, which preferentially absorbs blue and red light. Under shaded conditions, relatively low amounts of blue and red light may reach the stream benthos because light of these wavelengths already has been absorbed by the chlorophyll a in the leaves of the canopy (Salisbury and Ross 1985). Therefore, green algae may be both quantitatively and qualitatively light-limited under these conditions. A seasonal survey of macroalgal dynamics in Rhode Island streams revealed that during summer months, filamentous green algae were abundant in streams with no canopy, but were absent in heavily shaded streams of the same order (Sheath and Burkholder 1985). Experimental manipulations employing selective filters could be informative in assessing the influence of light quality on the dynamics of algal populations in streams.

The role of competition in structuring algal assemblages in lotic ecosystems is unknown because of inherently fast growth rates of most species, high frequencies of perturbation to the communities, and difficulties in performing experimental manipulations. In addition, the structural and taxonomic complexity of the assemblages on very small scales makes it extremely difficult to tease apart indirect effects that may be occurring among individuals or populations. It would appear that new approaches to the study of these assemblages are necessary before the importance of competition can be assessed.

Grazing: Grazing by animals in lotic ecosystems has been shown to have at least four distinct effects on benthic algal assemblages: (1) reduce the biomass (Gregory 1980, Sumner and McIntire 1982, Lamberti and Resh 1983, McAuliffe 1984a, Jacoby 1985); (2) change the taxonomic composition (Eichenberger and Schlatter 1978, Sumner and McIntire 1982, Hart 1985, Jacoby 1985); (3) stimulate primary production (Gregory 1980, Lamberti et al. 1987); and (4) influence nutrient recycling (Mulholland et al. 1983).

Results from this study have shown that grazers can reduce biomass and change the taxonomic structure of algal assemblages. *Juga silicula* and *Dicosmoecus gilvipes* were capable of reducing algal biomass to 10% of the amount found in non-grazed streams, although reduction levels were a function of grazer density. Changes in taxonomic structure involved the removal of upright, clumped, and filamentous growth forms (*Synedra* spp.,

chlorococcalean taxa, and *Stigeoclonium tenue*, respectively), with subsequent dominance by adnate cells which grazer mouthparts apparently were unable to reach (e.g. *Achnanthes* spp. and *Stigeoclonium* basal cells).

Aquatic invertebrates exhibit a wide range of mouthpart morphologies and modes of feeding. Hence, these characteristics often delimit the size, shape and location of food that can be ingested (Cummins and Klug 1979). Attempts to attribute the greater efficacy of *Dicosmoecus* at removing algal biomass, relative to *Juga*, to a specific factor were complicated by the fact that at any given density, the tissue dry weight of the caddisflies was slightly greater than that of the snails. However, the difference was relatively small. Thus, the large disparity in algal biomass between streams with the lowest densities of *Juga* and *Dicosmoecus* was attributable, at least in part, to differences in their rates and modes of feeding. *Juga* grazed in discrete areas, moved at rates of less than 0.2 $cm \cdot min^{-1}$ (Judy Li, pers. comm.), and used radula to rasp at food items. *Dicosmoecus*, on the other hand, moved almost continuously, exhibited movement rates of between 10-58 $cm \cdot min^{-1}$ (Judy Li, pers. comm.), and used mandibles to scrape at food items. Consequently, at low densities *Dicosmoecus* grazed over a greater area per unit time than *Juga*, and was more effective at maintaining the algal assemblages in a simple physiognomy with relatively few vertically oriented cells. In regions where grazing by *Juga* was evident, however, algal community structure was very similar to

that observed in areas grazed by caddisflies, despite their different mouthpart morphologies. It appears that for laboratory stream assemblages grown on flat, relatively smooth tile surfaces, rasping and scraping do not result in very different types of algal community structure.

Integration: In this dissertation, three factors that potentially influence the dynamics, and in particular the successional trajectories, of lotic, benthic algal assemblages were studied. The study of succession in freshwater periphyton communities has been the focus of several recent studies (Hudon and Bourget 1981, Hoagland et al. 1982, Korte and Blinn 1983, Hamilton and Duthie 1984, Lowe et al. 1986, Steinman and McIntire 1986). Application of traditional successional theory (e.g. Connell and Slatyer 1977) to these communities has failed to provide a model which completely describes the temporal changes observed in them (Goldsborough and Robinson 1986). The facilitation model suggests that early colonists modify the environment and make it suitable for growth by later colonists. Bacteria and diatom-derived organic mucilage may facilitate settlement of early algal colonizers in aquatic habitats (Hoagland et al. 1982, Korte and Blinn 1983, Roemer et al. 1984). Apart from exuded mucilage, however (Stevenson 1983), it remains unclear whether or not facilitation by algae is common and/or effective in streams, since most algal species have relatively high growth rates and lotic communities are subject to a high frequency of disturbance.

The tolerance model of succession (Connell and Slatyer 1977)

implies that competition is occurring, as the species best adapted to the present environmental conditions dominates. Although competitive interactions have been inferred among algal species in streams (Steinman and McIntire 1986), evidence for the tolerance model is lacking among lotic algal assemblages due to the high frequency of disturbance and difficulty in manipulating these taxa for competition experiments. The rapid increase of a previously unobserved taxon after a drastic change in incident light level of a headwater stream (Sheath et al. 1986a) indirectly suggests that lotic algae can tolerate unfavorable growth conditions for long periods of time. The data from the present study provide additional indirect evidence that the tolerance model of succession may be operating in algal assemblages. Although all streams began with similar inocula in each experiment, low-irradiance streams consistently ended up with large amounts of *Achnanthes lanceolata*, suggesting that this taxon has a high tolerance for low light levels. Tolerances to grazing pressure provide additional complexity to the model, as some species (or growth forms) may be tolerant of a certain light regime and the presence or absence of grazers (e.g. *C. placentula*'s apparent tolerance of low light and grazing by *Juga*).

In the inhibition model of succession (Connell and Slatyer 1977), early colonizers preclude the growth of future species. The data from the present study fail to support this model, at least with respect to the earliest colonizers. *Synedra ulna* dominated

early seral stages in most experiments, but it was unable to inhibit the growth of other species, as it was eventually replaced in most treatments.

Grazing can alter successional trajectories, and in the process, potentially provide evidence for which model of succession, if any, is operating in the laboratory streams. For example, Lubchenco and Gaines (1981) cited examples in the marine intertidal where the removal of early colonizers by grazing resulted in an enhancement of the succession rate, thereby suggesting that the early colonists were inhibiting the growth of later colonists. Conversely, Brown (1984) showed that grazing of ruderal plant species slowed down the rate of succession, presumably because facilitation was prevented.

The mechanisms invoked by Lubchenco and Gaines (1981) and Brown (1984) by which grazing altered plant community succession may not be applicable to the algal assemblages examined in this study, since neither facilitation nor inhibition were apparent. It is possible, however, that given different physical/chemical conditions or a different species pool, these processes may have occurred. Two factors, in particular, complicate the study of succession and the influence of grazing upon it in lotic ecosystems: (1) succession in natural streams rarely occurs on substrates totally devoid of algal cells (Wehr 1981); hence, the presence of these algal propagules may influence the settlement and growth patterns of algal colonists; and (2) the time scale by which algal assemblages operate in lotic ecosystems is much shorter than

in terrestrial or marine intertidal systems. As a consequence, enhancement or retardation of succession rates by grazing are more difficult to assess. It certainly appears that grazing can alter the sere of an ungrazed assemblage, as grazing can remove taxa in the overstory and result in prolonged dominance of taxa with less vulnerable, adnate growth forms (see Chapter V). However, more information is needed on finer temporal and spatial scales before a better understanding can be obtained of how succession operates in algal stream assemblages. Ultimately, we may find that no one model adequately explains succession in these communities, and that several models will need to be invoked, depending upon local physical, chemical, and biological conditions.

Figure VIII.1 presents a process model that schematically represents a herbivory subsystem in a lotic ecosystem. The theory behind process models and the conventions used in their portrayal are reviewed by McIntire (1983). Briefly, solid arrows indicate an input/output of matter and/or energy while dashed arrows indicate a coupling to the process of interest that does not involve transfer of matter or energy. Circles denote a biological process (e.g. primary production and grazing), solid rectangles refer to the state variables internal to the process of interest, dashed rectangles indicate state variables coupled to the process of interest, and solid ovals denote physical and chemical variables controlling or affecting the process of interest.

In Figure VIII.1, current velocity is portrayed as a physical

(nonresource) variable, along with temperature and other physical processes that affect the process of primary production. Light energy is viewed as a resource variable that influences primary production. Grazing is depicted as a separate process that is energetically coupled to primary production, with the arrow denoting the transfer of energy that occurs when autotrophs are consumed by grazers. It should be noted that consumption of primary producers also has a quantitative and qualitative effect on the process capacity of the primary production subsystem. Quantitatively, grazing reduces the biomass of autotrophs, while qualitatively, grazing changes the physiognomic, taxonomic, and chemical structure of the primary producers. Thus, the process of herbivory, which McIntire and Colby (1978) conceptualized as encompassing both primary production and grazing subsystems, should be viewed as an interactive process (Gregory 1983).

The data collected in this study make it possible to predict the responses of both the quantitative (i.e. biomass) and qualitative (i.e. taxonomic structure, chemical composition) components of the process capacity associated with the primary production subsystem. Different responses are proposed for each unique set of input functions (e.g. high/low irradiance, fast/slow current) and grazing parameters (e.g. Juga/Dicosmoecus, high/low/zero density) in Tables VIII.1 and VIII.2. The biomass and community structure responses proposed in these tables stem from the experimental results of this dissertation. However, not every one of the 20 unique conditions in Tables VIII.1 and VIII.2 was

actually examined. For those conditions not investigated, responses are hypothetical constructs based on the collective results of two or more separate experiments.

A number of interesting points arise from the proposed responses in these tables:

(1) Current velocity had an effect on biomass under only one set of conditions: high irradiance and grazer-absent (conditions [A] and [B]); a fast current resulted in larger biomasses than slower currents, presumably because of enhanced exchange rates. Differences in flow regime alone never affected the structure of mature assemblages. The relatively small difference in the current velocities used (5 and 15 cm$\cdot$ s^{-1}) and the fact that even the higher current velocity was relatively slow compared to natural stream conditions may have been responsible for the lack of a more pronounced effect.

(2) As discussed previously, high irradiance levels resulted in both a large accumulation of biomass and the growth of filamentous chlorophytes.

(3) Because grazing by *Juga* was localized, patches of grazed and ungrazed algal regions developed, regardless of snail density. Under high irradiances, ungrazed patches were characterized by dense algal mats with chlorococcalean taxa, diatoms, and filamentous chlorophytes, while adnate diatoms and *Stigeoclonium* basal cells and short filaments dominated

the grazed areas. Ungrazed patches exposed to low irradiances were composed primarily of adnate, rosette- and chain-forming diatoms. The grazed patches also were composed primarily of diatoms (and some *Phormidium*), but these cells all exhibited an adnate growth form.

(4) Unlike streams with *Juga*, grazed and ungrazed patches never developed in streams with *Dicosmoecus*, regardless of density, because of the caddisfly's vagility and ability to remove material with its tarsi. As a consequence, the algal assemblages were comprised mostly of adnate forms. Under high irradiances, both diatoms and chlorophytes were present, while diatoms and some adherent cyanophytes were observed in streams exposed to low irradiance levels.

(5) Chemical structure can also be used to express the qualitative component of the process capacity of the primary production subsystem, even though it was not included in Tables VIII.1 and VIII.2. Results from this study suggest that under certain conditions, algal assemblages contained relatively predictable fatty acid profiles. For example, assemblages exposed to low irradiances and heavy grazing pressure were characterized by high proportions of 16:1 and 20:5 fatty acids, while assemblages exposed to high irradiances and low grazing pressure exhibited high relative abundances of 16:3 and 18:3 fatty acids.

Taken together, Figure VIII.1 and Tables VIII.1 and VIII.2 provide a conceptual model of algal dynamics in lotic ecosystems

and integrate the responses of both quantitative and qualitative components. Although the model proposed is incomplete, it can be used to generate hypotheses about how algal assemblages respond at the process or organismal level to irradiance, current velocity, and grazing in natural streams. As more information becomes available concerning how nutrients, substrate type, disturbance patterns, grazer mouthpart morphology and feeding behavior, and mechanisms and rates of algal dispersal and colonization affect lotic algal assemblages, the model can be updated and refined. A more complete model will enhance our understanding of the dynamics of benthic algal assemblages and how they interrelate with other biological processes in lotic ecosystems.

Table VIII.1 Proposed responses of biomass and community structure of a "mature" algal assemblage to the combined effect of fast/slow current velocity, high/low irradiance, and different densities of *Juga silicula*.

	Current Velocity		Irradiance		Density			Biomass	Community Structure
	Fast	Slow	Hi	Low	Hi	Low	Abs		
A)	+		+				+	Very High	Dense mats; filamentous greens; various diatoms
B)		+	+				+	High	Similar to "A"
C)	+			+			+	Mod. Low	Loose mats; adherent blue-greens; various diatoms
D)		+		+			+	Mod. Low	Similar to "C"
E)	+		+			+		High	Dense mats (see "A"); patches of adnate cells
F)		+	+			+		High	Similar to "E"
G)	+			+		+		Low	Various diatoms--forms differ among patches
H)		+		+		+		Low	Similar to "G"
I)	+		+		+			Mod. Low	Similar to "G"
J)		+	+		+			Mod. Low	Similar to "G"
K)	+			+	+			Very Low	Adnate diatoms
L)		+		+	+			Very Low	Adnate diatoms

Table VIII.2 Proposed responses of biomass and community structure of a "mature" algal assemblage to the combined effect of fast/slow current velocity, high/low irradiance, and different densities of *Dicosmoecus gilvipes*.

	Current Velocity		Irradiance		Density			Biomass	Community Structure
	Fast	Slow	Hi	Low	Hi	Low	Abs		
A)	+		+				+	Very High	Dense mats; filamentous greens; various diatoms
B)		+	+				+	High	Similar to "A"
C)	+			+			+	Mod. Low	Loose mats; adherent blue-greens; various diatoms
D)		+		+			+	Mod. Low	Similar to "C"
E)	+		+			+		Mod. Low	Adnate forms (diatoms; "Stig" basal cells
F)		+	+			+		Mod. Low	Similar to "E"
G)	+			+		+		Low	Adnate diatoms
H)		+		+		+		Low	Adnate diatoms
I)	+		+		+			Low	Similar to "E"
J)		+	+		+			Low	Similar to "E"
K)	+			+	+			Very Low	Adnate diatoms
L)		+		+	+			Very Low	Adnate diatoms

Figure VIII.1 Schematic representation of herbivory system showing factors influencing the processes of primary production and grazing in lotic ecosystems. Symbols and conventions are discussed in text. Aspects of the model covered in this dissertation are presented in boldface.

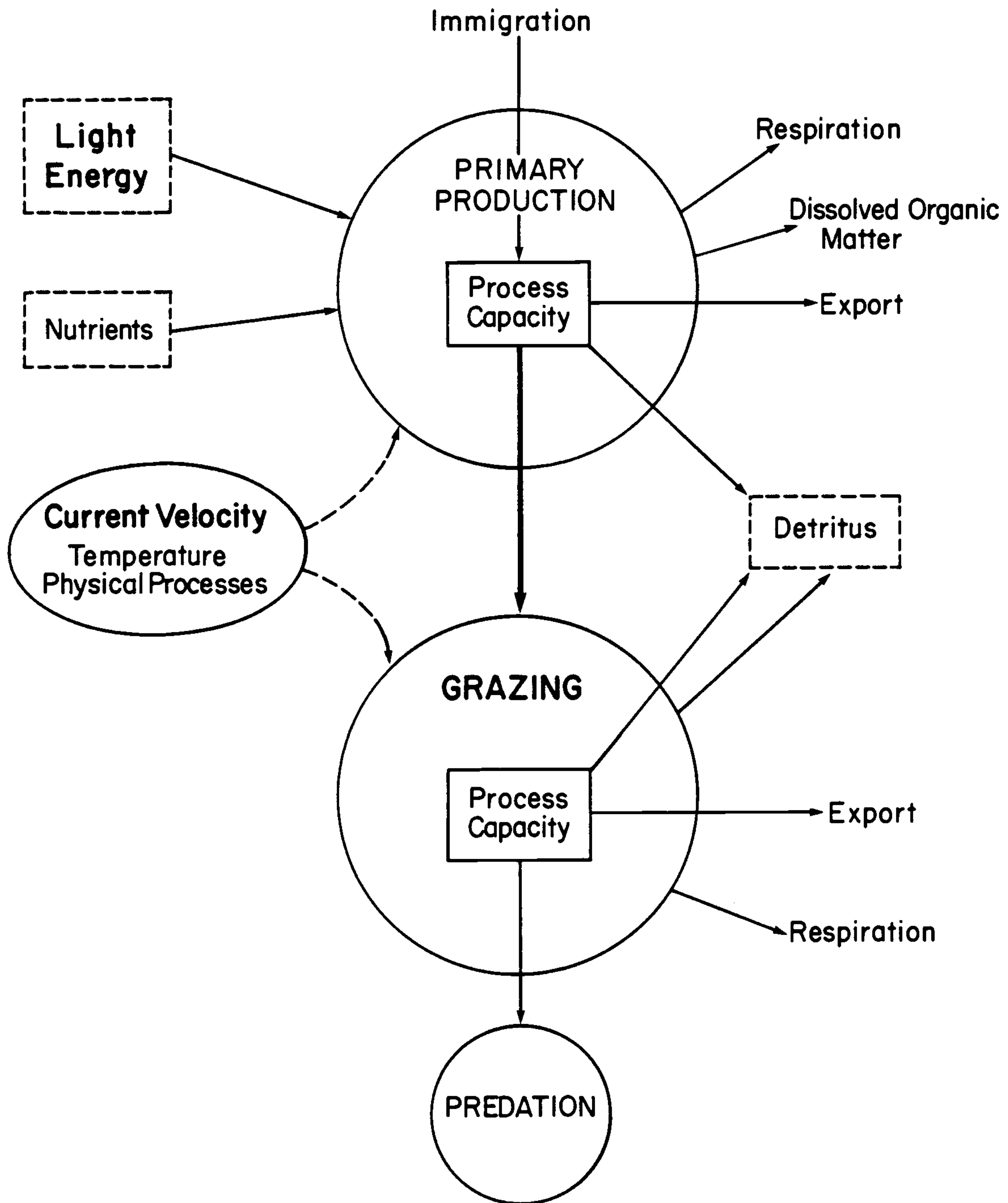

Figure VIII.1

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X. APPENDICES

Appendix I

Table AII.1 Relative abundance of selected algal taxa on day 8 in laboratory streams expressed as % biovolume of total assemblage biovolume. The values for both replications of each treatment are given. Treatment designators are defined in the text. Stig = Stigeoclonium; Klebs = Klebsormdium; Frag = Fragilaria; Ach = Achnanthes.

	Day 8			
Taxa	450:5	450:15	50:5	50:15
Chlorophyta				
Stig tenue[1]	0.5/4.2	1.3/0.3	1.9/0.6	0.3/1.0
Ulothrix zonata	0/0	0/75.3	0/0	0/29.8
U. tenerrima	7.0/1.6	7.7/6.2	7.3/0	7.0/1.9
Klebs fluitans	0/0	0/0	0/12.8	1.2/0
Bacillariophyta				
Synedra ulna	47.9/26.9	44.2/7.0	18.6/43.4	49.2/30.4
S. rumpens v. familiaris	17.2/22.1	20.3/4.5	13.7/8.8	13.1/9.8
Frag vaucheriae	4.9/6.8	6.0/1.6	5.8/3.8	5.6/5.0
Nitzschia oregona	3.3/4.9	1.5/0.9	7.3/2.9	1.9/2.3
N. dissipata	1.2/1.7	0.6/0.2	7.6/2.3	1.7/3.0
N. linearis	4.3/4.0	5.1/1.0	4.6/4.7	4.1/5.0
Ach lanceolata	2.3/7.8	4.4/2.2	4.5/1.6	3.6/6.4

[1] includes both filamentous and basal cells.

Table AII.2 Relative abundance of selected algal taxa on day 16 in laboratory streams expressed as % biovolume of total assemblage biovolume. The values for both replications of each treatment are given. Treatment designators are defined in the text. Stig = Stigeoclonium; Klebs = Klebsormdium; Frag = Fragilaria; Ach = Achnanthes.

	Day 16			
Taxa	450:5	450:15	50:5	50:15
Chlorophyta				
Stig tenue[1]	39.3/21.4	5.5/9.3	0.3/0.1	0.1/0
Ulothrix zonata	4.8/0	0/0	0/0	0/0
U. tenerrima	0/1.1	0/0	0/0	0/0.3
Klebs fluitans	0/0	0/0	0/0	4.5/0
Bacillariophyta				
Synedra ulna	30.6/44.9	45.4/35.1	14.9/45.5	41.7/35.9
S. rumpens v. familiaris	12.8/13.8	12.9/6.7	24.0/14.2	8.3/6.1
Frag vaucheriae	2.5/2.1	5.9/4.4	6.0/3.7	2.1/2.7
Nitzschia oregona	0.8/1.9	1.5/1.6	2.9/1.9	0.6/1.6
N. dissipata	0.3/0.6	0.4/0	1.7/1.8	0.9/0.6
N. linearis	2.5/4.3	2.7/3.6	15.7/8.7	6.0/6.3
Ach lanceolata	1.8/2.9	18.6/31.3	25.4/14.0	30.6/42.1

[1] includes both filamentous and basal cells.

Table AII.3 Relative abundance of selected algal taxa on day 32 in laboratory streams expressed as % biovolume of total assemblage biovolume. The values for both replications of each treatment are given. Treatment designators are defined in the text. Stig = Stigeoclonium; Klebs = Klebsormdium; Frag = Fragilaria; Ach = Achnanthes.

	Day 32			
Taxa	450:5	450:15	50:5	50:15
Chlorophyta				
Stig tenue[1]	29.6/53.8	39.4/56.8	2.8/1.2	0/35.4
Ulothrix zonata	13.3/0	0/0	0/0	0/0
U. tenerrima	0/0	0/0	0/0	0/0
Klebs fluitans	0/0	0/0	0/0	0/0
Bacillariophyta				
Synedra ulna	17.5/9.1	35.1/24.2	7.0/18.4	24.1/6.7
S. rumpens v. familiaris	11.5/13.2	5.6/1.3	10.6/8.7	12.2/10.1
Frag vaucheriae	5.4/2.5	4.0/2.1	3.9/4.0	2.6/6.3
Nitzschia oregona	2.2/4.0	1.1/0.5	2.0/3.9	1.7/2.5
N. dissipata	0/0	0/0	1.8/0.3	0.4/1.0
N. linearis	5.8/5.1	2.9/3.9	14.0/15.7	19.1/2.2
Ach lanceolata	7.8/4.1	5.4/6.4	47.7/35.3	34.7/26.1

[1] includes both filamentous and basal cells.

Appendix II

Table AIV.1 Quantities of fatty acids and total crude lipid in laboratory stream algal assemblages on days 8, 15, and 31, exposed to photon flux densities of 15, 50, 150 and 400 uE m^{-2} s^{-1}. Fatty acid data are expressed as percentage of total in each sample and are the mean of two replications. Total crude lipid is expressed as mg lipid/g AFDW and is a mean (± SD) of 4 replications. T denotes a trace amount (less than 0.2%).

	Day 8				Day 15				Day 31			
Fatty Acid	15	50	150	400	15	50	150	400	15	50	150	400
12:0	2.92	1.97	3.32	2.74	0.84	3.90	6.24	2.42	3.12	3.44	6.68	3.99
14:0	3.43	10.65	9.29	8.74	2.88	6.34	7.55	6.76	5.51	5.83	7.58	7.14
14:1	1.56	0.85	0.85	0.75	0.97	T	T	T	T	T	T	0.48
Unk A[a]	1.33	1.10	1.21	0.74	0.57	0.91	3.19	0.52	0.65	1.15	3.59	1.57
16:0	19.75	14.57	11.12	11.95	21.33	11.49	9.72	11.24	14.99	13.39	18.21	15.76
16:1	9.24	12.02	14.07	15.19	6.60	15.10	14.91	17.09	16.76	22.69	22.47	23.51
16:2	3.71	6.66	8.57	8.83	2.87	8.49	8.71	7.42	6.09	5.73	3.27	3.58
16:3	0.30	0.90	1.09	1.00	T	T	2.35	0.58	T	T	0.75	1.22
18:0	11.51	2.21	T	T	11.97	0.77	T	T	2.30	0.33	0.20	T
18:1[b]	15.52	23.39	18.44	17.86	24.50	21.90	13.77	17.72	19.96	14.96	8.27	9.18
18:2	2.17	2.66	2.39	2.55	3.02	2.49	4.60	2.82	2.17	1.91	2.56	2.78
18:3	7.77	3.05	3.57	2.25	11.88	1.07	4.20	1.17	2.57	1.06	2.80	2.93
Unk C[c]	0.86	1.27	0.35	T	T	0.35	T	0.55	0.21	0.36	T	T
20:0	T	0.57	1.26	1.27	T	1.01	1.77	1.15	0.31	0.66	0.64	0.71
Unk D[d]	1.68	T	0.54	T	T	T	0.35	T	—	—	—	—
20:2	T	T	1.21	1.50	0.60	1.03	1.75	0.90	0.46	0.82	0.77	0.85
20:5	7.68	14.38	17.70	19.23	11.91	23.85	16.81	24.30	22.29	22.74	17.42	20.21
22:0	1.61	1.75	1.65	1.18	T	0.95	1.94	2.47	2.32	3.42	3.09	4.01
22:2	4.66	0.84	0.77	0.20	—	—	1.83	—	—	—	—	—
24:0	3.46	—	—	T	—	—	—	—	—	—	0.28	T
Total Lipid	102	169	99	110	139	134	140	126	174	170	117	71
(± SD)	(43)	(41)	(5)	(10)	(35)	(18)	(14)	(3)	(21)	(9)	(6)	(22)

[a]Relative retention time of Unknown A was 0.61, with 18:0 = 1.00.
[b]This fatty acid apparently was comprised of two unresolvable isomers.
[c]Relative retention time of Unknown C was 1.95.
[d]Relative retention time of Unknown D was 2.47.