

AN ABSTRACT OF THE THESIS OF

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Title: SUCCESSIONAL CHANGES ASSOCIATED WITH BENTHIC

ASSEMBLAGES IN EXPERIMENTAL STREAMS

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Experimental streams constructed by the Weyerhaeuser Company, Tacoma, Washington, at Kalama Springs, Washington, were used to observe successional changes in the benthos. Community changes were observed relative to experimental manipulations of light intensity and nitrate concentration in two experiments. The development of benthic assemblages was followed for 150 days after a simulated freshet that removed most of the plant and animal biomass from the streams.

The development of the benthic assemblages was quantified with measures of composite properties (organic matter and pigment concentrations); primary production and community respiration; the taxonomic structure, biomass, and export of plants; and the taxonomic structure, biomass, and export of animals. A photosynthesis-respiration chamber was used to measure the rate of benthic primary production at light saturation and to establish the relationship between primary production and light intensity. Multivariate analyses (discriminant and principal components analyses) were used to analyze temporal changes in algal taxonomic structure within a riffle and differences among riffles exposed to different experimental conditions.

Successional changes in benthic assemblages that occurred in all riffles were described by a series of three stages taxonomically distinguished by Diatoma hiemale v. mesodon (stage I), chironomids (stage II), and Zygnuma (stage III). These stages were characterized by a rapid increase of algae (stage I), an increase of faunal biomass and export (stage II), and a subsequent increase of algae with a decrease in faunal export (stage III). The rate of primary production was higher in

riffles exposed to high solar radiation than riffles receiving low radiation, and higher in the nitrate-enriched riffles than in the unenriched riffles if solar radiation was high. High algal biomasses (stage I and III) and high faunal export (stage II) were observed in riffles subjected to relatively high solar radiation.

The behavior of the benthic assemblages with time was interpreted as the reorganization and stabilization of two levels of organization - the benthos and stream system - within the structural hierarchy of the lotic ecosystem. The developmental stages were the reorganization of the producer (algal) subsystem that resulted in an increase in primary production (stage I), stabilization of the producer and consumer (faunal) subsystems of the benthos system (stage II), reorganization of the benthos system that resulted in an increase in primary production and a decrease in community respiration (stage III), and stabilization of the stream system (hypothesized stage IV). Conceptually, benthic assemblages of natural streams are perceived to exist in a tension between environmental stress and the evolution of hierarchical organization that represents the decomposition and composition of structure in the lotic ecosystem, respectively.

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with Benthic Assemblages
in Experimental Streams

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SUCCESSIONAL CHANGES ASSOCIATED WITH BENTHIC ASSEMBLAGES IN EXPERIMENTAL STREAMS

INTRODUCTION

Investigations of ecosystems utilize two sources of information: natural systems and artificial (man-made) systems. In stream ecology, these sources are natural streams and experimental streams. The use of natural streams to understand phenomena in the stream ecosystem is a direct and intuitively desirable approach to a problem of interest. However, this approach is often hampered by the complexity of natural ecosystems and by the heterogeneity among and within streams. An alternative approach, using man-made systems, gives better opportunities to simplify, control, manipulate, measure, and spatially limit problems. A consequence of this simplification is that all factors of the complex natural ecosystem are not reproduced in any one design of experimental streams. Therefore, information obtained from given experimental streams must be evaluated to separate that which is relevant to a particular problem and that which is artifact, a product of artificial design.

An area of study that has been constrained by the characteristics of many experimental streams is successional changes of the benthos (plants and animals associated with the streambed). Successional change in lotic benthos is a process that can not be appropriately examined in experimental streams of a closed or partially closed design (Warren and Davis, 1971). In these streams, water is recirculated in a trough with little or no replacement. The water is usually filtered before entering the trough, and the streams are often located inside buildings. These conditions tend to prevent or inhibit colonization. The recovery of benthic assemblages in natural streams, particularly the faunal components, is largely influenced by dispersal mechanisms of organisms (Siegfried and Knight, 1977). Therefore, reasonable doubt exists whether realistic successional changes can be observed in these experimental streams.

The inappropriateness of certain experimental streams to the problem of successional change is unfortunate, considering the importance of successional change in lotic ecosystems. Margalef (1963), Minckley (1963), and Eichenberger and Wuhrmann (1975) suggest that stream communities are kept in pioneer stages by the impact of current. The flow of the stream during periods of high discharge scours organisms from the substrate, thereby preventing the establishment of more mature stages. In this perspective, stream ecosystems are continually recovering from catastrophic freshets, and successional change is an omnipresent aspect of benthic assemblages. These changes are difficult to isolate in natural systems because seasonal changes in environmental factors may also affect changes in the benthos. The investigations of successional change in benthic assemblages requires open, flow-through channels that are located in the field where dispersal is not artificially inhibited and in which the environment of the streams can be controlled. Experimental streams of this design have been constructed by the Weyerhaeuser Company at their Kalama Springs laboratory (southwestern Washington) and were used for the research reported here.

The primary objective of this research was to describe and understand successional changes in benthic assemblages of streams after a catastrophic event (i. e., the removal of flora and fauna during a simulated freshet). Another objective was to examine the effect of light intensity and nutrient enrichment on the structure and function of benthic assemblages. This latter objective is particularly relevant to streams of the Pacific Northwest, as logging activities affect the lotic ecosystem through these factors. The light intensity in a stream ecosystem can increase from less than 100 ft-c to more than 10,000 ft-c after tree removal, while the concentration of dissolved inorganic materials often increases several fold (Likens, et al., 1967). Proper and profitable utilization of aquatic and terrestrial resources requires an understanding of the effects of logging practices on lotic ecosystems.

The investigation of light and nutrient effects on benthic assemblages of streams also represents a continuation of previous work. In a study of the response of these assemblages to light intensity and

current velocity, McIntire (1968) noted a dichotomy in previous research - studies of taxonomic structure and studies of functional attributes (e. g., primary production and community respiration). His study attempted to relate measures of algal taxonomic structure to common measures of primary producer abundance (e. g., organic matter and chlorophyll a). Investigations of this type are necessary to reconcile structure and function in lotic benthos. This thesis represents a continuation of these studies by examining responses of benthos to different nutrient regimes and light intensities relative to measures of organic matter, chlorophyll a, taxonomic composition, primary production, and community respiration. The effects of light intensity and nutrient enrichment were investigated within the context of successional change in benthic assemblages after a simulated freshet (scour event).

HISTORICAL PERSPECTIVE

The history of research on autotrophic stream ecosystems has involved the successive development and maturation of two paradigms where the term "paradigm" is used to mean the perspectives, techniques, and goals of members of a given scientific community (Kuhn, 1970). An early paradigm of stream ecologists was based on the perspective that the distribution and abundance of floral taxa in streams are controlled primarily by the physical environment. This hypothesis also implied that the ambient environment of the community is predictable from the kinds and quantities of taxa present. The paradigm related to these hypotheses developed from observations of recurrent spatial and temporal distributional patterns of algal taxa (Kofoid, 1903; Brown, 1908; Pearsall, 1923; Butcher, 1932; Budde, 1936). Research during this period was characterized by descriptive analyses of the occurrence of algal taxa, and the subsequent cataloging of these taxa relative to preceived responses to environmental factors. The maturation of the paradigm occurred with the ecological classification of taxa relative to current velocity (Picken, 1936; Butcher, 1947), depth (Blum, 1960), turbidity (Blum, 1956), pH (Lackey, 1938), nitrogen concentration (Kolkwitz, 1946), and channel size (Eddy, 1934). Classifications also were presented that cataloged taxa on "spectral ranges" for individual chemical and physical factors, and groups of taxa as distinctive algal communities. The former classification of organisms described the habitat of taxa in one of five or more ranks relative to ranges of pH (Hustedt, 1937), salinity (Kolbe, 1927), organic pollution (Fjedingstad, 1964), current velocity (Hustedt, 1937), calcium concentration (Nissen, 1956) and others (Wilhm, 1975). The latter classification system described recurrent associations of taxa within streams and on a regional basis (Butcher, 1946; Blum, 1954; Whitford, 1956; Margalef, 1960).

The limitations of the early paradigm became more evident as the data base increased. While some environmental properties often were associated with different algal taxa, conditions of occurrence for most taxa were too broad to allow adequate predictions of the physical

environment from descriptions of taxonomic structure (Fjedingstad, 1964). In addition, classification of algal communities led to a seemingly endless series of loose associations (Blum, 1956) in which no constant relationship between taxa was evident (Patrick, et al., 1967). These limitations and the emergence of an alternative approach resulted in the transition to a second paradigm in lotic ecology.

The second paradigm was the energy-based perspective of ecosystems as presented by Lindeman (1942) in which system dynamics were investigated by the examination of energy flows between components of the ecosystem. In autotrophic streams, this paradigm involved measurements of primary production and community respiration. The development of this research approach was slow because of the sampling difficulties associated with streams (Wetzel, 1975). Some early studies derived organic budgets from crude measurements of system variables from each trophic level (Odum, 1957; Teal, 1957). The sophistication of estimates of community metabolism increased from colonization rates on artificial substrates (Cooke, 1956; Kevern, et al., 1966; Vollenweider, 1969), diurnal changes in gas concentrations (Odum, 1957; Duffer and Doris, 1966; Wright and Mills, 1967), and light-dark bottle studies (McConnell and Sigler, 1959; Kobayasi, 1961) to respirometer studies (McIntire, et al., 1964; Hansmann, et al., 1971). In addition, experimental streams were developed for more controlled examination of energy flow in streams (McIntire, et al., 1964; Whitford and Schumacher, 1964; Warren and Davis, 1971; McIntire, 1975). Maturation of the energy-based paradigm occurred with the presentation of theoretical models specific to the lotic ecosystem (Fraleigh and Wiegert, 1975; McIntire and Colby, 1978). The current state of autotrophic stream ecology is this maturation period in which previously developed techniques are used to examine the value of a paradigm oriented toward energy flows.

The concept of ecological succession in autotrophic stream ecosystems has not been reconciled with either paradigm of lotic ecology. During the period of classification, the perspective of succession in lotic ecology was largely influenced by successional concepts developed for terrestrial ecosystems (e. g., Clements, 1916). These concepts

were considered inappropriate for streams by some workers because no successional sequences of algal communities were observed (Blum, 1956). The flora was considered to be opportunistic with an algal community developing without prior modification of the environment by other communities. Other workers considered the sequential appearance of constituent taxa in a community to represent a nonobligatory form of succession (Eddy, 1925; Butcher, 1949), and "climax" communities of algae were proposed and described for permanent streams (Margalef, 1960).

According to the energy-based perspective of ecosystems, general trends of community development were postulated for all ecosystems (Odum, 1969). Succession was considered a directional change in community structure and function which resulted from the modification of the physical environment by the community and culminated in a large organic structure maintained per unit of energy flow (Cooke, 1967). Succession was observed relative to changes in "composite" ecosystem properties (Table 1). The most comprehensive application of these concepts to lotic ecosystems has been done by Margalef (1960, 1963, 1968). Margalef observed that successional changes occurred in streams, and that higher concentrations of carotenoid pigments relative to chlorophyll a, indicative of biochemical diversity, also occurred in more mature communities. However, these concepts were directed towards "longitudinal" succession in streams, the examination of differences between upstream (immature) and downstream (mature) communities. The problem with this perspective of succession is that changes are defined spatially instead of temporally. The examination of ecological (temporal) succession requires the observation of communities within one site in which all independent factors of the environment except time are constant. Such observations have not yet been reported in the literature of lotic ecology. The observation of community development in the experimental streams at Kalama Springs is an attempt to describe and understand temporal succession in autotrophic stream ecosystems.

Table 1. General trends of temporal succession in autotrophic ecosystems (Cooke, 1967; Margalef, 1968; Odum, 1969).

Ecosystem Attribute	Developmental Stage	
	immature	mature
Community Structure		
Total Biomass	low	high
Chlorophyll <u>a</u>	low	high
Chlorophyll <u>a</u> /Total Biomass	high	low
Biochemical Diversity (480:665)	low	high
Community Energetics		
Gross Primary Production	low	high
Gross Primary Production/Chlorophyll <u>a</u>	high	low
Community Respiration	low	high
Community Respiration/Total Biomass	high	low

DESCRIPTION OF THE EXPERIMENTAL STREAMS

The experimental streams used in this research were constructed and maintained by the Weyerhaeuser Company (Tacoma, Washington). The streams are located on the company's St. Helens Tree Farm in Cowlitz County, Washington (Section 7, T7N, R4E). This field laboratory is adjacent to the Kalama River, a tributary of the Columbia River, and is at an elevation of 335 m. The Weyerhaeuser Company developed this field laboratory in 1964 with the long range goal of contributing basic information concerning stream productivity and the impact of the logging industry on the water resources of the Pacific Northwest.

The streams are fed at the site by Kalama Springs, a cold-water spring. Water flows from this spring to the Kalama River at a rate of 27,000 to 44,000 m³ day⁻¹. Approximately 10 % of this flow is diverted into a series of ponds above the artificial streams (Figure 1).

Manipulation of weirs between the ponds allows a constant flow of 2200 m³ day⁻¹ to be maintained in each stream. The water temperature of the streams is 5 to 7 C throughout the year. Chemical composition also is relatively constant with a dissolved solids concentration of less than 50 mg l⁻¹ (Table 2).

The artificial streams are designed as a series of alternating pools and riffles. The riffles are 6 to 10 cm deep and 1.2 m wide in alternating lengths of 7.6 m (9.3 m² in area) and 15.2 m (18.6 m² in area). The pools are 13.7 m² in area and 0.3 to 0.5 deep. The riffles have a current velocity of 55 cm sec⁻¹, a gradient of 0.5 %, and a substrate of small, smooth stones, 1.8 to 4.0 cm in diameter, overlying a fine pumice base. The two riffles immediately below the distribution pond in each of the three streams were used in this research.

Figure 1. Diagram of the Kalama Springs experimental streams indicating the springs (S), the distribution pond (D), a riffle (R), a pool (P), the flow of water to the Kalama River (F), and where nitrate-nitrogen was introduced into the streams (N).

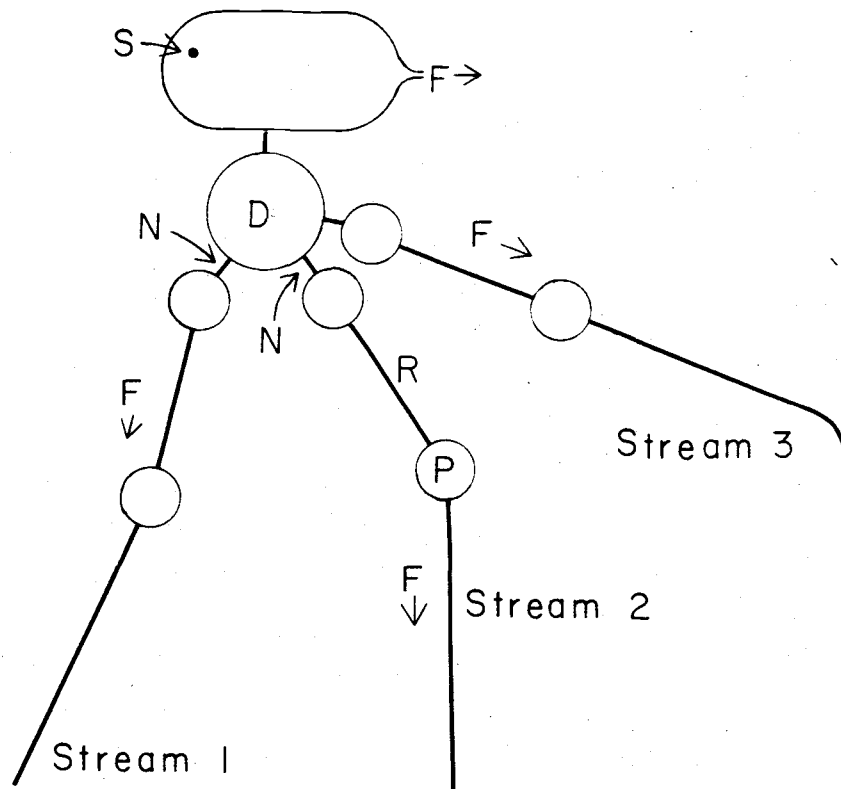


Table 2. Water quality summary for the experimental streams, 1972-1974 (Bisson, et al, 1975).

	December - February	March - May	June - August	September - November
Silica mg/l	8.2 - 16.6	9.0 - 19.0	24.1 - 25.0	23.0 - 24.0
Sodium mg/l	2.8 - 5.3	3.0 - 4.5	3.9 - 4.4	2.8 - 4.5
Magnesium mg/l	0.9 - 1.0	0.8 - 0.9	1.1 - 1.2	1.2
Calcium mg/l	3.0 - 3.6	2.1 - 3.8	4.1 - 4.6	2.6 - 4.4
Potassium mg/l	0.5 - 0.6	0.5 - 0.6	0.6	0.6 - 0.8
Sulfate mg/l	1.8 - 3.2	1.0 - 1.2	1.1 - 2.0	1.4 - 2.0
Chloride mg/l	1.25 - 1.4	-	-	-
Phosphate-P µg/l	18.0	24.0	19.0	-
Nitrate-N µg/l	40.0 - 50.0	26.0 - 33.0	24.0 - 26.0	41.0 - 42.0
Aluminum µg/l	2.1 - 19.0	0.6 - 9.4	3.9 - 4.1	2.4 - 2.7
Beryllium µg/l	0.1	0.1	0.1	0.1
Cadmium µg/l	0.1	0.1	0.1	0.1
Chromium µg/l	0.1 - 1.2	0.1 - 0.2	0.1	0.1
Cobalt µg/l	2.0 - 1.1	0.1 - 0.5	0.1 - 0.2	0.4
Copper µg/l	0.8 - 1.5	0.2 - 0.8	0.5 - 0.8	0.2 - 0.4
Iron µg/l	10.1 - 11.0	1.1 - 2.5	1.4 - 1.5	1.1 - 3.2
Lead µg/l	0.1	0.1	0.1	0.1 - 0.2
Manganese µg/l	0.1 - 0.4	0.1 - 0.1	0.1 - 0.2	0.1 - 0.3
Nickel µg/l	1.4 - 6.0	4.7 - 11.0	0.5 - 2.0	0.1 - 0.4
Vanadium µg/l	3.2 - 5.0	3.7 - 5.0	3.6 - 11.0	4.0 - 8.3
Zinc µg/l	0.2 - 1.1	0.1 - 0.7	0.1 - 0.1	0.2 - 1.0
Molybdenum µg/l	0.7 - 0.8	0.5 - 1.0	0.4 - 0.7	0.8

Experimental Design

This research consisted of two experiments at the Kalama Springs station. The first experiment was an examination of the replicability among identical streams and a contrast of community development in two different environments after a simulated freshet. The freshet was simulated on December 5, 1975, by agitating the substrate with rakes until no algal or animal material was visible in the riffles. The different environments were created by shading the three upstream riffles on each stream. This treatment allowed a contrast between unshaded riffles and riffles where the solar radiation had been reduced 85 %. The shade was established by placing a wooden framework of lathes and supports over the stream. Benthic assemblages in the two sets of three riffles were sampled six times after the scour event on December 15, 1975, January 3, January 19, February 8, March 21, and May 9, 1976 - 10, 30, 45, 65, 105, and 155 days after the simulated freshet.

The second experiment expanded the number of environments in which community development was described. After another simulated freshet on July 5, 1976, benthic assemblages were observed in six environments. The three upstream riffles were shaded (85 % reduction of solar radiation) with nylon-mesh material stretched across wooden frames. The three downstream riffles were exposed to normal light intensities. Stream 1 received a constant enrichment of nitrogen at $100 \mu\text{l l}^{-1}$ nitrate-nitrogen above background levels. Stream 3 received no nitrate enrichment. Stream 2 received no nitrogen enrichment until 40 days after the freshet, after which it received an addition of $100 \mu\text{g l}^{-1}$ nitrate-nitrogen from this time to the conclusion of the experiment. Nitrate-nitrogen was put into stream 1 and 2 by dripping sodium nitrate below the weirs of the distribution pond (Figure 1). Benthic assemblages were sampled eight times after the scour event on July 12, July 19, July 26, August 10, August 24, September 7, October 4, and November 8, 1976 - 7, 14, 21, 35, 49, 63, 90,

and 125 days after the freshet. Fishes were not present in the streams during either experiment.

Sampling and Analysis

Environment

Solar radiation at the Kalama Springs experimental streams was monitored with a Beaufort recording pyr heliometer. Nitrate-nitrogen concentration during the nutrient enrichment experiment was determined for each sampling date by the cadmium-reduction method (Wood, Armstrong, and Richards 1967).

Plants and Composite Properties

Benthic assemblages were sampled for composite properties (biomass and pigment concentration and the abundance of plant taxa) from plexi-glass trays (0.1 m^2) placed below the rock substrate at the beginning of each experiment. A tray of substrate with intact assemblages was removed from each riffle on each sampling date. Enough trays were placed in the riffles so that an area of riffle was sampled only once during the experiment. The riffles were not large enough to permit the removal of more than one tray per sampling date and, therefore, no estimate of variance within riffles was available for the various attributes measured.

The benthos was separated from the rock by hand scrubbing, and the material was fragmented for 20 seconds in a 3.8-l blender according to the method of McIntire (1968). The volume of this suspension was measured and subsamples were removed for analysis. Three 50-ml subsamples of the blended benthos were dried at 70 C and ignited in a muffle furnace at 500 C. The mean weight lost on ignition (ash-free dry weight) was considered to estimate organic matter in the benthic assemblage. Percent organic matter was derived from the quotient of ash-free dry weight and dry weight before ignition. Three 25-ml samples of the blended benthos were removed for pigment analyses. The mean concentration of chlorophyll a and c and light absorbance at 480

and 665 nm were determined spectrophotometrically after acetone extraction (Strickland and Parsons, 1972).

Two 25-ml samples of the blended benthos were preserved in a solution of water, alcohol, and formaldehyde for the determination of algal densities. One ml of a preserved sample was placed in a sedimentation slide and examined with an inverted microscope. Fifteen fields of sedimented materials were inspected for estimates of algal cell number and filament lengths. Diatom and Hydrurus cells were counted at a magnification of 400 X. Schizothrix filaments were counted at 200 X; and Microcoleus, Tolypothrix, Nostoc, Tribonema, Batrachospermum, and Zygnema filaments were counted at 100 X. Filament lengths were approximated by a grid method (Olson, 1950) using a 400 intersection ocular grid. This procedure was repeated for each of the two 25-ml samples, and estimates of algal abundance in a benthic assemblage were based on the examination of a total of 60 microscopic fields. To analyze the composition of the diatom flora in isolation, one 25-ml subsample of the blended benthos was boiled in nitric acid. The cleaned diatom frustules were mounted in Hyrax and counted at 1000 X. Community structure measures were based on counts of 500 valves (McIntire and Overton, 1971).

The export of plant material was collected for 15-minute periods at 0830, 1230, 1630, 2030, 0030, and 0430 hours with a 200 um mesh net that spanned the width and depth of the riffles. The first three samples were pooled for a measure of day drift while the latter three samples were pooled for a measure of night drift. The combined samples were blended for 20 seconds, and estimates of organic matter and pigment concentration were derived from 50-ml and a 25-ml subsample, respectively. Drift was sampled simultaneously below each riffle and above the upper riffles.

Animal Assemblages

The collection and analysis of animal assemblages was conducted by Weyerhaeuser Company biologists under the direction of Dr. Peter Bisson. Assemblages of invertebrate organisms were sampled with a

metal coring device (0.02 mm^{-2}) that enclosed a portion of the substrate down to the compacted pumice base. Organisms and substrate were removed from the core manually with a 200 μm mesh dip net. The material was washed on a 250 μm mesh sieve. Four samples were obtained from the longer riffles and pooled into one, while two samples were pooled for the shorter riffles. The combined samples were preserved in alcohol and stored for sorting and identification. Individuals of the microfauna were counted, while individuals of insect taxa were counted and sorted by size class. Estimates of biomass expressed as g m^{-2} were based on number-weight and length-weight conversions previously estimated by Weyerhaeuser Company biologists.

The export of invertebrate organisms was collected for 15-minute periods at 0800, 1200, 1600, 2000, 0000, and 0400 hours with 200 μm mesh nets positioned below each riffle and above the upper riffles. The first three samples were pooled for a measure of day drift, while the other samples were pooled for a measure of night drift. Estimates of drifting biomass for taxa were based on the sorting and counting method described in the preceding paragraph. The export rate has been considered to be indicative of turnover rates of the faunal taxa (Waters, 1961 b) and was used to distinguish taxa with "fast turnover rates" (mean export more than 1 % of the biomass per day).

Diversity

Diversity of each taxon was expressed as Shannon's H' (base e), where abundance was an estimate of biomass. Total cell volume for each algal taxon was estimated by the product of length and mean cross-sectional area for filamentous taxa, and cell number and mean cell volume for nonfilamentous taxa. This volumetric estimate of algal biomass is recommended by Allen and Koonce (1973). The diatoms were considered as one taxa for estimating the diversity of all algal taxa; the diversity of the diatom flora was determined in a separate analysis. Estimates of biomass for animal taxa used a number-length-weight conversion as the many immature stages of these aquatic organisms made species identification impossible. Taxonomic categories ranged from

the species level to family (e. g., Chironomidae) and class (e. g., Gastropods).

Multivariate Analyses

The sampling of algal assemblages during each experiment in the Kalama Springs streams resulted in a data matrix in which the columns and rows were observations (i. e., algal assemblages) and abundances of the alga taxa, respectively. A principal components or discriminant analysis (Cooley and Lohnes, 1971) was used to collapse most of the information (i. e., variance) in the data matrices to two or three variables which represented linear transformations of the original variables (i. e., taxa). The differences among assemblages during an experiment were assessed by the position of the assemblages in these transformed variables. This approach allowed the comparison of assemblages among riffles and within a riffle with time in a dimensional space less than that of the original data matrix.

The discriminant analysis was used for the data from the first experiment in which algal assemblages were sampled from shaded and unshaded riffles of the three experimental streams. The 36 assemblages observed in this experiment represent 12 groups (two treatments and six sampling dates) with triplicate observations (i. e., the algal assemblages in the three streams) in each group. The location of observations in the transformed variables was based on an algorithm that maximized the ratio of variance among to that within the 12 groups. Therefore, the plane of the first and second canonical variables represented the plane of maximum dispersion of these groups. The principal components analysis was used for the data from the second experiment in which no replicates existed. The location of the 48 observations (six treatments and eight sampling dates) in the transformed variables was based on an algorithm that maximized the variance among the observations. In this analysis, the plane of the first and second factors represented the plane of maximum dispersion

of the observations. Similiar discriminant and principal components analyses were performed on the diatom data of experiments 1 and 2.

Primary Production and Community Respiration

Rates of primary production and community respiration for the benthic assemblages were measured using a field respirometer. This approach involved: (1) enclosing a tray of substrate with attached benthos in a plexiglass chamber, (2) maintaining a constant temperature within the chamber with a surrounding water bath, (3) simulating current within the chamber by recirculating the water with pumps, and (4) measuring the change in dissolved gas (oxygen or carbon dioxide) concentration within the chamber over a period of time (McIntire, et al., 1964). The chambers (13-l in volume) were submerged in a pool of the experimental streams, and water was recirculated inside the respirometer with two battery-powered, submersible centrifugal pumps. Rates of oxygen evolution and uptake were based on measurement periods of one hour between initial and final water samples. The water samples were taken with 300-ml BOD (biological oxygen demand) bottles with the dissolved oxygen concentration measured with an IBC (International Biological Company) probe and meter. Prior to the initial sample, the water introduced to the respirometer was bubbled with nitrogen gas to lower the oxygen concentration below saturation. Rates of community respiration were estimated from measurements of the oxygen uptake rate by the benthos in the dark. Rates of gross primary production were estimated by adding the rate of community respiration to the rate of oxygen evolution in the light for an equivalent period of time.

The rate of primary production for each benthic assemblage was measured in a series of higher light intensities. The rapid increase of light intensity at Kalama Springs through the course of the day necessitated placing filters of 58, 45, and 33 %, over the respirometer to expand the time of increasing intensity. Six one-hour measurements of oxygen evolution at light intensities of 15, 15, 15, 55, 67, and 100 % of direct insolation were taken. Water was exchanged in

the chamber for a 15-minute interval between measurements to minimize the effects of nutrient depletion. The estimate of maximum rate for an assemblage was the highest observed rate during the series of measurements of oxygen uptake for a one-hour period.

The method used for the measurement of primary production in this experiment assumed the rate of primary production for a benthic assemblage increased with increasing light intensity up to some asymptotic value, a maximum rate at which the system becomes light saturated. This assumption allowed the separate examination of maximum rate and productive activity of benthic assemblages relative to light intensity (Parsons and Takahashi, 1973). The maximum rate of primary production for a benthic assemblage will be a function of the mass of primary producers, the acclimation of the producers to their environment, and environmental factors that limit production (e. g., nutrients or temperature). The productive activity of the benthic assemblages was indicated by the relationship between relative production (the quotient of production rate and the maximum rate of production) and light intensity. Assemblages that have a high productive activity will attain their maximum rate of production (i. e., relative production is equal to one) at a low light intensity. The use of relative production rates allowed the comparison of productive activity among benthic assemblages with different maximum production rates.

RESULTS

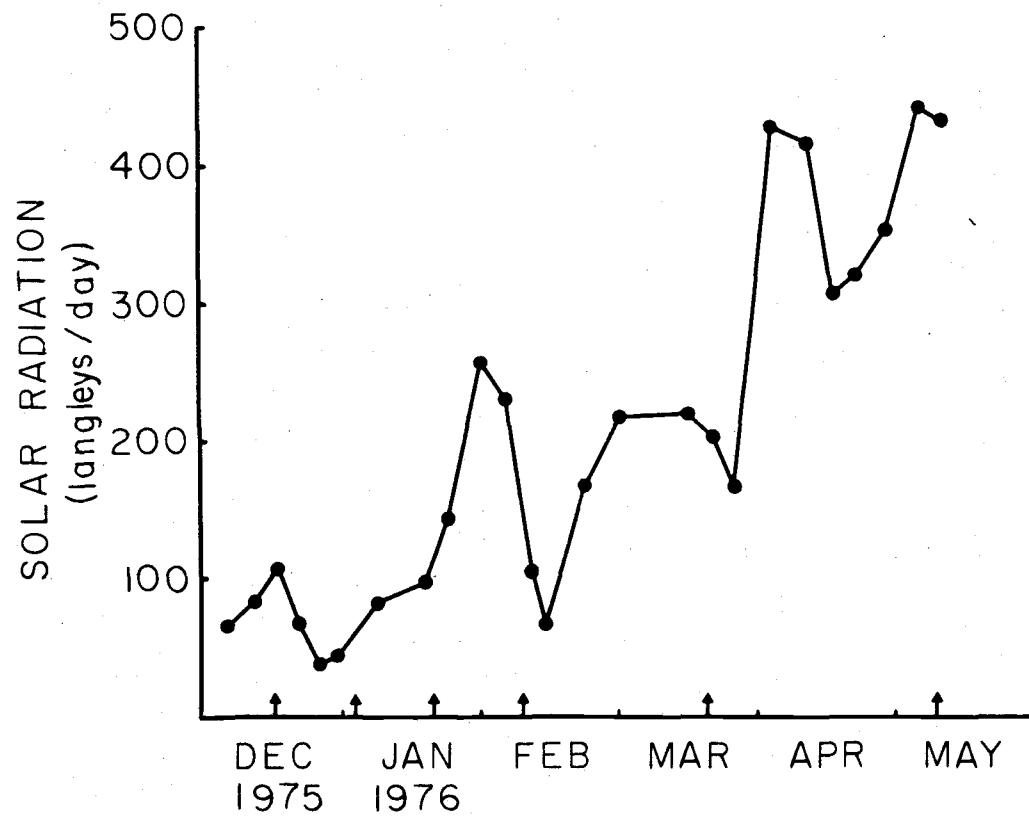
The results of the study of successional change associated with benthic assemblages in experimental streams are divided into two sections. The first section is entitled "Community Development in Shaded and Unshaded Riffles," and presents the results of experiment 1 in which the development of benthic assemblages was observed in high and low light environments, 100 % and 15 % of incident solar radiation, respectively. The second section - "Community Development in Nitrate-Enriched Riffles" - presents the results of experiment 2 in which the development of benthic assemblages was observed in six environments that differed with respect to available solar radiation and nutrient (nitrate-nitrogen) concentration.

Experiment 1 - Community Development in Shaded and Unshaded Riffles

During experiment 1, solar radiation at Kalama Springs increased from 68 ly day^{-1} in December to 408 ly day^{-1} in April and May (Figure 2), while the daylength increased from nine hr day^{-1} in December to 14 hr day^{-1} in May. Insolation was 100 % and 15 % of solar radiation in the unshaded and shaded riffles, respectively. Benthic assemblages were sampled on December 15, 1975, and January 3, January 19, February 8, March 21, and May 9, 1976. Henceforth, these dates will be referred to as observations 1, 2, 3, 4, 5, and 6, respectively.

Agitation of the rock substrate (i. e., the simulated freshet) removed a mass of filamentous algae and associated fauna from the streams. Relatively little plant or animal life was observed on the substrate after this agitation. At the first sampling date ten days after the disturbance, the rock were covered with golden-brown, gelatinous algae, and little difference was apparent between shaded and unshaded streams. At the second sampling date 30 days after the freshet, golden-brown filaments covered the substrate, and the density of these filaments was greater in the unshaded riffles. Fifteen days after this observation, the carpet-like mass of filaments was gone in

Figure 2. Daily solar radiation at Kalama Springs, experiment 1.
Arrows indicate the sampling dates.



all riffles, and little algal material was apparent. Algal biomass remained relatively low in both the shaded and unshaded riffles between observations 3 and 4. At the time of observation 5 patches of a filamentous green alga were observed on the substrate and by observation 6, 155 days after the simulated freshet, this alga was growing in long filaments (> 10 cm) in length uniformly over the rocks of the unshaded riffles. This alga covered the substrate in the shaded riffles to a lesser extent.

Composite Ecosystem Properties

Organic matter increased to more than 26 g m^{-2} in all riffles within 30 days after the simulated freshet (Figure 3 a,b). This accumulation stopped after observation 2, and this attribute varied between 24 and 38 g m^{-2} during the next 85 days. Subsequently, organic matter increased to a mean of 51 g m^{-2} in the shaded riffles and to a mean of 68 g m^{-2} in the unshaded riffles by observation 6.

The percentage organic matter in the benthic assemblage remained relatively constant (26 - 40 %) in all riffles during the first 155 days after the simulated freshet (Figure 3 c,d), and this percentage was significantly higher in the shaded riffles than the unshaded riffles (paired t-test, $\alpha = 0.05$). The percentage organic matter increased in all riffles by observations 5 (33 - 41 %) and 6 (42 - 51 %).

Chlorophyll a concentration increased to means of 263 and 375 mg m^{-2} in the shaded and unshaded riffles, respectively, by observation 2 (Figure 4 a,b). This attribute varied between 67 and 209 mg m^{-2} in both the shaded and unshaded riffles during the rest of the experiment.

The ratio of chlorophyll a to organic matter initially increased to means of 0.006 in the shaded riffles and 0.011 in the unshaded riffles in observation 2 (Figure 4 c,d). Between observations 3 and 5, the ratio ranged from 0.003 to 0.008 for all riffles, and subsequently the value decreased to 0.001 and 0.002 for the shaded and unshaded riffles, respectively, by observation 6. The decrease in

Figure 3. Organic matter and percentage organic matter in the benthos of unshaded (a,c) and shaded (b,d) riffles in stream 1 (small circle), 2 (square), and 3 (triangle), experiment 1. The large circle is the mean of the replicate riffles.

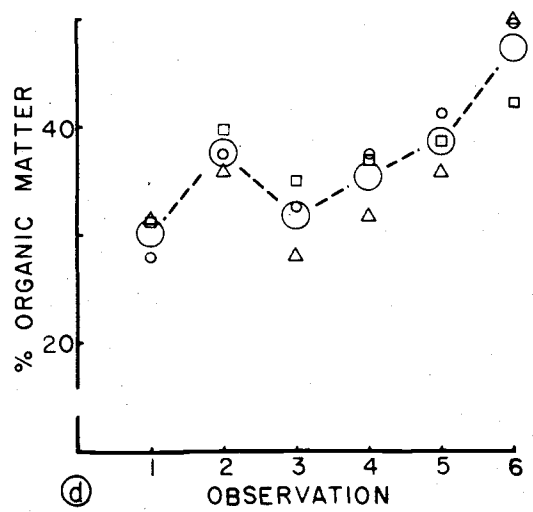
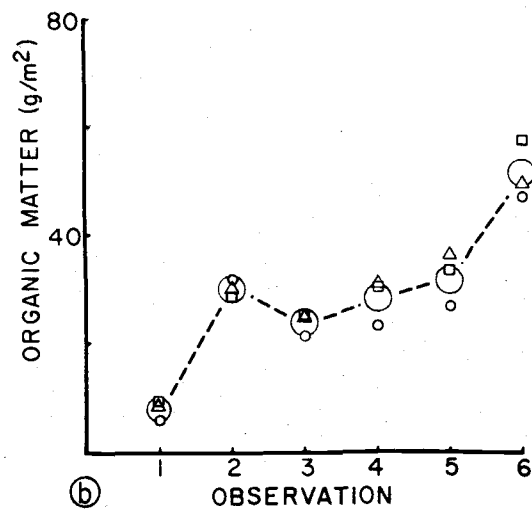
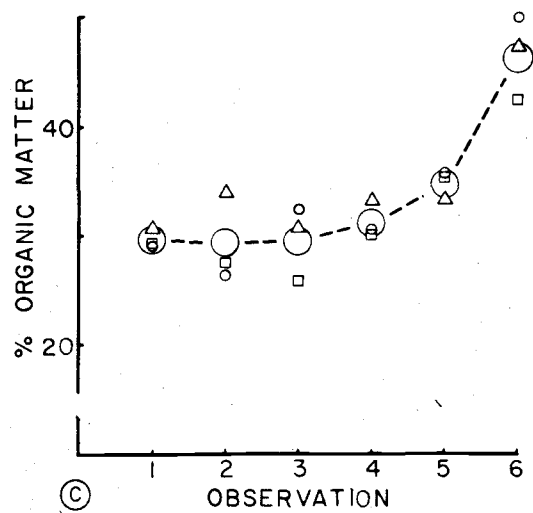
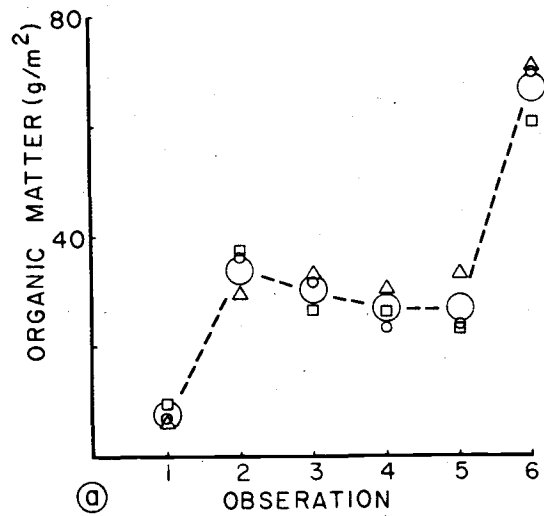
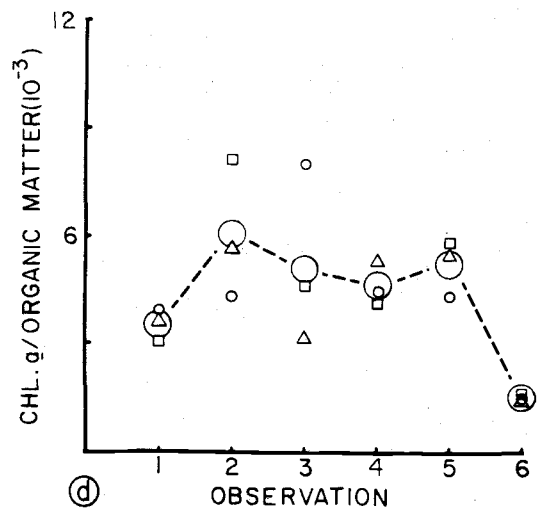
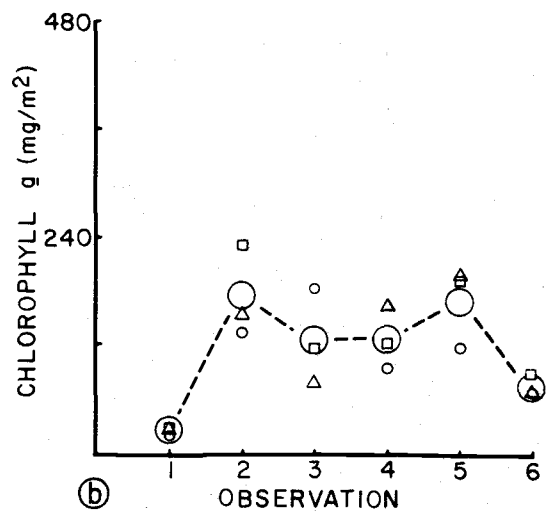
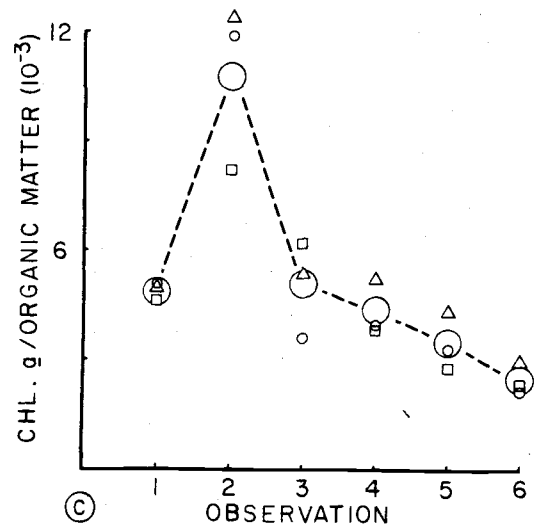
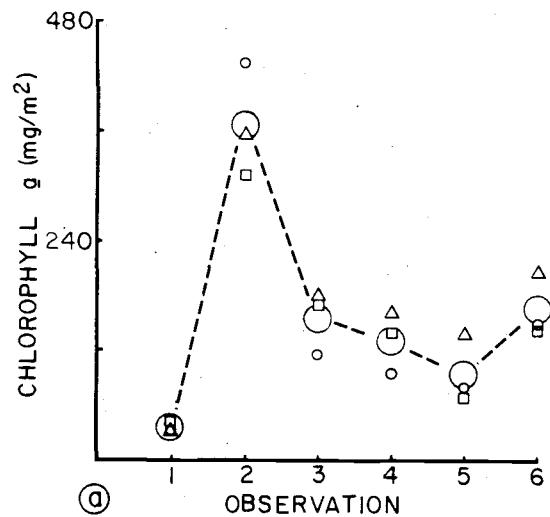


Figure 4. Chlorophyll a concentrations and the ratio of chlorophyll a to organic matter in the benthos of unshaded (a,c) and shaded (b,d) riffles in streams 1 (small circle), 2 (square), 3 (triangle), experiment 1. The large circle is the mean of the replicate riffles.



the ratio after the initial increase was particularly evident in the unshaded riffles.

The ratio of light absorbances at 480 and 665 nm was significantly higher in the unshaded riffles than the shaded riffles (Figure 5 a,b; paired t-test, $\alpha = 0.05$). The largest differences were at observations 1 and 2. The ratio of chlorophyll c to a also exhibited a similar pattern (Figure 5 c,d). Little difference in this ratio was observed between treatments for observations 3 through 6, while it decreased from more than 0.26 to less than 0.15 in all riffles.

The export of chlorophyll a varied from 0.1 to 4.1 % of the chlorophyll a in all riffles per day during the experiment (Figure 6 a,b). The largest percentage losses occurred in the unshaded riffles at the time of observations 2 (2.0 to 3.3 % day⁻¹) and 6 (3.4 to 4.1 % day⁻¹). Of the chlorophyll a exported from the riffles in a 24-hour day, a mean of 56 % occurred between 0600 and 1800 hours.

Floral Assemblages

The taxonomic composition of the floral component of the benthic assemblages included a moss, a liverwort, and algae (Table 3). The moss and liverwort occurred infrequently in both experiments. Frequently-occurring algal taxa were Batrachospermum, Microcoleus, Schizothrix, Tribonema, Zygnema and diatoms. The abundances of these taxa (cell number and filament lengths per square meter) increased during the experiment (Figure 6 c,d and 7 a-d). These abundances were similar among the shaded and unshaded riffles except for higher concentrations of Zygnema in the unshaded riffles and Batrachospermum in the shaded riffles. The abundance of diatoms was higher in the unshaded riffles than the shaded riffles at observations 1 and 2.

Most (86 %) of the information expressed in the six preceding figures was retained in two canonical axes after the discriminant analysis of the 36 observations of algal assemblages. While this multivariate analysis could not increase the information presented in the six univariate analyses, the distribution of algal assemblages in the plane of the first and second canonical axes distinctly indicated

Figure 5. Ratios of 480 to 665 nm absorbancies and chlorophyll a concentrations in the benthos of unshaded (a,c) and shaded (b,d) riffles in streams 1 (small circle), 2 (square), and 3 (triangle), experiment 1. The large circle is the mean of the replicate riffles.

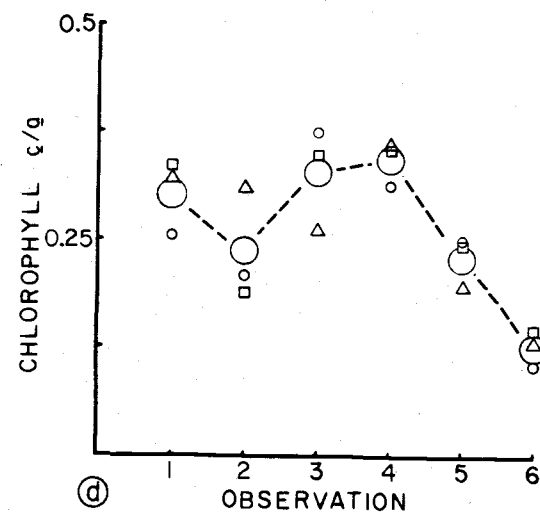
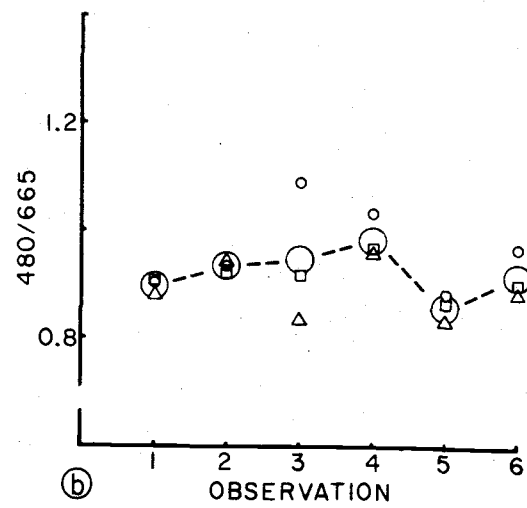
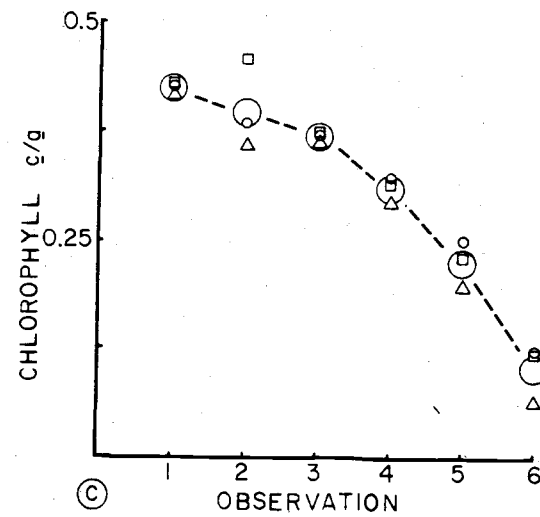
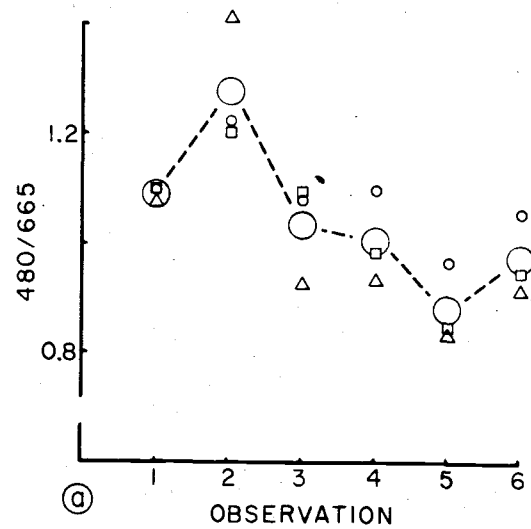


Table 3. List of floral taxa in the experimental streams.

Bacillariophyta	
<u>Achnanthes lanceolata</u> Breb.	<u>Navicula contenta</u> var. <u>biceps</u>
<u>A. minutissima</u> Kuetz.	(Arn.) V. H.
<u>Achnanthes</u> sp. 1	<u>N. minuscula</u> Grun.
<u>Achnanthes</u> sp. 2	<u>N. pelliculosa</u> (Breb.) Hilse
<u>Achnanthes</u> sp. 3	<u>N. radiosa</u> Kuetz.
<u>Caloneis bacillaris</u> var. <u>thermalis</u>	<u>N. radiosa</u> var. <u>tenella</u> (Breb.)
(Grun.) A. Cl.	Grun.
<u>Cocconeis placentula</u> var. <u>lineata</u>	<u>N. rhychocephala</u> Kuetz.
(Ehr.) Cl.	<u>N. secreta</u> var. <u>apiculata</u> Patr.
<u>C. ventricosa</u> Kuetz.	<u>N. seminulum</u> Grun.
<u>Diatoma hiemale</u> var. <u>mesodon</u>	<u>Navicula</u> sp. 1
(Ehr.) Grun.	<u>Navicula</u> sp. 2
<u>Diploneis ovalis</u> (Hilse) Cl.	<u>Nitzschia dissipata</u> (Kuetz.) Grun.
<u>Epithemia turgida</u> (Ehr.) Kuetz.	<u>N. flexa</u> Schum.
<u>Eunotia pectinalis</u> (Mull.) Rabh.	<u>N. frustulum</u> var. <u>perminuta</u> Grun.
<u>E. perpusilla</u> Grun.	<u>N. linearis</u> W. Sm.
<u>Fragilaria construens</u> var.	<u>Nitzschia</u> sp. 1
<u>venter</u> (Ehr.) Grun.	<u>Nitzschia</u> sp. 2
<u>F. vaucheriae</u> (Kuetz.) Peters.	<u>Opephora martyi</u> Herib.
<u>F. virescens</u> Ralf.	<u>Pinnularia borealis</u> Ehr.
<u>Frustulia rhomboides</u> (Ehr.) DeT.	<u>P. braunii</u> var. <u>amphicephala</u> (May.)
<u>Gomphonema intricatum</u> var.	Hust.
<u>pumila</u> Grun.	<u>P. viridis</u> (Nitz.) Ehr.
<u>G. montanum</u> var. <u>subclavatum</u>	<u>Rhoicosphenia curvata</u> (Kuetz.)
Grun.	Grun.
<u>Gomphoneis</u> sp. 1	<u>Staruroneis kriegeri</u> Patr.
<u>Melosira italica</u> (Ehr.) Kuetz.	<u>S. phoenicentron</u> Ehr.
<u>Meridion circulare</u> (Grev.) Arg.	<u>Stenopterobia intermedia</u> (Lewis)
	Hust.
	<u>Synedra famelica</u> Kuetz.
Chlorophyta	
<u>Chlamydomonas globosa</u> Snow	<u>Vaucheriae</u> sp.
<u>Spirogyra</u> sp.	<u>Zygnema</u> sp.
Chrysophyta	
<u>Tribonema bombycinum</u> (Ag.) Derb. et Sol.	
<u>Hydrurus foetidus</u> (Vill.) Trev.	
Cyanophyta	
<u>Chamaesiphon</u> sp.	<u>Nostoc parmelioides</u> Kuetz.
<u>Microcoleus lyngbyaceus</u>	<u>Schizothrix calcicola</u> (Ag.) Gom.
(Kuetz.) Crouan	
Rhodophyta	
<u>Batrachospermum</u> sp.	
Bryophyta	
<u>Chiloscyphus polyanthos</u> (L.) Corda	
<u>Fontinalis neo-mexicana</u> Sull. et Lesq.	

Figure 6 a,b. The percentage of chlorophyll a exported per day from the unshaded (a) and shaded (b) riffles of streams 1 (small circle), 2 (square), and 3 (triangle), experiment 1. The large circle is the mean of the replicate riffles.

Figure 6 c,d. The density of diatom cells (c) and Batrachospermum (d) in the benthos, experiment 1. The circle and square are the means of assemblages in unshaded and shaded riffles, respectively.

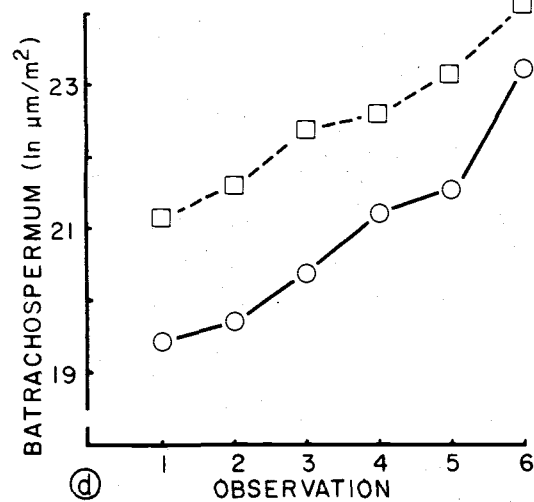
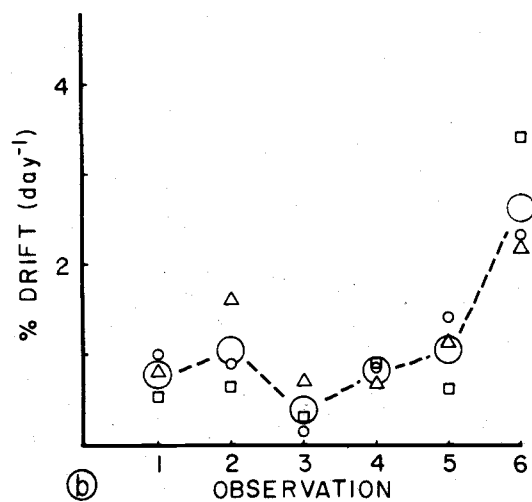
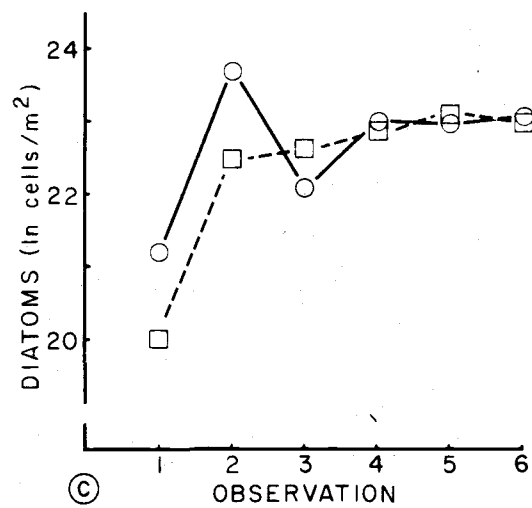
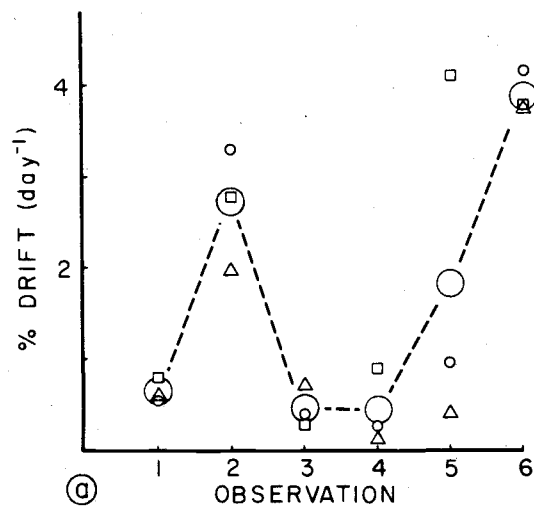
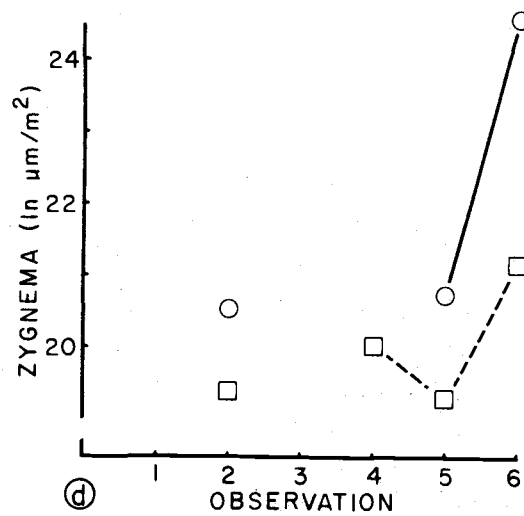
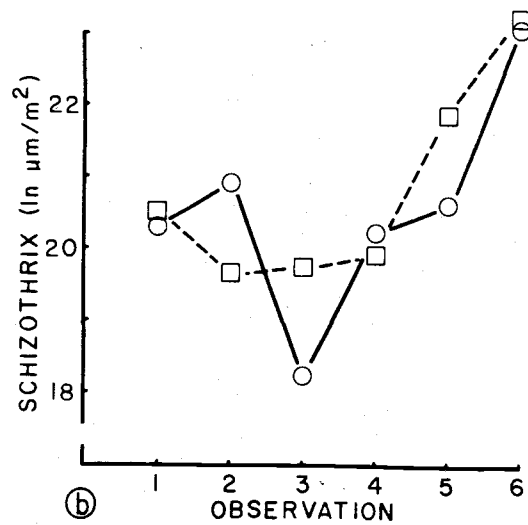
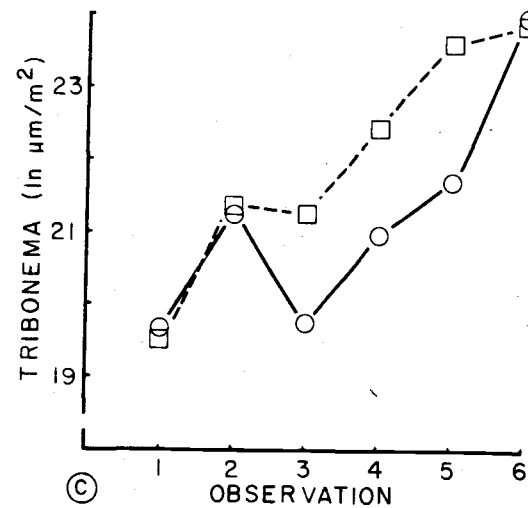
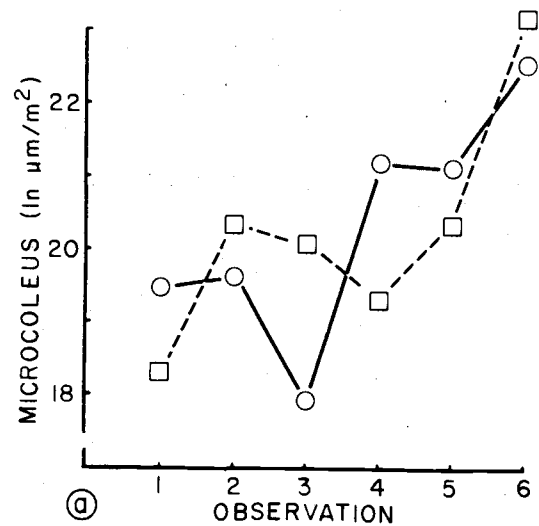


Figure 7. The density of Microcoleus (a), Schizothrix (b), Tribonema (c), and Zygnema (d) in the benthos, experiment 1. The circle and square are the means of assemblages in unshaded and shaded riffles, respectively.

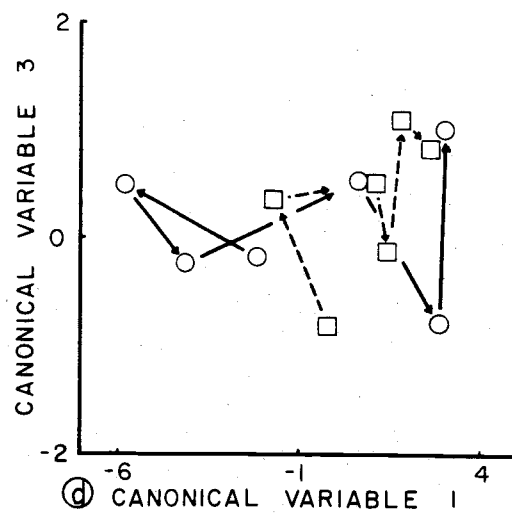
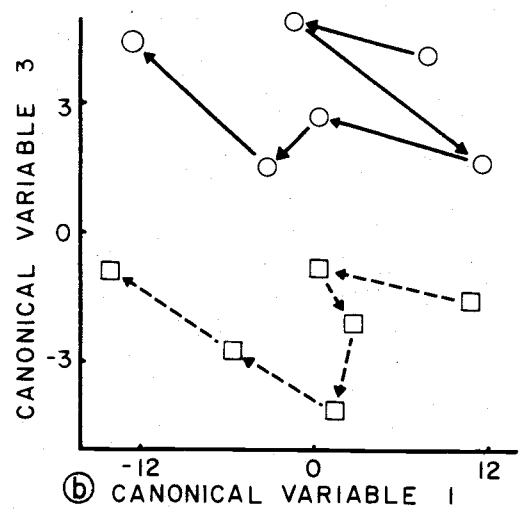
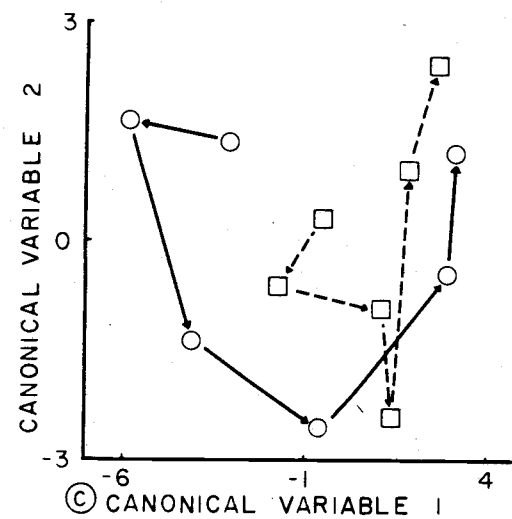
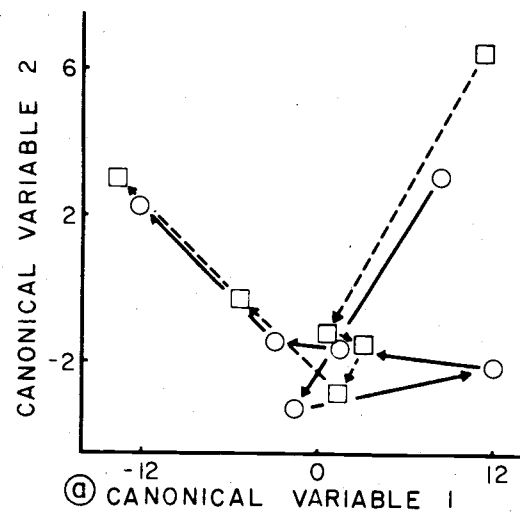


that the transition of assemblages was similar between shaded and unshaded riffles (Figure 8 a). Differences between the assemblages of shaded and unshaded riffles were expressed in the third canonical axis which accounted for only 9 % of the information (Figure 8 b).

The multivariate analysis of the algal assemblages also indicated the changes of the individual algal taxa when the original and canonical variables were correlated. This correlation indicated that the first canonical axis expressed the abundances of diatoms ($r = -.70$), Batrachospermum ($r = -.69$), Microcoleus ($r = -.94$), Schizothrix ($r = -.86$), Tribonema ($r = -.69$), and Zygnema ($r = -.80$), while the second and third axes expressed the abundances of diatoms ($r = -.68$) and Batrachospermum ($r = .68$), respectively. This portion of the analysis indicated that the abundance of all taxa increased during the experiment, the abundance of diatoms increased rapidly between observations 1 and 2, and the abundance of Batrachospermum was greater in the shaded riffles than the unshaded riffles. Because the relationship between the univariate and multivariate analyses has been established with the interpretation of the algal assemblages, only the multivariate analysis of the diatom assemblages will be presented.

The discriminant analysis of the 36 diatom assemblages collapsed 91 % of the variance in the relative abundances of seven taxa (Achnanthes lanceolata, A. minutissima, Diatoma hiemale v. mesodon, Eunotia pectinalis, Fragilaria construens v. venter, F. vaucheriae, and Nitzschia frustulum v. perminuta) into three canonical axes. The analysis indicated that the transition in diatom assemblage was similar between the shaded and unshaded riffles (Figure 8 c,d). Correlations between original and canonical variables for the diatom data indicated that the first canonical axis expressed the abundances of Diatoma hiemale v. mesodon ($r = -.87$), A. lanceolata ($r = .68$), A. minutissima ($r = .80$), F. pectinalis ($r = .90$), and F. construens v. venter ($r = .82$). The second canonical axis expressed the abundance of A. lanceolata ($r = -.63$), and the third axis reflected the abundance of N. frustulum v. perminuta ($r = -.79$). The highest abundance of D. hiemale v. mesodon occurred 30 days after the simulated freshet in

Figure 8. Discriminant analysis of algal (a,b) and diatom (c,d) assemblages in the benthos, experiment 1. The circle and square are centroids of assemblages in unshaded and shaded riffles, respectively. The arrows indicate the sequence of assemblages observed.



the unshaded riffles. The abundance of Diatoma decreased in all riffles in subsequent observations, with the reciprocal increases of the other diatom taxa, particularly taxa other than A. lanceolata, after observation 3.

Faunal Assemblages

The faunal component of the benthic assemblages was a diverse group of invertebrate animals (Table 4). Abundant and frequently-occurring faunal taxa in the benthos and drift were chironomids, ostracods, copepods, mites (Acarina), nematodes, turbellarians, snails, oligochaetes, Rhyacophila verrula, Paracapnia oswegaptera, and a species of the family Limnephilidae (Table 5). The biomass of faunal taxa with relatively high turnover rates (i. e., those taxa with an export rate of more than 1 % day⁻¹) increased to more than 2.7 g m⁻² in all riffles by 30 days after this simulated freshet (Figure 9 a,b). In the unshaded riffles, this biomass was high (4.3 - 10.9 g m⁻²) through observation 4 and then decreased to less than 4.1 g m⁻² by observations 5 and 6. The biomass in the shaded riffles decreased to a mean of 2.8 g m⁻² by observation 4 and subsequently increased to 8.1 g m⁻² by observation 6. Export of this faunal biomass ranged from 50 to 250 mg m⁻² day⁻¹ in the unshaded riffles and remained less than 90 mg m⁻² day⁻¹ in the unshaded riffles between observations 2 through 4 (Figure 9 c,d). Subsequently, the rate increased in the shaded riffles, while it changed relatively little in the unshaded riffles. Faunal export was 66 to 278 mg m⁻² day⁻¹ in all riffles by observation 6.

The family Chironomidae was the most abundant taxon during the experiment (Table 5). Mean biomass and export of the larval and post-larval stages of this taxon were greater in the unshaded riffles than in the shaded riffles. This difference between treatments was the result of a greater abundance of chironomids in the unshaded riffles in observation 2 through 4 (Figure 10). However, by observation 5, little difference in biomass and export between treatments existed. Mean dry weight of individual chironomid larvae was greater in the unshaded riffles than shaded riffles for the initial four observations.

Table 4. List of faunal taxa in the experimental streams (Thut and Hermann, 1969).

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<u>Ameletus</u> sp. 1	Ephemeroptera
<u>Ameletus</u> sp. 2	<u>Ephemerella grandis</u>
<u>Baetis</u> sp. 1	<u>E. heterocaudata</u>
<u>Cinygma</u> sp. 1	<u>E. inermis</u>
<u>Cinygmula</u> sp. 1	<u>E. spinifera</u>
<u>Epeorus longimanus</u>	<u>E. tibialis</u>
<u>Ephemerella coloradensis</u>	<u>Ephemerella</u> sp. 1
<u>E. delantala</u>	<u>Paraleptophlebia</u> sp. 1
<u>E. doddsi</u>	<u>P. debilis</u>
	<u>Rhithrogena morrisoni</u>
<u>Acroneuria californica</u>	Plecoptera
<u>Alloperla borealis</u>	<u>Leuctra augusta</u>
<u>A. exquisita</u>	<u>L. saea</u>
<u>Arcynopteryx curvata</u>	<u>Magaleuctra complicata</u>
<u>A. subtruncata</u>	<u>Nemoura besametsa</u>
<u>Brachyptera occidentalis</u>	<u>N. cinctipes</u>
<u>Paracapnia oswegaptera</u>	<u>N. californica</u>
<u>Capnia oenone</u>	<u>N. frigida</u>
<u>C. projecta</u>	<u>N. oregonensis</u>
<u>Isogenus nonus</u>	<u>N. producta</u>
<u>I. sordida</u>	<u>Peltoperla brevis</u>
<u>Isogenus</u> sp. 1	<u>P. mariana</u>
	<u>Rickera sorpta</u>
<u>Dysmicohermes crepusculus</u>	Megaloptera
<u>Agraylea</u> sp. 1	Trichoptera
<u>Discosmoecus</u> sp. 1	<u>Neophylax</u> sp. 1
<u>Ecclisomyia simulata</u>	<u>Psychoglypha alaskensis</u>
<u>Goerita genota</u>	<u>P. ulla</u>
<u>Glossosoma</u> sp. 1	<u>Rhyacophila arnaudi</u>
<u>Hydroptila rono</u>	<u>R. grandis</u>
<u>Imania</u> sp. 1	<u>R. vaccua</u>
<u>Limnephilus aequalis</u>	<u>R. vaefes</u>
<u>L. occidentalis</u>	<u>R. vagrita</u>
<u>L. nogus</u>	<u>R. vepulsa</u>
<u>Micrasema dimmicki</u>	<u>R. verrula</u>
	<u>Rhyacophila</u> sp. 1
<u>Agabus tristis</u>	Coleoptera
<u>Ametor scabrosus</u>	<u>Hydroporus vilis</u>
<u>Cymbiodyta</u> sp. 1	<u>Rhantus bintatus</u>

Table 4. Continued

Diptera	
(* indicates the family Chironomidae)	
<u>Antocha</u> sp. 1	<u>Limnophora</u> sp.1
<u>Bittacomorpha</u> sp.1	* <u>Orthocladius</u> sp.1
* <u>Chaetocladius</u> sp.1	* <u>Parastia</u> sp.1
* <u>Cheatocladius</u> sp. 2	* <u>Pseudodiamesa</u> sp.1
* <u>Chironomus galaptera</u>	* <u>Syncricotopus</u> sp.1
* <u>Corynoneura</u> sp.1	* <u>Synorthocladius</u> sp.1
* <u>Diamesa</u> sp.1	* <u>Trissocladius</u> sp.1
<u>Dicranota</u> sp.1	<u>Wiedemannia</u> sp.1
<u>Hexatoma</u> sp.1	
Other Taxa	
Acari	Oligochaeta
Collembola	Ostracoda
Copepoda	Tardigrada
Gastropoda	Turbellaria
Nematoda	

Table 5. Mean biomass and export of fauna in shaded and unshaded riffles during experiment 1.

Taxa	Biomass (mg m^{-2})		Export ($\text{mg m}^{-2} \text{d}^{-1}$)		% Export	
	Light Intensity		Light Intensity		Light Intensity	
	15 %	100 %	15 %	100 %	15 %	100 %
chironomid larvae	2027	3008	49.0	66.3	2.4	2.2
chironomid pupae/adults	52	133	17.6	37.8	33.9	28.4
oligochaetes	1619	951	14.7	46.4	0.9	4.9
snails	504	564	2.5	0.7	0.5	0.1
Limnephilidae sp. 1	302	375	1.2	0.9	0.4	0.2
ostracods	195	464	11.0	19.6	5.5	4.6
flatworms	156	215	2.2	3.4	1.4	1.6
nematodes	66	104	0.1	0.1	0.2	0.1
<u>Rhyacophila verrula</u>	54	66	2.8	4.6	5.1	7.0
mites	52	20	4.0	2.8	7.6	14.2
<u>Paracapnia oswegaptera</u>	26	12	0.3	0.3	1.3	2.1
copepods	21	9	0.9	1.3	4.5	13.9
collembola	3	6	45.1	35.5	1556.4	622.1

Figure 9. Faunal biomass in the benthos and the export of faunal biomass from the benthos of unshaded (a,c) and shaded (b, d) riffles of streams 1 (small circle), 2 (square), and 3 (triangle), experiment 1. The large circle is the mean of the triplicate riffles.

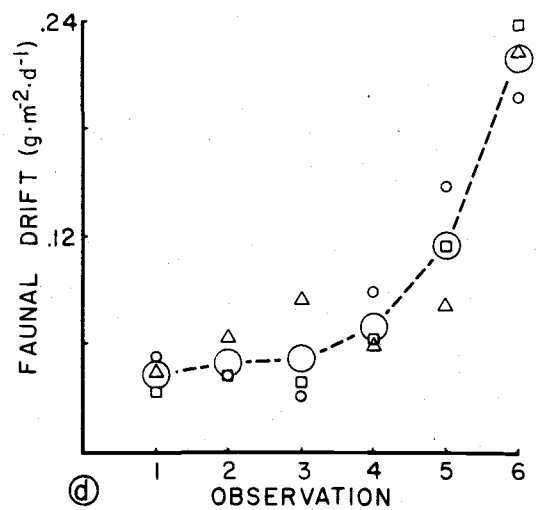
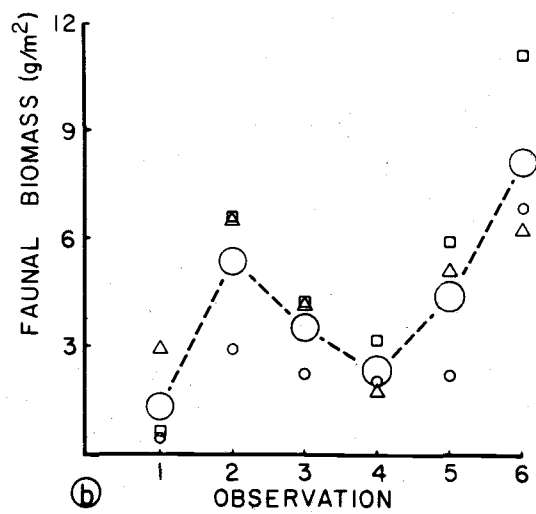
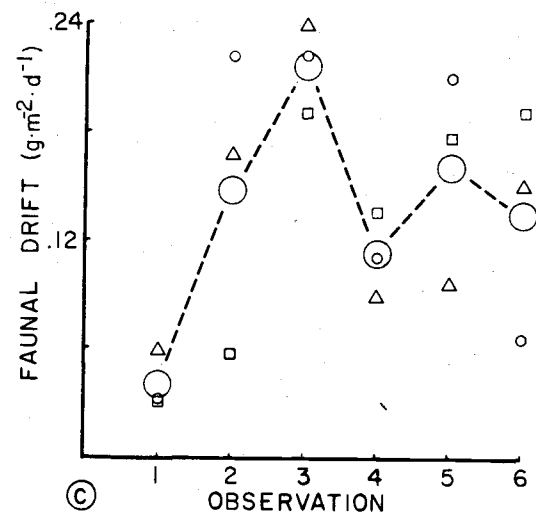
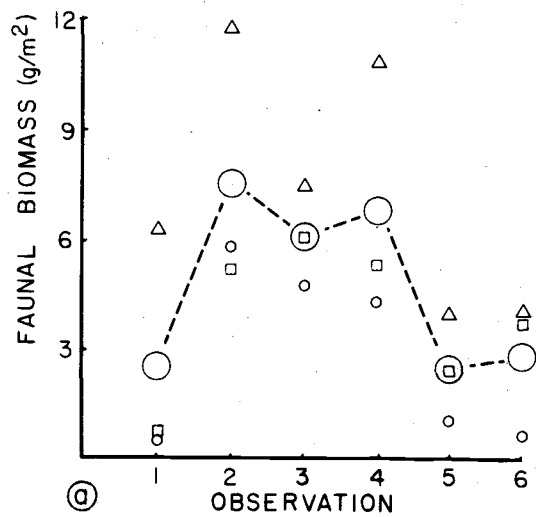
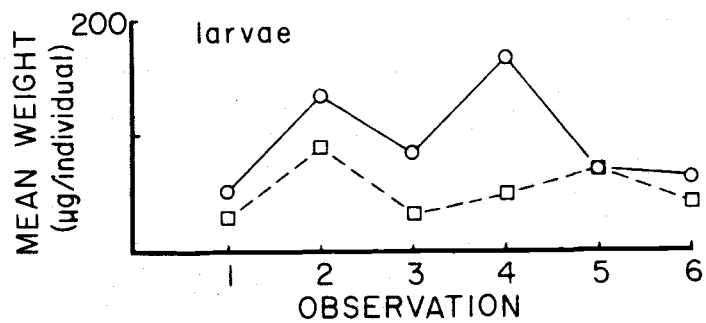
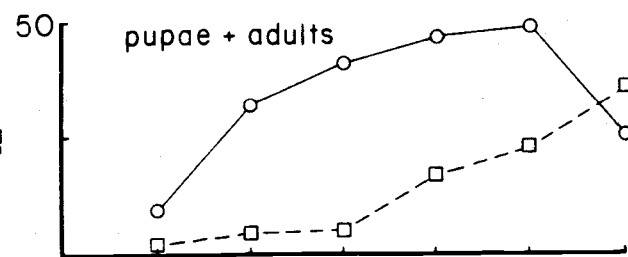
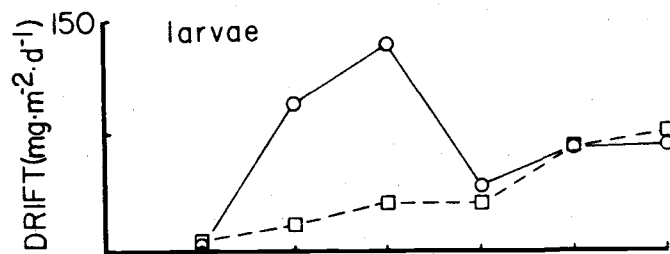
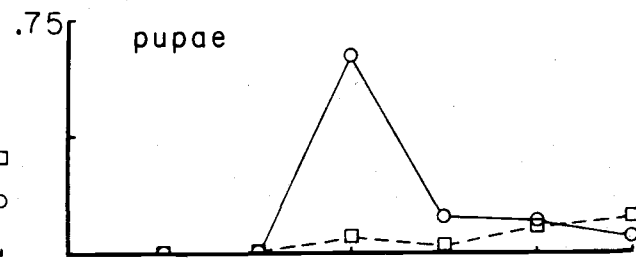
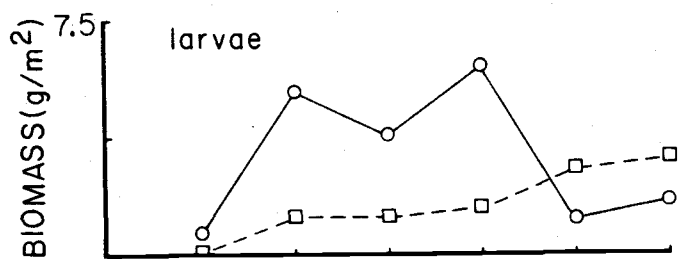


Figure 10. Biomass and export of chironomid larvae and pupae/adults, and larval mean weight, experiment 1. The circle and square indicate the means of the unshaded and shaded riffles, respectively.



Chironomid mean weight increased in both shaded and unshaded riffles between observations 1 and 2 and between observations 3 and 4. Little difference in the mean weight of larvae was observed between treatments.

The relative abundance of chironomids in the faunal biomass in both the benthos and drift of the shaded and unshaded riffles increased between observations 1 and 3, and decreased between observations 4 and 6 (Figure 11 a,b). The relative abundance of this taxon in the benthos and drift of all riffles increased from less than 40 % of the faunal biomass in observation 1 to a range of 58 - 92 % by observation 4. Chironomid relative abundance decreased to means of 65 % (benthos) and 59 % (drift) for all riffles by observation 6.

The export rate of animals was highest between 0600 and 1800 hours (Table 6). Chironomid pupae/adults and collembola had the greatest difference between day and night drift rates, as more than 75 % of the export of these taxa for the 24-hr drift occurred between 0600 and 1800 hours. Drift of turbellarians, Rhyacophila, Paracapnia, and the Limnephilidae species was not significantly higher ($\alpha = 0.05$) in the day.

Diversity

The diversity of algal taxa was lower in the unshaded riffles than the shaded riffles in the initial three observations (Figure 11 c,d). In observation 4 and 5, little difference in this measurement was apparent between shaded riffles and unshaded riffles. The diversity of algal taxa was again lower in the unshaded riffles by observation 6. The diversity of diatom taxa followed a similar pattern except that little difference was apparent between shaded and unshaded riffles between observations 4 through 6 (Figure 12 a,b). The diversity of animal taxa was lower in the unshaded riffles than the shaded riffles between observations 2 and 4 (Figure 12 c,d). Little difference in diversity of these taxa was apparent in observations 1, 5, and 6.

Figure 11 a,b. Relative abundance of chironomids in the biomass (a) and export (b) of the faunal assemblages, experiment 1. The circle and square are the means of assemblages in unshaded and shaded riffles, respectively.

Figure 11 c,d. The diversity of algal taxa in the benthos of unshaded (c) and shaded (d) riffles of streams 1 (small circle), 2 (square), and 3 (triangle), experiment 1. The large circle is the mean of the replicate riffles.

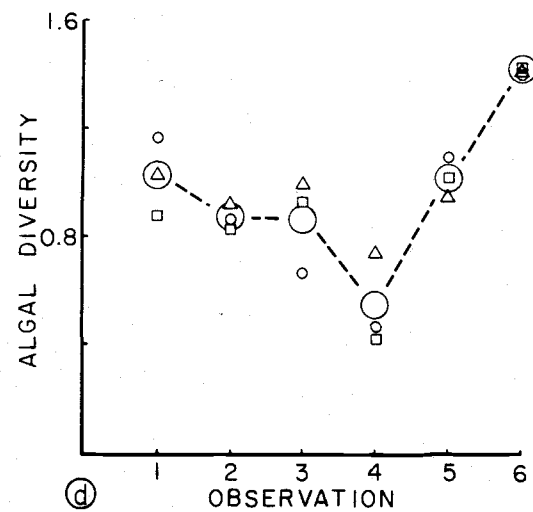
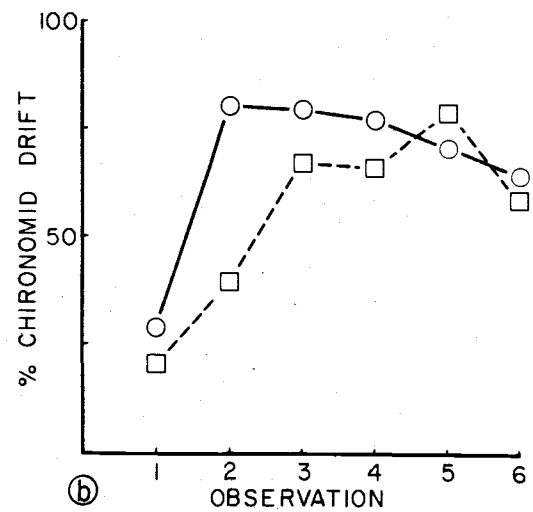
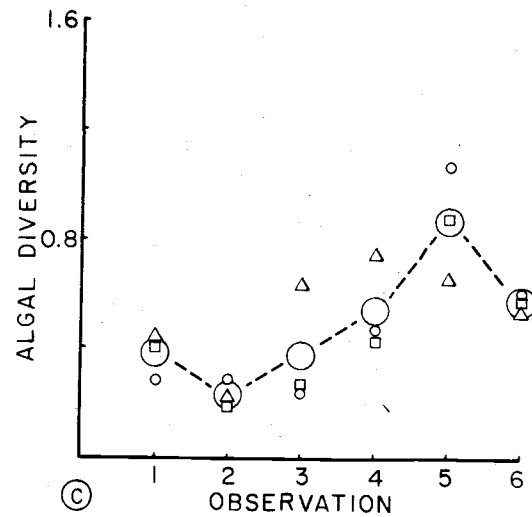
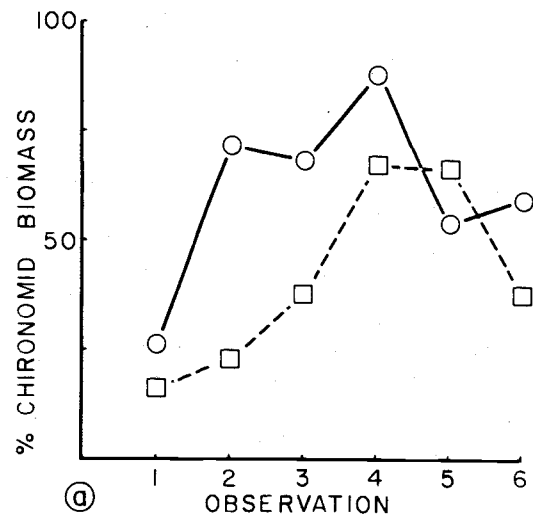
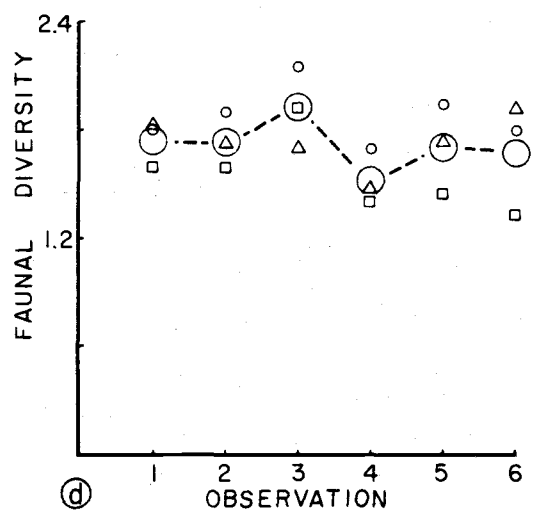
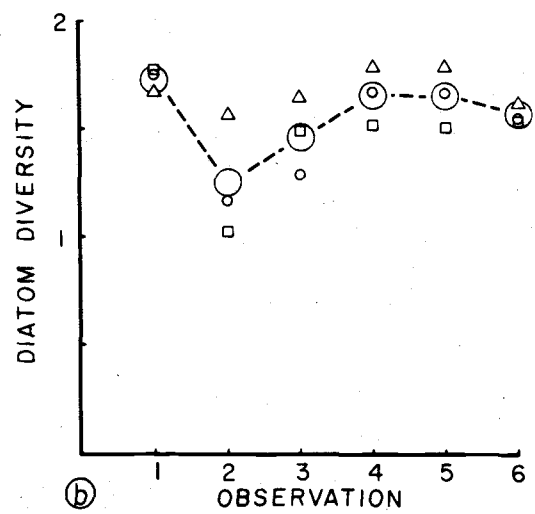
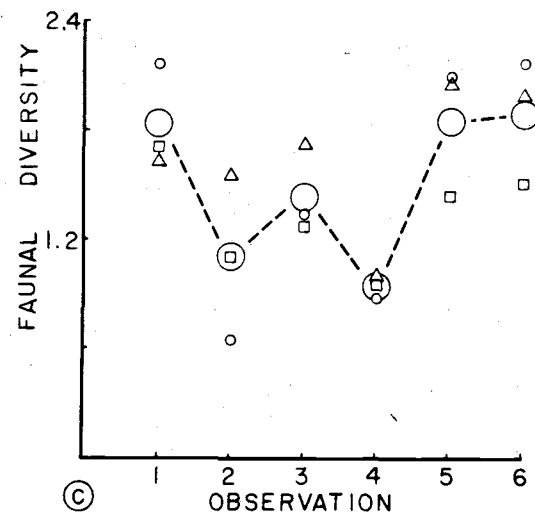
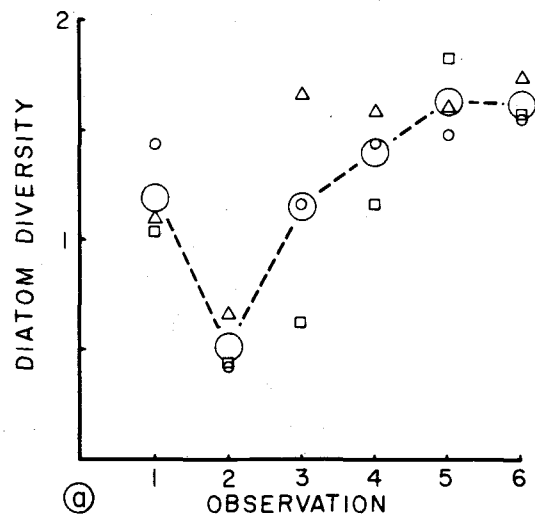


Table 6. Comparison of day versus night faunal drift, experiment 1.

Taxa	% of drift during 24-hr day between 0600 & 1800	Significant difference ($\alpha = 0.05$)
chironomid adults/pupae	87.3	*
collembola	77.9	*
mites	69.5	*
<u>Paracapnia oswegaptera</u>	67.6	*
chironomid larvae	64.1	*
copepods	62.3	*
oligochaetes	61.6	*
<u>Rhyacophila verrula</u>	57.5	
Limnephilidae sp. 1	55.7	
flatworms	50.9	

Figure 12. Diversity of diatom faunal taxa in the benthos of unshaded (a,c) and shaded (b,d) riffles of streams 1 (small circle), 2 (square), and 3 (triangle), experiment 1. The large circle is the mean of replicate riffles.



Experiment 2 - Community Development in Nitrate-Enriched Riffles

During experiment 2, solar radiation at Kalama Springs decreased from 410 ly day^{-1} in July to 93 ly day^{-1} in November (Figure 13), while the daylength decreased from 15 hr day^{-1} in July to 9 hr day^{-1} in November. Insolation was 100 % and 15 % of solar radiation in the unshaded and shaded riffles, respectively. In addition, stream 1 received continuous enrichment of nitrate-nitrogen ($100 \mu\text{g l}^{-1}$ over background) during the experiment, while stream 3 was not enriched (Figure 1). Stream 2 was unenriched for 40 days after the simulated freshet and then continuously enriched for the duration of the experiment. Benthic assemblages were sampled on July 12, July 19, July 26, August 10, August 24, September 7, October 4, and November 8, 1976. Henceforth, samples will be referred to as observations 1, 2, 3, 4, 5, 6, 7, and 8, respectively.

Little plant or animal material was apparent on the substrate of the streams immediately after the simulated freshet on July 5. The rocks in the riffles were covered with golden-brown, gelatinous algae within seven days after this disturbance and golden-brown filaments were observed by observation 2, 14 days after the freshet. Algal biomass decreased in all riffles between observations 3 and 4, and little algal material was apparent in the riffles between 35 and 63 days after the freshet. A filamentous green alga covered the substrate of all riffles from September to the end of the experiment. The density of the golden-brown algae in the early observations and the green alga in the later observations was greater in the unshaded riffles than the shaded riffles, while little difference was apparent between nitrate-enriched and unenriched streams.

Composite Ecosystem Properties

Organic matter increased to more than 25 g m^{-2} in the shaded riffles and more than 37 g m^{-2} in the unshaded riffles within 14 days after the freshet (Figure 14 a,b). This attribute decreased to a mean of 26 g m^{-2} by observation 4 in all riffles. By observation 8, organic

Figure 13. Daily solar radiation at Kalama Springs, experiment 2.
Arrows indicate the sampling dates.

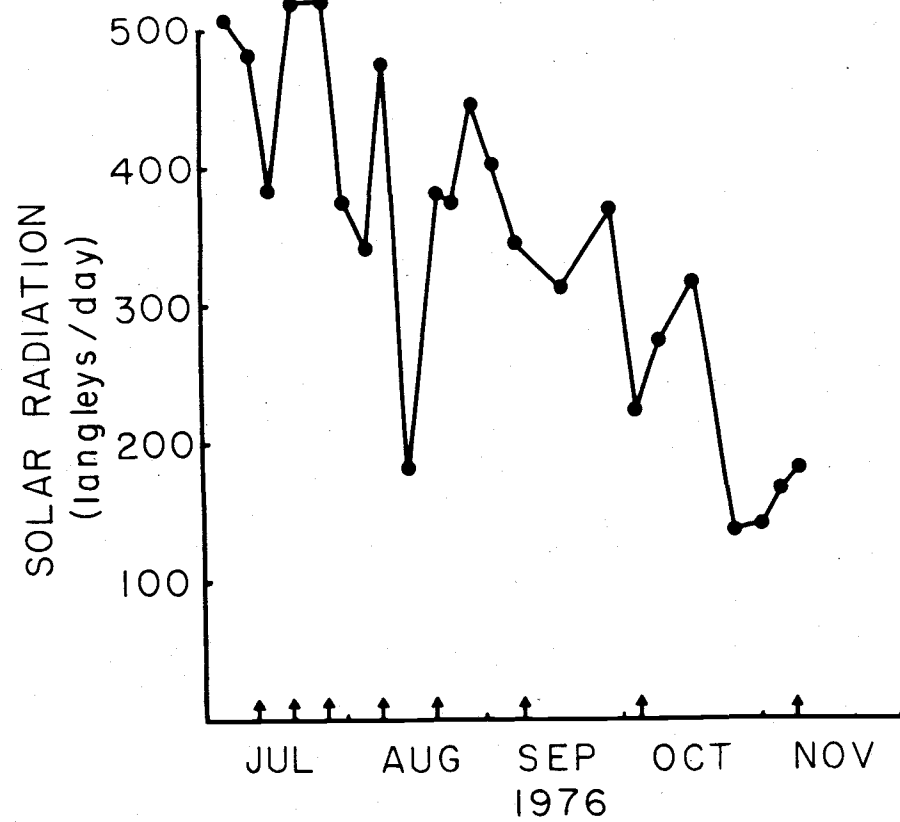
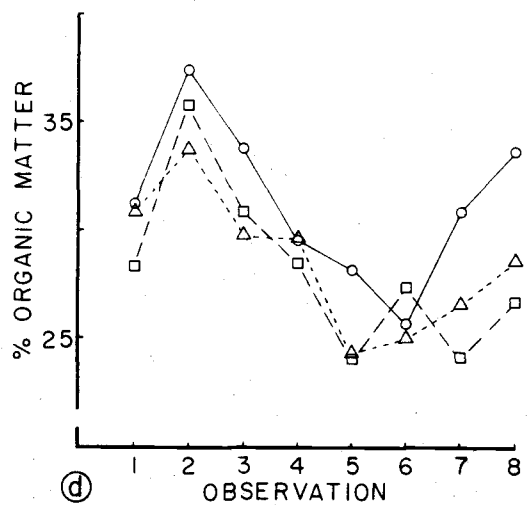
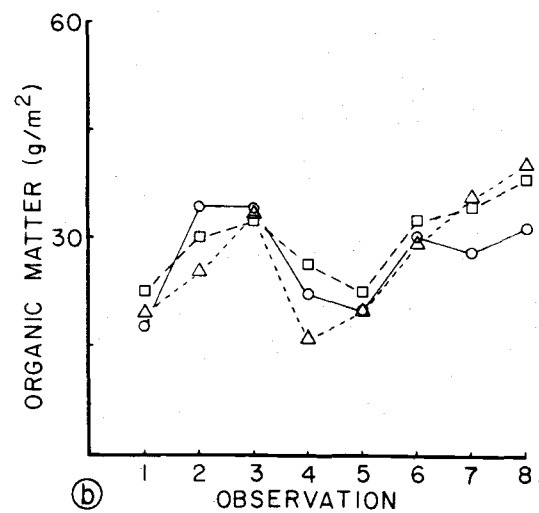
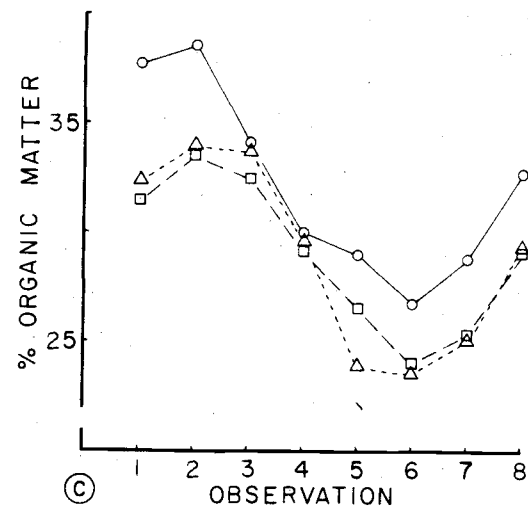
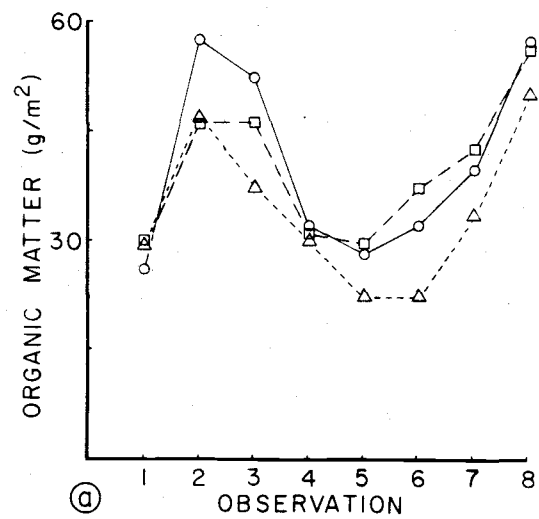


Figure 14. Organic matter and percentage organic matter in the benthos of unshaded (a,c) and shaded (b,d) riffles of streams 1 (circle), 2 (square), and 3 (triangle), experiment 2.



matter increased to means of 37 g m^{-2} and 55 g m^{-2} in the shaded and unshaded riffles, respectively. The amount of organic matter was greater in the nitrate-enriched, unshaded riffles than in unenriched, unshaded riffles after observation 1. Little difference in this attribute was observed between nitrate-enriched and unenriched shaded riffles.

The percentage organic matter increased to a mean of 36 % for all riffles by observation 2 (Figure 14 c,d). This attribute subsequently decreased to a mean of 26 % by observation 5, and increased again to a mean of 30 % by observation 8.

Chlorophyll a concentration increased to a mean of 272 mg m^{-2} in the shaded riffles, a mean of 383 mg m^{-2} in the unenriched, unshaded riffles and 587 mg m^{-2} in the nitrate-enriched, unshaded riffle within 14 days after the simulated freshet (Figure 15 a,b). The concentration decreased to less than 180 mg m^{-2} in all riffles between observations 3 and 4, and varied from 101 to 176 mg m^{-2} between observations 4 and 8 in the shaded riffles. In the unshaded riffles, the chlorophyll a concentration increased to more than 187 mg m^{-2} by observation 8, with higher concentrations in the nitrate-enriched riffles than the unenriched riffles.

The ratio of chlorophyll a to organic matter initially increased to a mean of 0.009 in all riffles within 14 days after the simulated freshet (Figure 15 c,d). This ratio decreased to less than 0.005 by observation 4 in the unshaded riffles and by observation 7 in the shaded riffles; it varied between 0.003 to 0.005 for the subsequent observations.

The ratio of light absorbances at 480 and 665 nm increased to means of 1.3 in the shaded riffles and 1.5 in the unshaded riffles by observation 3 (Figure 16 a,b). This ratio decreased to less than 1.00 in all riffles by observation 8. The ratio of chlorophyll c to a increased to means of 0.40 in the shaded riffles and 0.54 in the unshaded riffles by observation 3 (Figure 16 c,d). This ratio decreased to less than 0.24 in all riffles by observation 8. Little difference in the ratios of light absorbances or chlorophyll c to a was apparent between nitrate-enriched and unenriched riffles.

Figure 15. Chlorophyll a concentrations and the ratio of chlorophyll a to organic matter in the benthos of unshaded (a,c) and shaded (b,d) riffles of streams 1 (circle), 2 (square), and 3 (triangle), experiment 2.

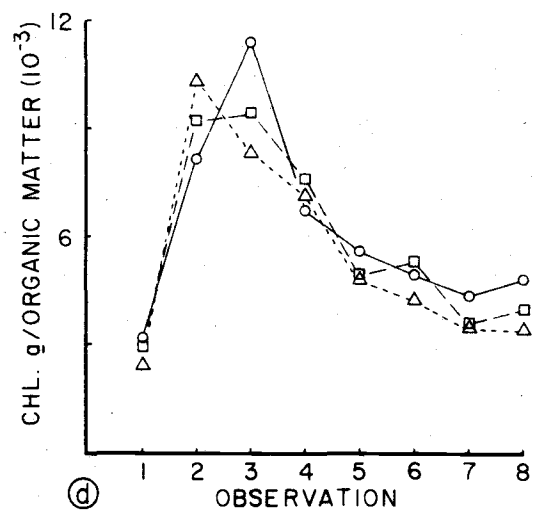
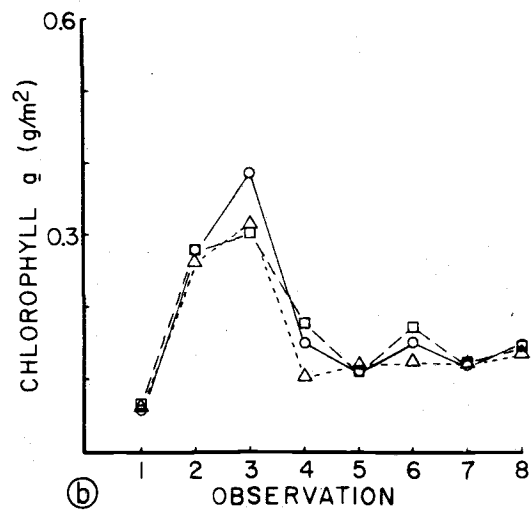
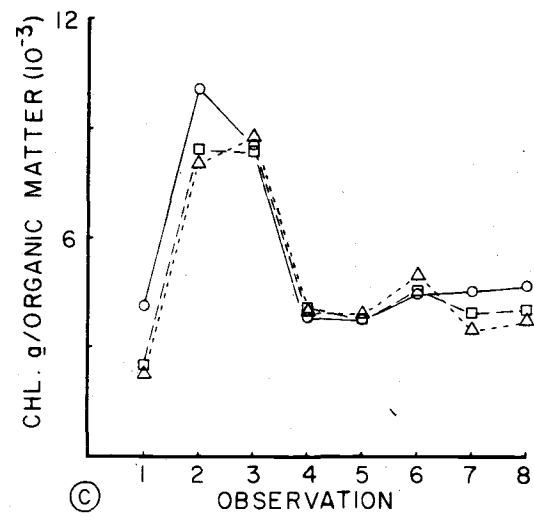
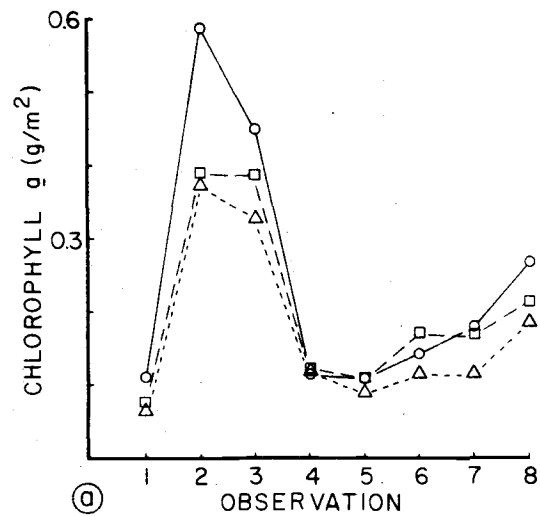
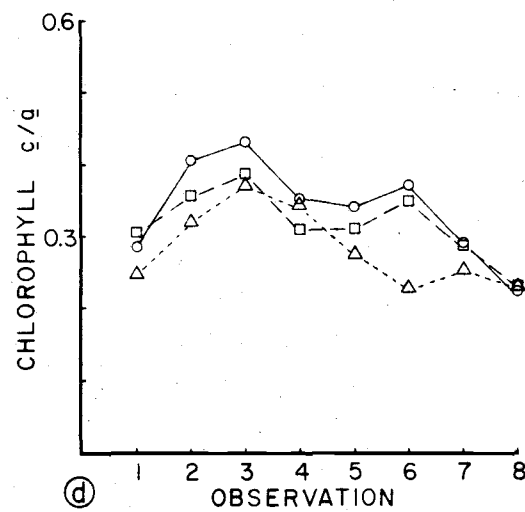
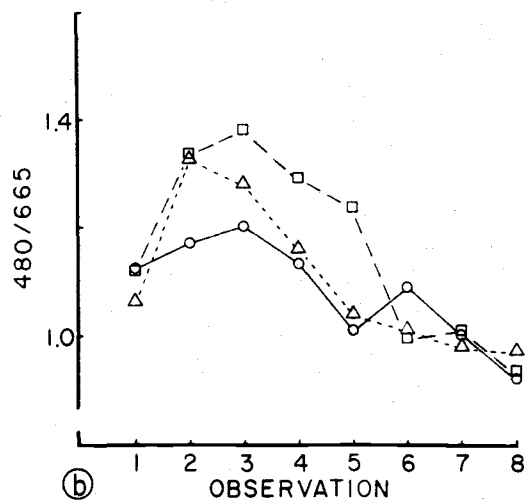
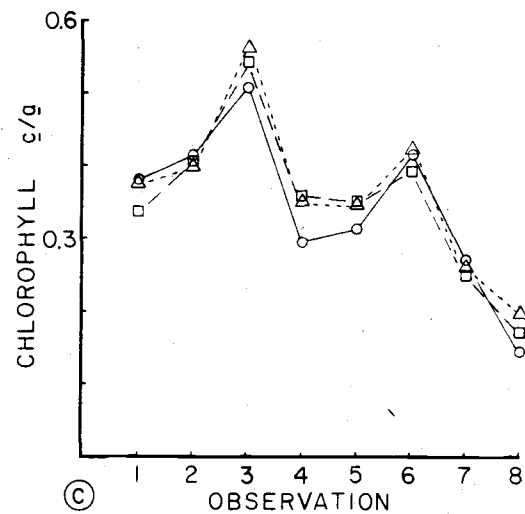
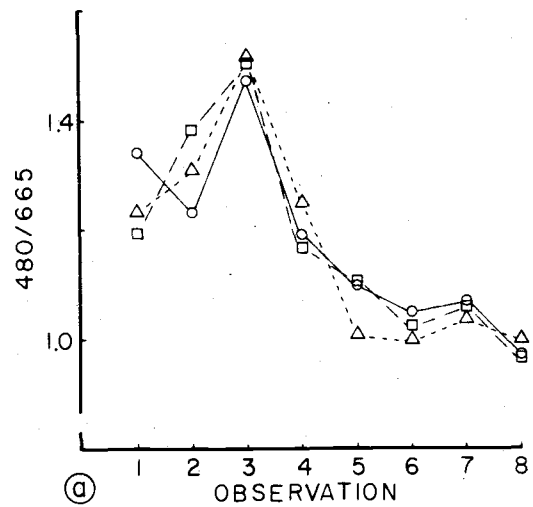


Figure 16. Ratios of 480 to 665 nm absorbancies and chlorophyll c to a concentrations in the benthos of unshaded (a,c) and shaded (b,d) riffles of streams 1 (circle), 2 (square), and 3 (triangle), experiment 2.



The rate of chlorophyll a export can be described as a linear function of chlorophyll a concentration in the riffle (Figure 17 a, b) or as the percentage daily loss of chlorophyll a from the riffles (Figure 17 c,d). This export ranged from 0.4 to 2.0 % of the chlorophyll a in the riffles per day during the experiment. In general, export increased between observations 1 and 3, decreased between observations 3 and 4, and increased between observations 4 and 8.

Primary Production and Community Respiration

The maximum rate of gross primary production (i. e., the rate at light saturation) increased to a mean of $434 \text{ mg O}_2 \text{ m}^{-2} \text{ hr}^{-1}$ in the shaded riffles, a mean of $654 \text{ mg O}_2 \text{ m}^{-2} \text{ hr}^{-1}$ in the unenriched, unshaded riffles; and $881 \text{ mg O}_2 \text{ m}^{-2} \text{ hr}^{-1}$ in the nitrate-enriched, unshaded riffle within 14 days after the simulated freshet (Figure 18 a,b). Subsequently, this rate decreased in all riffles to less than $340 \text{ mg O}_2 \text{ m}^{-2} \text{ hr}^{-1}$ by observation 4. In the unshaded riffles, the rate increased again to more than $530 \text{ mg O}_2 \text{ m}^{-2} \text{ hr}^{-1}$ by observation 8, with higher production rates observed in the nitrate-enriched riffles than the unenriched riffles.

The maximum rates of gross production were positively correlated to chlorophyll a concentration in the riffles (Figure 19). However, the relationship was not linear, and the ratio of maximum rate to chlorophyll a decreased with increasing chlorophyll a concentration. This ratio was higher in benthic assemblages of nitrate-enriched, unshaded riffles than those of unenriched, unshaded riffles. The parameters of a rectangular hyperbola ($Y = b_1 X / (b_2 + X)$) were fitted to the maximum rates (Y) and chlorophyll a concentrations (X) in the nitrate-enriched and unenriched, shaded and unshaded riffles. The resulting equations indicated that at saturating concentrations of chlorophyll a, the highest achievable rates of gross primary production were $693 \text{ mg O}_2 \text{ m}^{-2} \text{ hr}^{-1}$ (unenriched, shaded riffles), $575 \text{ mg O}_2 \text{ m}^{-2} \text{ hr}^{-1}$ (nitrate-enriched, shaded riffles), $915 \text{ mg O}_2 \text{ m}^{-2} \text{ hr}^{-1}$ (unenriched, unshaded riffles), and $1065 \text{ mg O}_2 \text{ m}^{-2} \text{ hr}^{-1}$ (nitrate-enriched, unshaded

Figure 17 a,b. The relationship of chlorophyll a export to the concentration of chlorophyll a in unshaded (a) and shaded (b) riffles of streams 1 (circle), 2 (square), and 3 (triangle), experiment 2.

Figure 17 c,d. The percentage of chlorophyll a exported per day from unshaded (c) and shaded (d) riffles of streams 1 (circle), 2 (square), and 3 (triangle), experiment 2.

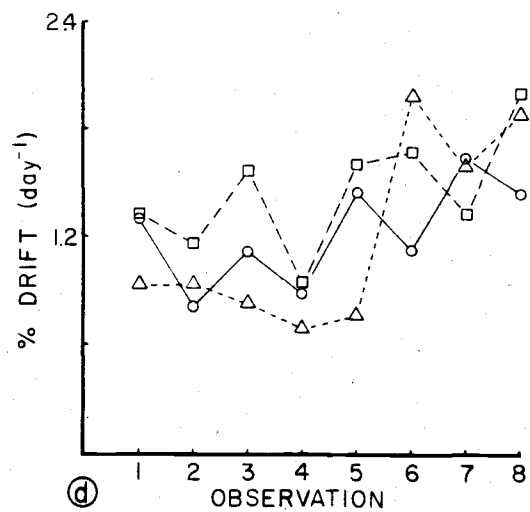
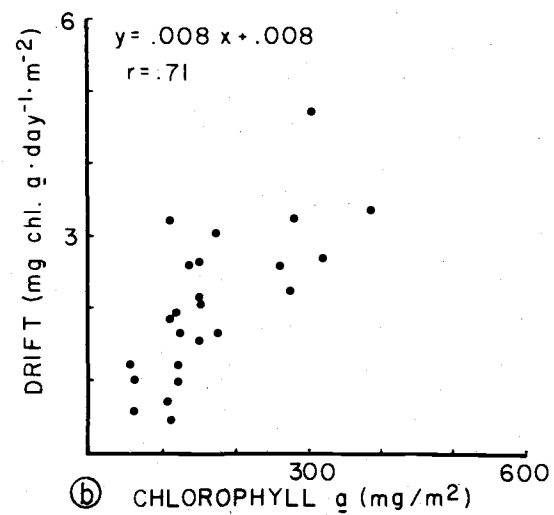
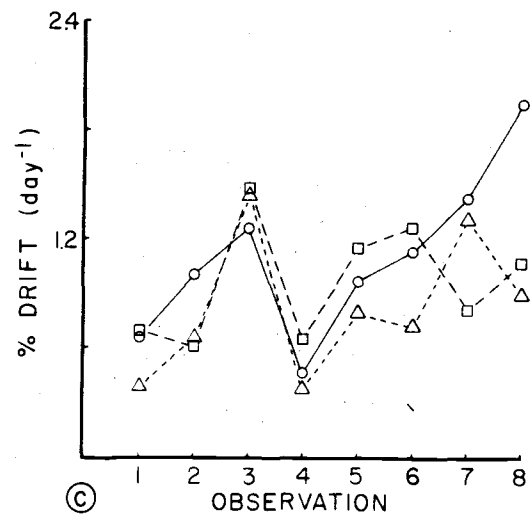
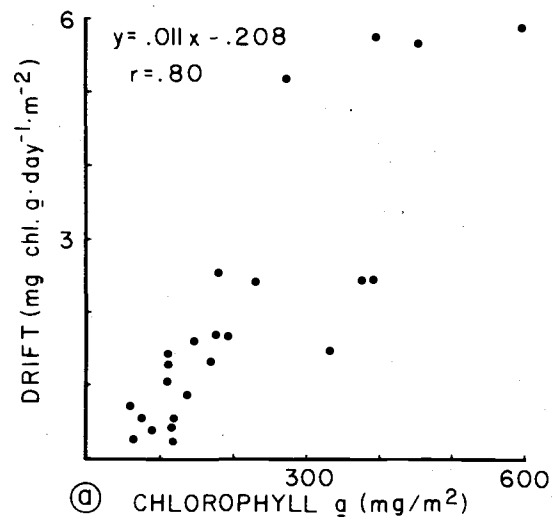


Figure 18. Maximum rate of gross primary production by benthic assemblages in unshaded (a) and shaded (b) riffles of streams 1 (circle), 2 (square) and 3 (triangle), experiment 2.

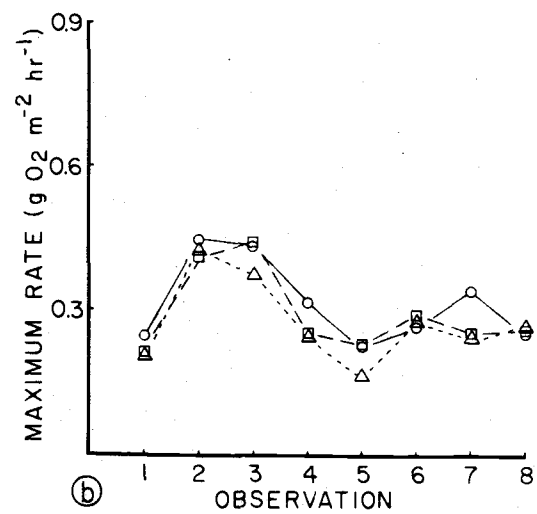
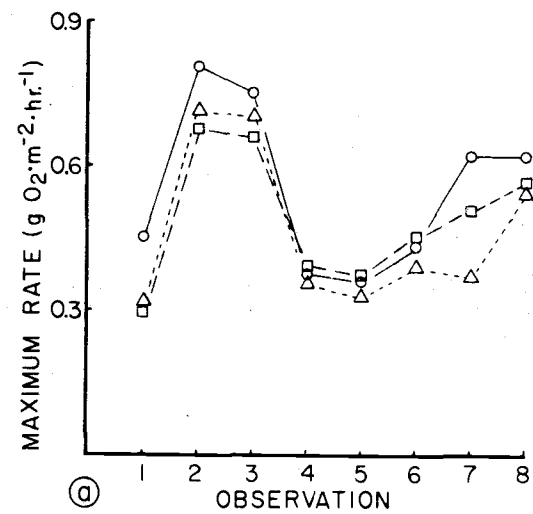
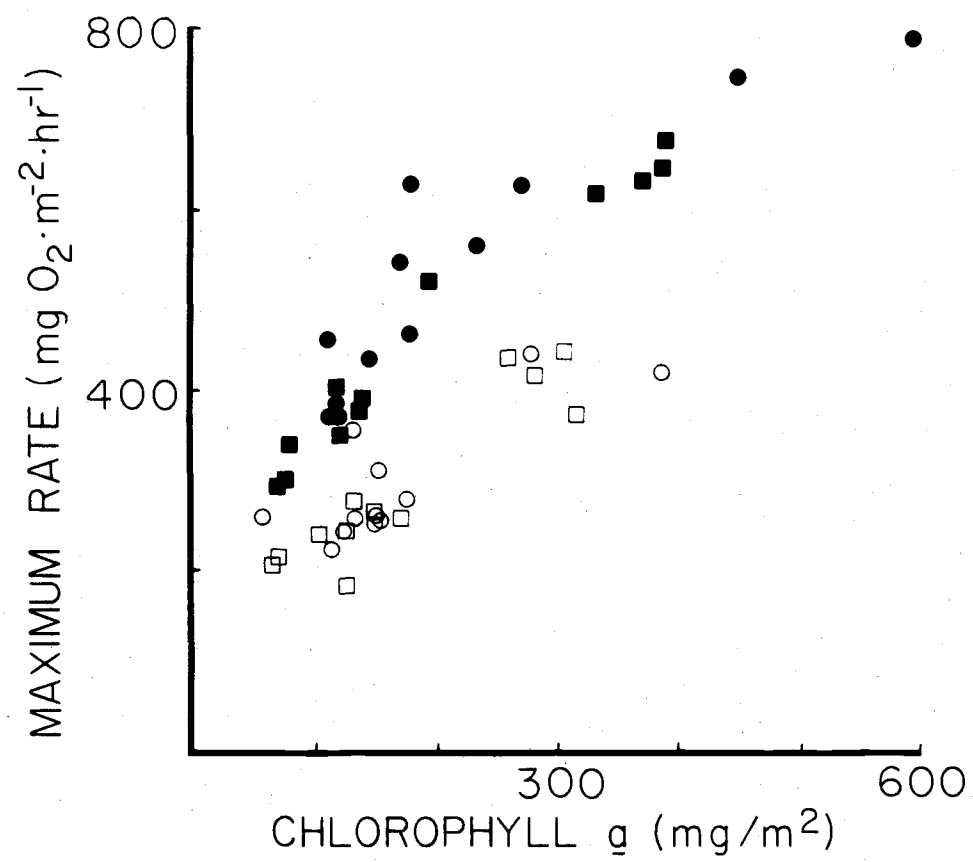


Figure 19. The relationship of maximum rates of gross primary production to chlorophyll a concentrations in nitrate-enriched, unshaded (closed circle); unenriched, unshaded (closed square); nitrate-enriched, shaded (open circle); and unenriched, shaded (open square) riffles, experiment 2.



riffles). The production rate was 50 % of these maximum velocities at chlorophyll a concentrations of 140-210 mg m^{-2} in the riffles.

A plot of the relative rate of gross primary production against light intensity for the shaded and unshaded riffles indicated that light saturation occurred around 0.1 ly min^{-1} (Figure 20). Fifty percent of the maximum rate of production occurred between 0.01 and 0.03 ly min^{-1} . At Kalama Springs, solar radiation of the unshaded riffles was greater than 0.1 ly min^{-1} during more than 90 % of the daylength in July and 80 % in December. For the shaded riffles, insolation was greater than 0.1 ly min^{-1} for more than 85 % of the daylength in July and 50 % in December.

Community respiration in the benthic assemblages increased between observations 1 and 3, and subsequently decreased to a relatively constant level between observations 4 and 8 (Figure 26 a,b). In the shaded riffles, community respiration increased to a mean of $78 \text{ mg O}_2 \text{ m}^{-2} \text{ hr}^{-1}$ by observation 3 and then decreased to less than $61 \text{ mg O}_2 \text{ m}^{-2} \text{ hr}^{-1}$ for the remainder of the experiment. In the unshaded riffles, this rate increased to a mean of $136 \text{ mg O}_2 \text{ m}^{-2} \text{ hr}^{-1}$ by observation 3 and then decreased to less than $93 \text{ mg O}_2 \text{ m}^{-2} \text{ hr}^{-1}$ between observations 4 and 8.

The ratio of community respiration to organic matter increased between observations 1 and 3, and decreased between observations 4 and 8 (Figure 21 c,d). In the shaded riffles, this ratio increased to a mean of $2.3 \text{ mg O}_2 \text{ g}^{-1} \text{ hr}^{-1}$ by observation 3 and decreased to less than $1.3 \text{ mg O}_2 \text{ g}^{-1} \text{ hr}^{-1}$ by observation 8. In the unshaded riffles, this ratio increased to a mean of $3.0 \text{ mg O}_2 \text{ g}^{-1} \text{ hr}^{-1}$ by observation 3 and decreased to less than $1.6 \text{ mg O}_2 \text{ g}^{-1} \text{ hr}^{-1}$ by observation 8.

Floral Assemblages

Abundant and frequently occurring taxa of the flora in experiment 2 were Batrachospermum, Microcoleus, Schizothrix, Tribonema, Zygnema, and diatoms. The abundances of these taxa were similar among riffles, except for the abundances of diatoms and Zygnema which were greater in the unshaded riffles than shaded riffles (Figure 22, 23, and 24). The principal components analysis of the 48 algal assemblages collapsed

Figure 20. The relationship of relative production and light intensity in benthic assemblages of unshaded (a) and shaded (b) riffles, experiment 2.

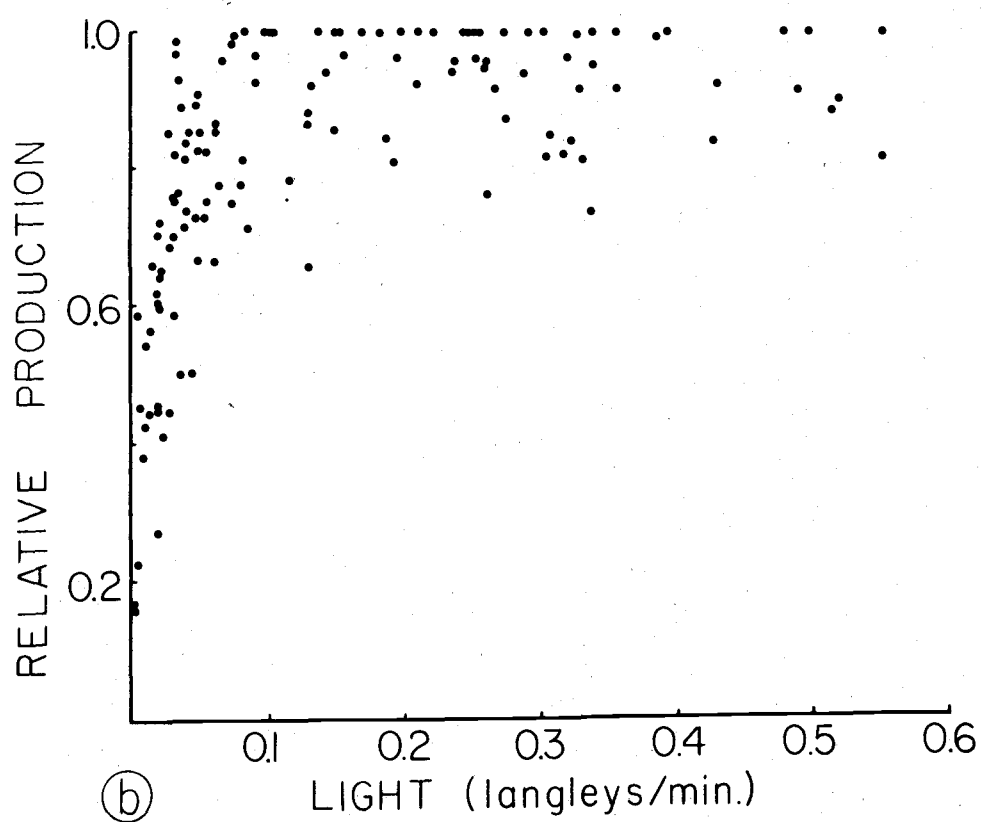
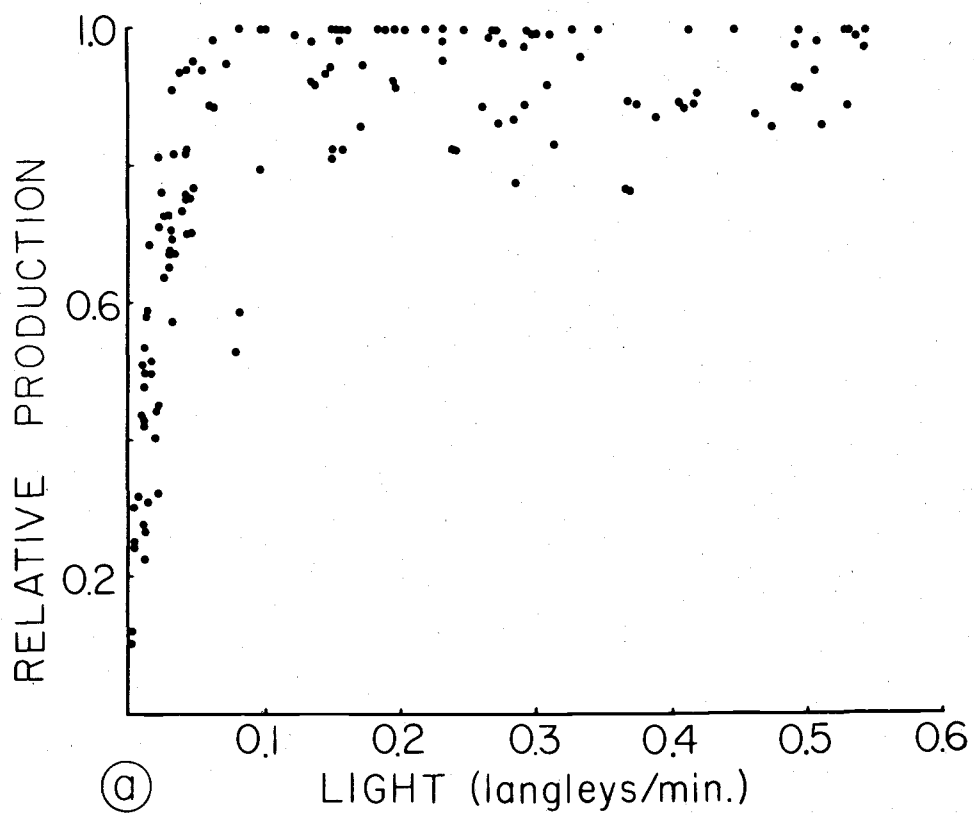


Figure 21. Rates of community respiration and the ratio of community respiration to organic matter of the benthos of unshaded (a,c) and shaded (b,d) riffles of streams 1 (circle), 2 (square), and 3 (triangle), experiment 2.

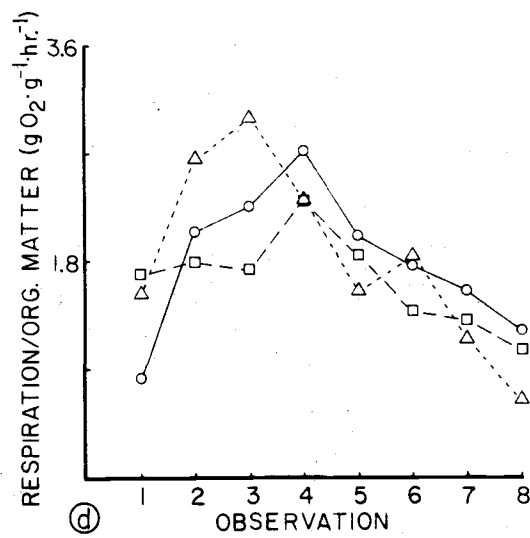
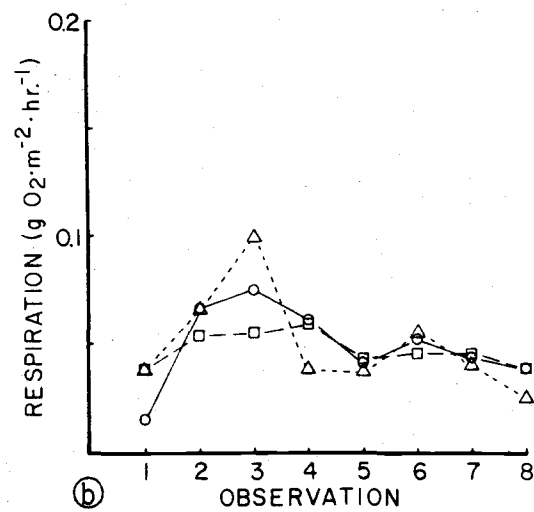
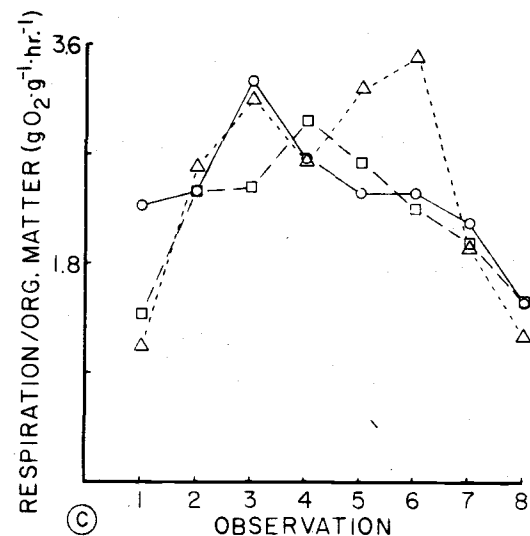
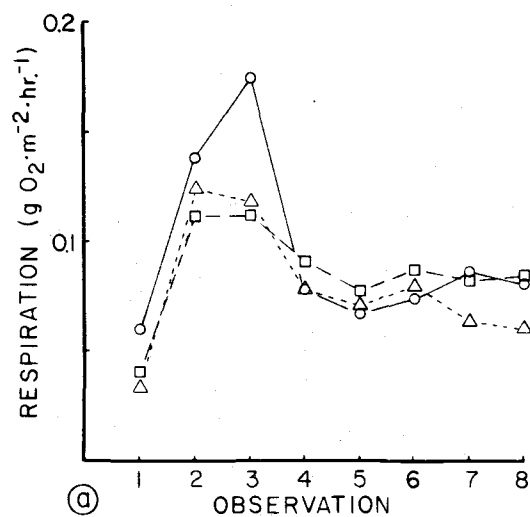


Figure 22. Density of diatom cells and Batrachospermum in the benthos of unshaded (a,c) and shaded (b,d) riffles of streams 1 (circle), 2 (square), and 3 (triangle), experiment 2.

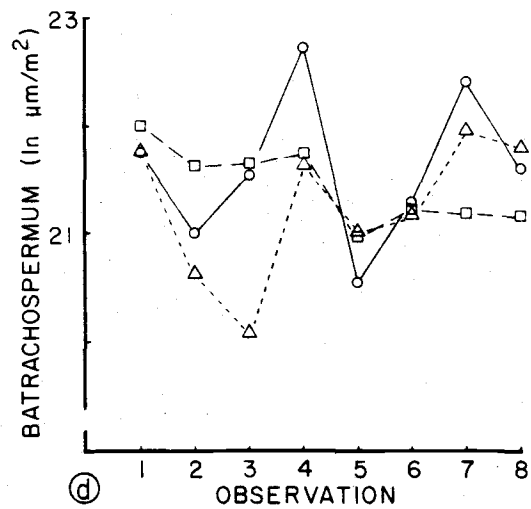
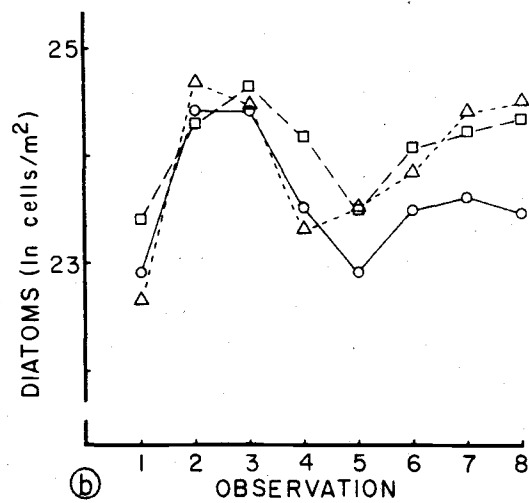
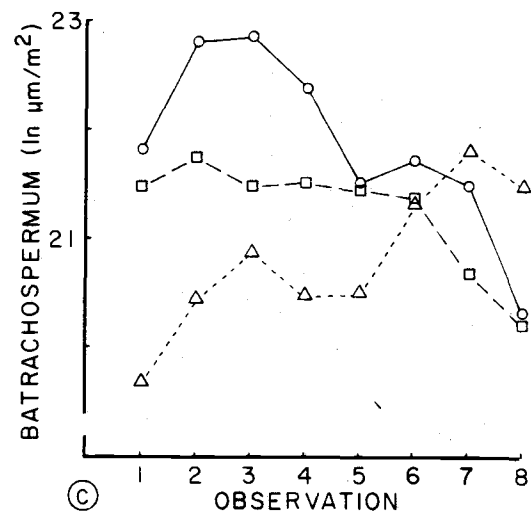
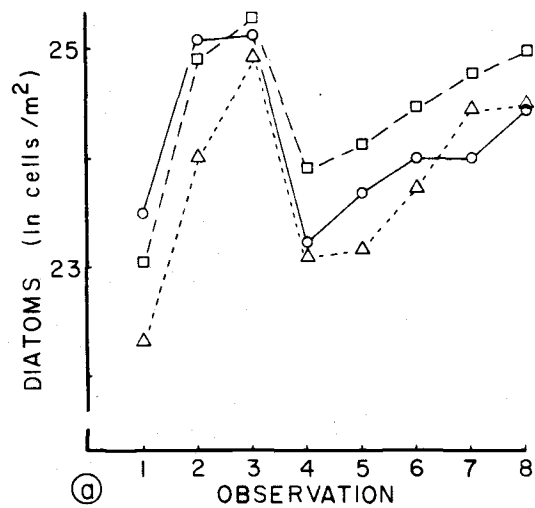


Figure 23. Density of Microcoleus and Schizothrix in the benthos of unshaded (a,c) and shaded (b,d) riffles of streams 1 (circle), 2 (square), and 3 (triangle), experiment 2.

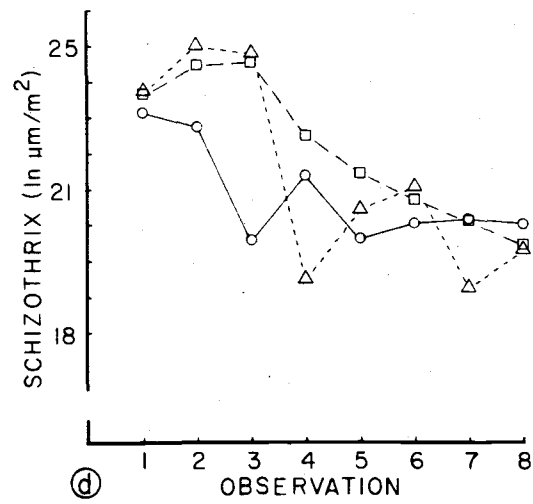
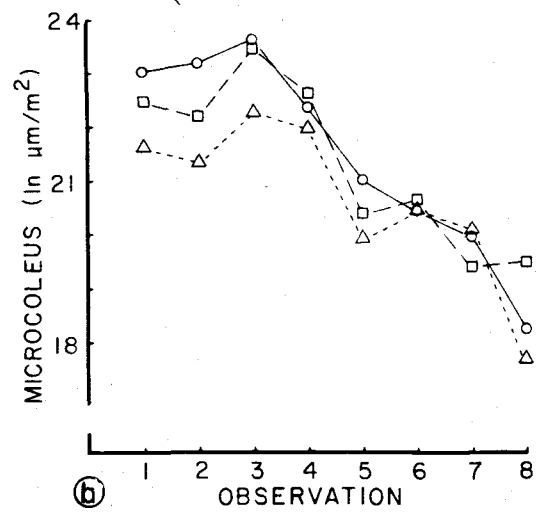
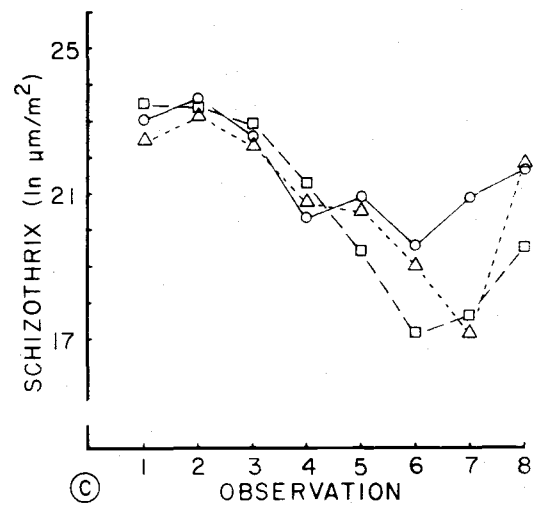
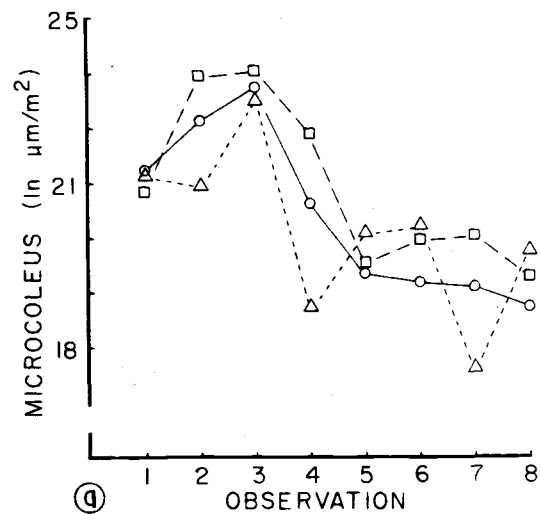
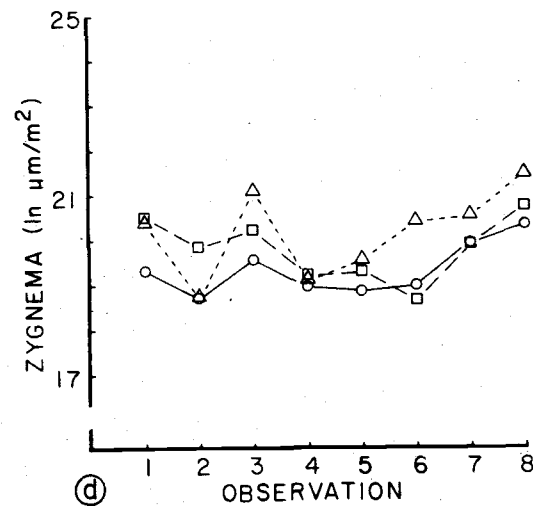
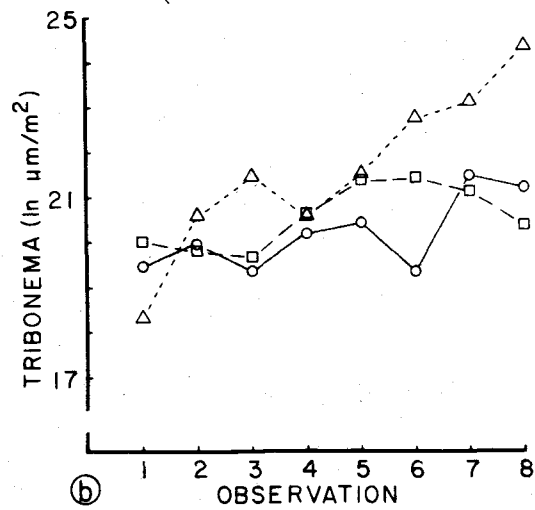
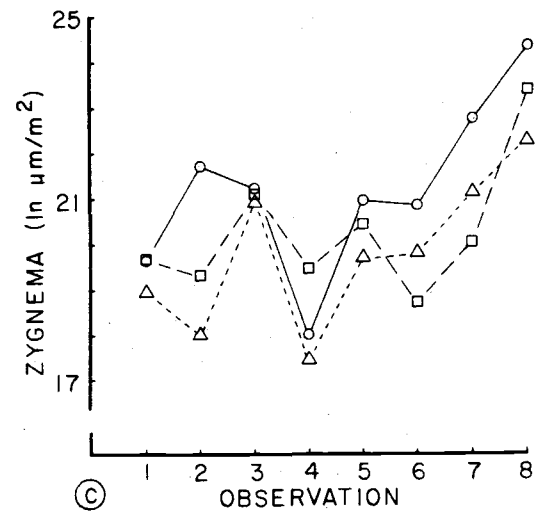
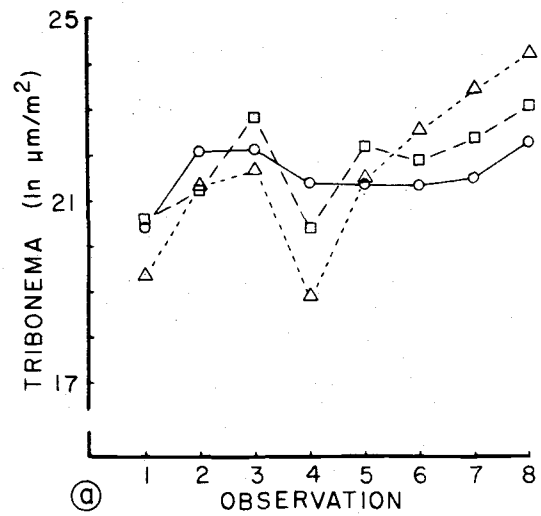


Figure 24. Density of Tribonema and Zygnema in the benthos of unshaded (a,c) and shaded (b,d) riffles of streams 1 (circle), 2 (square), and 3 (triangle), experiment 2.



70 % of the information associated with the six taxa into two factors. The distribution of assemblages in the plane of the first and second factors indicated that the transition of assemblages was similar among riffles (Figure 25 a,b). The first axis expressed the abundances of Microcoleus ($r = -.71$), Schizothrix ($r = -.75$), Tribonema ($r = .86$), and Zygnema ($r = .80$), and the second axis expressed the abundance of diatoms ($r = .80$). The analysis indicated that diatoms increased rapidly before observation 2 and decreased after observation 3. Between observation 4 and 8, a decrease in the abundances of Microcoleus and Schizothrix was concurrent with an increase in Tribonema and Zygnema.

The discriminant analysis of the 48 diatom assemblages collapsed 79 % of the variance in the relative abundances of seven taxa (Achnanthes lanceolata, A. minutissima, Diatoma hiemale v. mesodon, Eunotia pectinalis, Fragilaria construens v. venter, F. vaucheriae, and Nitzschia frustulum v. perminuta) into two factors. This analysis indicated that the transition in assemblages was similar among the riffles (Figure 25 c,d). The first factor expressed the abundances of A. lanceolata ($r = .81$), A. minutissima ($r = .85$), D. hiemale v. mesodon ($r = -.93$), E. pectinalis ($r = .75$), F. construens v. venter ($r = .68$), F. vaucheriae ($r = .62$), and N. frustulum v. perminuta ($r = .71$), while the second factor expressed the abundance of F. vaucheriae ($r = -.70$). This analysis indicated that the relative abundance of Diatoma increased between observations 1 and 2, and that of the other taxa increased between observations 3 and 8. The abundance of F. vaucheriae was greater in the unshaded riffles than the shaded riffles and was also more abundant in the nitrate-enriched, unshaded riffles than the unenriched, unshaded riffles.

Faunal Assemblages

Abundant and frequently occurring faunal taxa in the benthos and drift were chironomids, ostracods, copepods, mites, turbellarians, oligochaetes, nematodes, gastropods, Paracapnia oswegaptera, Arcynopteryx subtruncata, a species of the family Limnephilidae, a species of the genus Ephemerella, and collembola (Table 7). The

Figure 25. Principal components analysis of algal (a,b) and diatom (c,d) assemblages of unshaded (a,c) and shaded (b,d) riffles of streams 1 (circle), 2 (square), and 3 (triangle), experiment 2. The arrows indicate the sequence of assemblages observed. The closed squares indicate the period of nitrate enrichment in stream 2.

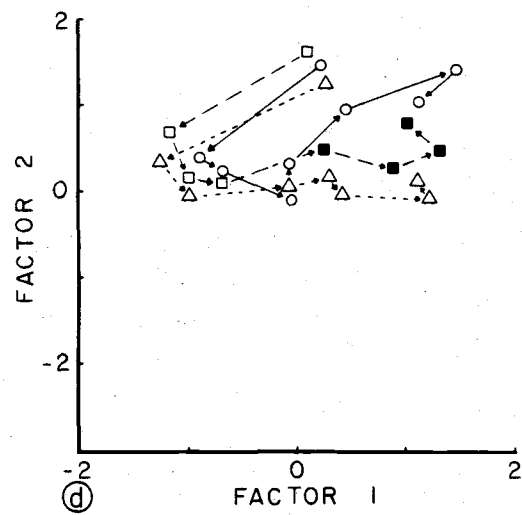
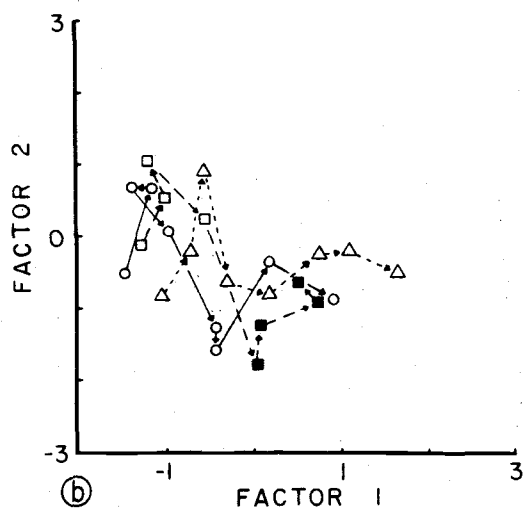
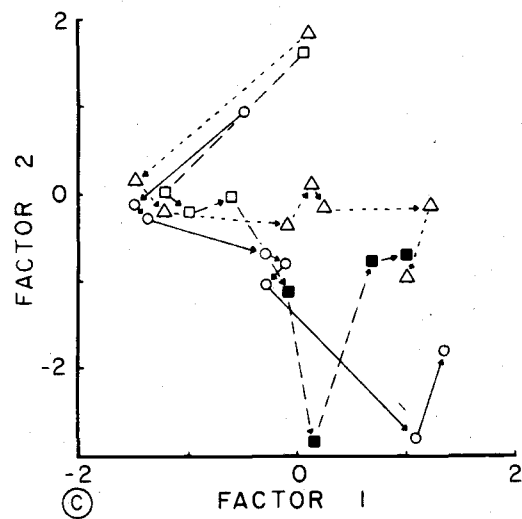
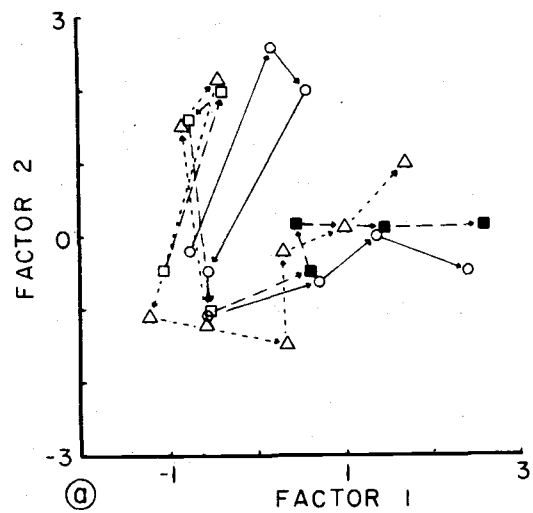


Table 7. Mean biomass and export of fauna in shaded and unshaded riffles during experiment 2.

Taxa	Biomass (mg m^{-2})		Export ($\text{mg m}^{-2} \text{d}^{-1}$)		% Export (d^{-1})	
	Light Intensity		Light Intensity		Light Intensity	
	15 %	100 %	15 %	100 %	15 %	100 %
chironomid larvae	2526	3562	88.4	119.7	3.5	3.4
chironomid pupae/adults	325	362	100.9	179.1	31.1	49.5
oligochaetes	1365	1300	58.0	31.4	4.3	2.4
<u>Arcynopteryx subtruncata</u>	1189	861	1.0	0.3	0.1	0.0
snails	129	318	0.8	8.8	0.6	0.3
ostracods	101	159	8.6	8.0	10.0	5.2
Limnephilidae sp. 1	110	105	8.3	0.6	0.8	0.6
nematodes	62	104	0.1	0.1	0.1	0.1
<u>Paracapnia oswegaptera</u>	62	99	0.7	1.4	1.1	1.4
flatworms	45	128	2.8	1.6	6.1	1.2
mites	38	19	5.5	4.3	14.4	23.3
copepods	8	16	0.8	0.8	10.0	5.2
<u>Ephemerella</u> sp. 1	3	5	0.0	0.3	0.3	0.7
collembola	6	9	76.9	66.0	1182.0	754.3

biomass of taxa with relatively high turnover rates (including those taxa with mean export rates greater than $1\% \text{ day}^{-1}$) increased to more than 2.8 g m^{-2} within 21 days after the simulated freshet (Figure 26 a,b). This biomass varied between 1.3 and 16.1 g m^{-2} for subsequent observations with little difference apparent among riffles of different light intensity and nitrate concentration. Export of this biomass was low ($0.03 - 0.17 \text{ g m}^{-2} \text{ day}^{-1}$) for the initial three observations and increased to means of $0.3 \text{ g m}^{-2} \text{ day}^{-1}$ in the shaded riffles and $0.9 \text{ g m}^{-2} \text{ day}^{-1}$ in the unshaded riffles by observation 5 (Figure 26 c,d). While the export of fauna was greater in the nitrate-enriched, unshaded riffles than the unenriched, unshaded riffles at this observation, the interpretation of this difference was complicated by differences in the average size of individual organisms. For example, the mean weight of chironomids, the most abundant faunal taxon in the riffles, was more than $175 \text{ ug individual}^{-1}$ in the nitrate-enriched riffles and less than $50 \text{ ug individual}^{-1}$ in the unenriched riffles. Therefore, the maximum rate of export in the unenriched riffles may have occurred prior to observation 5. The export of biomass was between 0.2 and $0.3 \text{ g m}^{-2} \text{ day}^{-1}$ in all riffles by the end of the experiment.

Chironomids were the most abundant taxon of the fauna in the benthos and drift (Table 7). The relative abundance of chironomids in the benthos increased in all riffles to a mean of 72 % of the faunal biomass within 21 days after the simulated freshet and to a mean of 84 % by observation 6 (Figure 27 a,b). This relative abundance decreased to less than 55 % in all riffles by observation 8 and was accompanied by higher abundances of other insect larvae, ostracods, oligochaetes, copepods, and mites. The relative abundance of chironomids in the drift of all riffles increased to more than 81 % within 35 days after the simulated freshet, and then decreased to a mean of 46 % by observation 8 (Figure 27 c,d).

Most of the faunal biomass exported from the riffles in a 24-hour day occurred between 0600 and 1800 hours (Table 8). Chironomids, copepods, and collembola had a significantly higher export rate during

Figure 26. Faunal biomass in the benthos and the export of faunal biomass from the benthos of unshaded (a,c) and shaded (b, d) riffles of streams 1 (circle), 2 (square), and 3 (triangle), experiment 2.

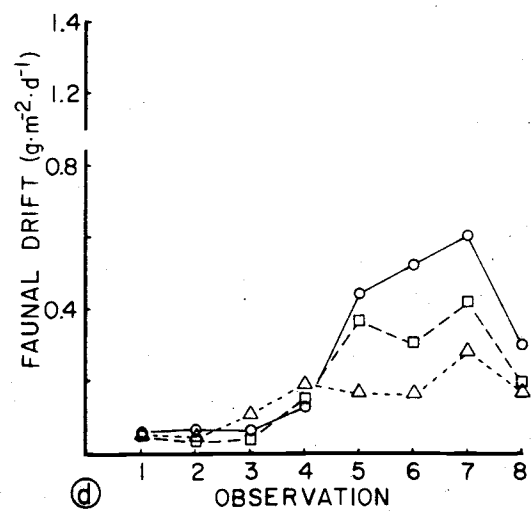
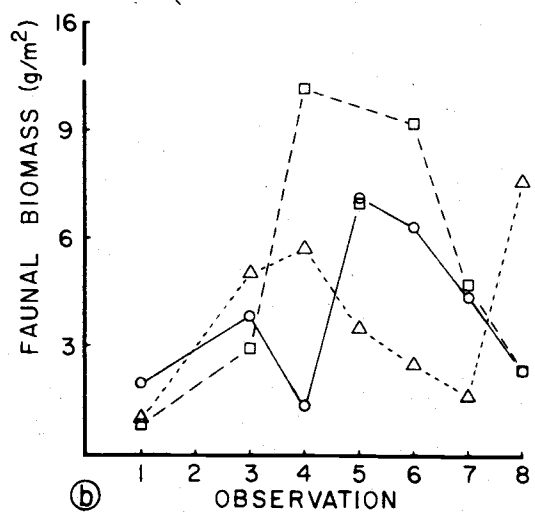
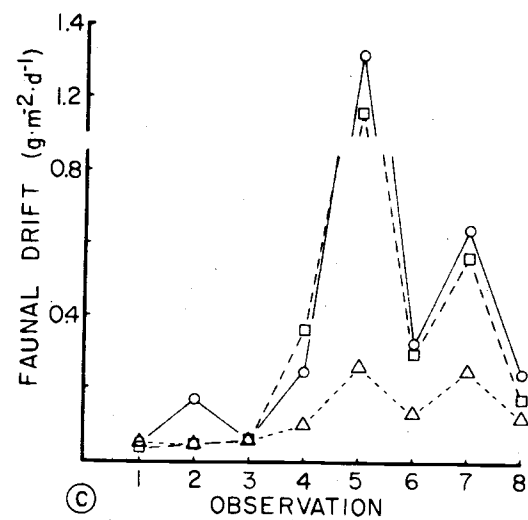
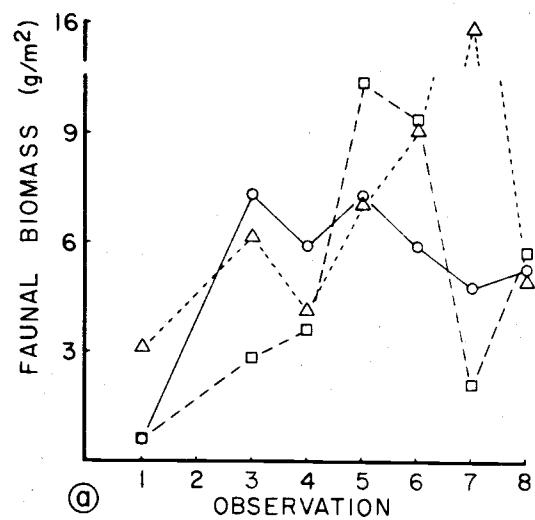


Figure 27. Relative abundance of chironomids in the biomass and export of the faunal assemblages in the benthos of unshaded (a,c) and shaded (b,d) riffles of streams 1 (circle), 2 (square), and 3 (triangle), experiment 2.

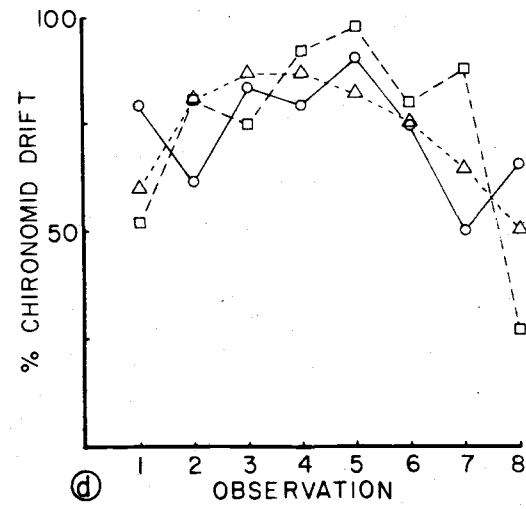
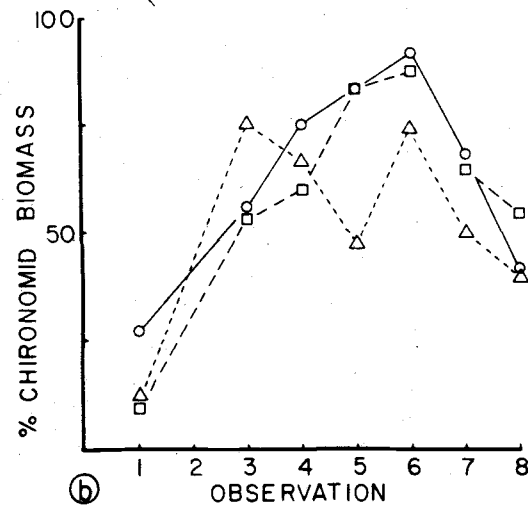
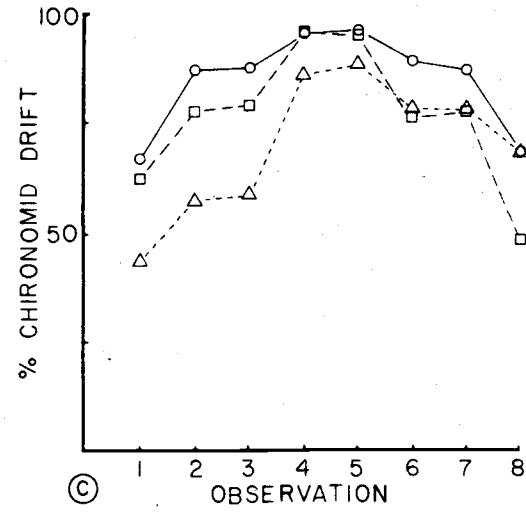
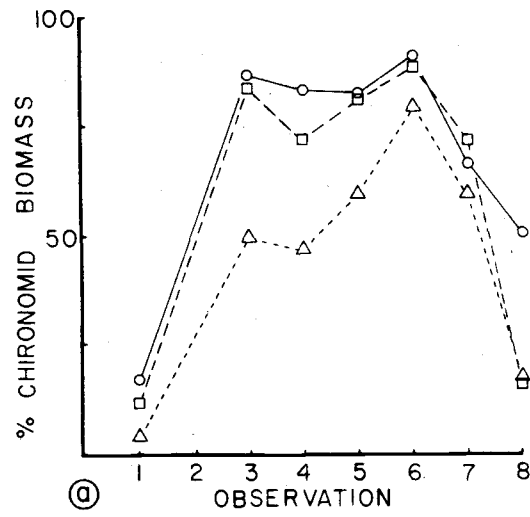


Table 8. Comparison of day versus night faunal drift, experiment 1 and 2.

Taxa	% of drift during the 24-hr day between 0600 & 1800	Significant difference ($\alpha = 0.05$)
chironomid pupae/adults	72.4	*
collembola	68.7	*
<u>Rhyacophila verrula</u>	61.1	
Limnephilidae sp. 1	60.3	
chironomid larvae	60.2	
mites	59.4	
copepods	59.3	*
ostracods	52.0	
<u>Paracapnia oswegaptera</u>	50.0	
oligochaetes	49.6	
flatworms	38.3	*

the day while turbellarians had a higher export rate at night. Mites, Rhyacophila verrula, and a species of the family Limnephilidae also had a higher export rate during day than during night, although this difference was not statistically significant.

DISCUSSION

Synthesis of Results

The synthesis of results from experiments 1 and 2 requires an appropriate time scale on which to describe observed behavior. The use of days is inappropriate for observations of autotrophic ecosystems at the Kalama Springs because of the disparity in daily solar radiation between experiments. The daily radiation increased during experiment 1 while it decreased during experiment 2. A means of reducing this disparity is to sequence behavior on the time scale of accumulated light hours (ALHr) after the simulated freshet. This time scale emphasizes the effect of primary production in the lotic ecosystem and is most appropriate if light saturation of primary production is achieved during the entire daily period of illumination. The relationship of relative production to light intensity observed in the benthic assemblages (Figure 20) indicates that light saturation was achieved in both shaded and unshaded riffles during most of the day. According to this time scale, observations 1, 2, 3, 4, 5, and 6 of experiment 1 occurred at 90, 270, 405, 600, 1040, and 1715 ALHr, respectively; while observations 1, 2, 3, 4, 5, 6, 7, and 8 of experiment 2 occurred at 110, 215, 320, 525, 720, 905, 1235, and 1610 ALHr, respectively.

The behavior common among riffles in experiments 1 and 2 can be summarized as a series of three stages (Table 9); 0 to 300 ALHr (stage I), 300 to 900 ALHr (stage II), and 900 to 1800 ALHr (stage III). Stage I was characterized by a rapid colonization of the substrate after the simulated freshet by diatoms, particularly Achnanthes lanceolata and Diatoma hiemale v. mesodon. D. hiemale v. mesodon is a filamentous diatom (Gasse, 1971) that became the predominant alga in the riffles by 300 ALHr. Stage II was characterized by an initial decrease in algal abundance and a subsequent low biomass of algae and high biomass of invertebrate fauna, primarily species of the family

Table 9. Temporal behavior of the benthic assemblages in experimental streams (+, -, and 0 indicate increase, decrease, and no change, respectively).

Ecosystem Attribute	Stage		
	I	II	III
Community Structure			
Total Organic Matter	+	-0	+
% Organic Matter	+	-0	+
Chlorophyll <u>a</u>	+	-0	+
Chlorophyll <u>a</u> /Organic Matter	+	-	-
Carotenoids/Chlorophyll <u>a</u> (480:665)	+	-	-
Community Energetics			
Gross Primary Production	+	-0	+
Gross Primary Production/Chlorophyll <u>a</u>	-	+0	-
Community Respiration	+	-0	0
Community Respiration/Organic Matter	+	-	-
Export			
Flora	+	-0	+
Fauna	0	+	-0
Diversity			
Flora	-	+	-
Fauna	0-	0	+0

Chironomidae. In stage III, algal biomass again increased with greater abundances of Tribonema and Zygnema. Concurrently, the faunal biomass remained high, while the export of fauna and abundance of chironomids was relatively low.

The trends in behavior presented in Table 9 were common to all riffles, but some differences attributable to the experimental alteration of light intensity and nitrate concentration were observed. In the contrast of riffles with a greater potential for primary production (relatively high light intensity and nitrate concentration) and riffles with lesser potential, rates of community respiration and gross primary production per unit chlorophyll a were higher in the former than the latter. The riffles with greater potential exhibited faster accumulation rates of algal biomass and higher export rates of faunal biomass than riffles with less potential. The abundance of Diatoma in stage I, chironomids in stage II, and Zygnema in stage III was greater in riffles of greater resource than those of lesser resource. These differences in benthic assemblages among riffles, however, were secondary to the differences in benthic assemblages temporally. Rates of primary production, community respiration, biomass accumulation, and biomass exported as well as taxonomic structure varied more within a riffle with time than among riffles at one observation.

The observed trends in some ecosystem properties were different than patterns reported by other workers. The ratio of carotenoid pigments to chlorophyll a was considered by Margalef (1960) to indicate biochemical diversity and was observed to increase with community development. This ratio was relatively high in riffles exposed to the high light intensities and generally decreased with community development in all riffles at Kalama Springs. In addition, the ratio of chlorophyll c to a has been reported to be higher in environments of relatively low light intensity (Brown and Richardson, 1968). This ratio was higher in the unshaded riffles than the shaded riffles at Kalama Springs and decreased during the experiments. These ratios indicate the transition from chlorophyll c - fucoxanthin assemblages (i. e., diatoms) to those dominated by more blue-green and green algae,

a transition which overrides an increase attributable to increasing biochemical diversity.

General trends in diversity of community components with time are difficult to predict (Odum, 1969). The diversity of algal and faunal taxa in the experimental streams decreased as the dominance of Diatoma, chironomids, and Zygnema increased in stages I, II, and III, respectively (Table 9). These patterns are compatible with Margalef's (1968) observation that a sudden increase in biomass is unevenly partitioned among constituent taxa and Paine's (1966) hypothesis that the diversity of the prey (i. e., diatoms) increased with predation (i. e., by the invertebrate fauna).

Analysis of Behavior

A "black box" problem is the examination of a system in which the organization and behavior of that system are not known although external quantities are available for observation and experimentation (Klir, 1969). Investigations of the stream ecosystem involve the examination of a biological black box. Few stream ecologists will dispute that the lotic ecosystem is a system in which organization is not completely known and behavior is not completely determined. Yet, reviews of stream ecosystem research (e. g., Hynes, 1970; Whitton, 1975) indicate that quantities and activities of the system have been extensively examined. Stream ecology is in a middle ground - some facets of streams are unknown, while some facets are well known.

The focus of this thesis is autotrophy in the lotic ecosystem; specifically, the response of the autotrophic stream system to different light intensity and nitrate concentration environments and to biomass reducing freshets. The examination of this system's response is dependent on the opportunity for and the appropriateness of the separation of systems within the lotic ecosystem on the basis of energy input form. The use of the Weyerhaeuser Company's Kalama Springs experimental streams presented the opportunity to isolate the

autotrophic system, because the amount of allochthonous energy input into these spring-fed streams is low relative to the amount of autochthonous input. The appropriateness of allochthonous and autochthonous subsystems is supported by the functional group perspective for lotic ecosystems (Cummins, 1974). The McIntire and Colby (1978) lotic ecosystem model reflects this perspective by separating the system into subsystems with either solar, detrital, or living organic energy inputs.

The examination of the autotrophic stream system black box is constrained by the powers of discrimination available, the temporal resolution of observation, and the encompassing conceptual model of the system considered appropriate (Klir, 1969). The external quantities that were measurable in the Kalama Springs experimental streams were algae, the larger animals, and composite ecosystem properties. A group of organisms not assayed was the micro-heterotrophic organisms (i. e., the bacteria, fungi, and protozoans). While exclusion of a group of varied and presumably important organisms in the ecosystem was undesirable, the omission is frequent and often unavoidable in lotic ecology (Jones, 1975). Because these micro-heterotrophs were beyond the power of discrimination, an algal taxon is considered to represent an entity - the periphyton - which includes the algal taxon plus associated micro-fauna. Micro-heterotrophs were considered a component of the periphyton instead of larger animals because the turnover rates of micro-heterotrophs is expected to be closer to algae than the larger animals and this perspective is consistent with previous examinations of energy flow within an autotrophic stream (McIntire, 1966; Brock, 1967).

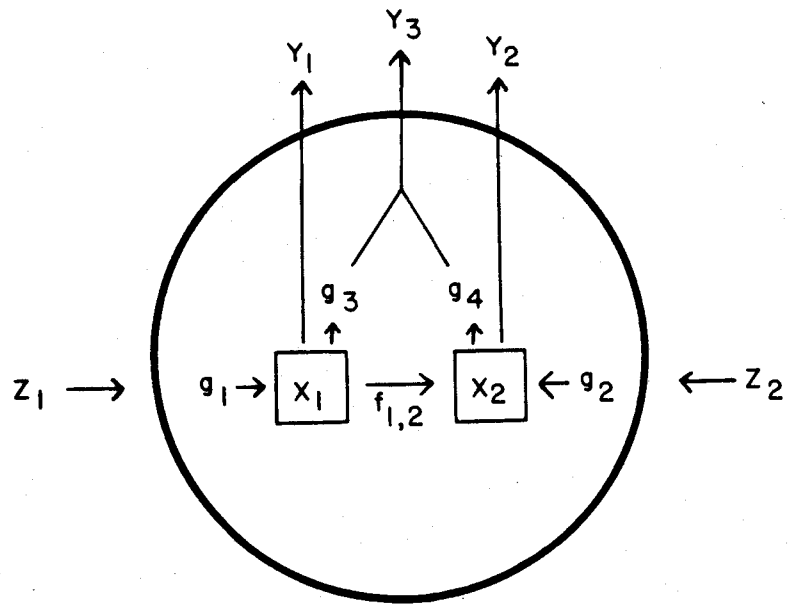
The resolution level of observation for monitoring the activity of the Kalama Springs black box, six and eight observations within 150 days, represented a balance between the number of sampling dates possible and the time span of events considered appropriate. Brock and Brock (1967) described a recovery of algae in a thermal spring within 150 days after a catastrophic hail storm. McIntire (1968) observed relatively uniform periphyton assemblages after 30 days. Grzenda and Brehmer (1960), Kevern, et al. (1966), and Waters (1961 a)

found chlorophyll a concentrations on artificial substrates to approach constant levels after 30, 30, and 35 days, respectively. Odum and Hoskin (1957) found organic matter in experimental streams to become relatively constant after 100 days. These previous studies indicated that 150 days would be a suitable time span for observations after the simulated freshet.

The conceptualized structure of the autotrophic stream system has two subsystems (Figure 28) and is presented according to the FLEX convention (White and Overton, 1974) for the identification of system inputs (z), outputs (y), state variables (x), internal flux (f), and intermediate flows (g). In this conceptualization, the quantities of periphyton and macro-fauna correspond to the producer (x_1) and consumer (x_2) subsystems of the system. Inputs to the system are solar radiation (z_1) and the drift of macro-fauna from upstream benthos (z_2). Energy flows into the subsystem by primary production (g_1) and recruitment from faunal drift (g_2). Recruitment from periphyton drift is assumed to be insignificant relative to primary production because the experiments involved the regrowth of organisms on the substrate (the simulated freshets did not eliminate periphyton on the rocks) and this assumption is considered appropriate by other workers (Waters, 1961 a; Kevern, et al., 1966; Fraleigh and Wiegert, 1975). Outputs of the system are producer export (y_1), consumer export (y_2), and community respiration (y_3) which is the sum of producer (g_3) and consumer (g_4) respiration. $F_{1,2}$ is an internal flow between components x_1 and x_2 (i. e., assimilation of producer biomass by consumers). The producer biomass consumed but not assimilated by consumers was considered to be subsumed in the producer biomass or export. Predation on herbivores by carnivores is an unquantified internal flow within x_2 . This ecosystem structure is compatible with Odum's (1976) conceptualization of ecosystems, and the McIntire and Colby (1978) and Webster, et al., (1975) models of lotic ecosystems.

Previous research and practical limitations of observation therefore presented external quantities, temporal resolution, and structure for the examination of the autotrophic stream ecosystem. The black

Figure 28. Conceptual model of the benthos system with producer (x_1) and consumer (x_2) subsystems, and energy inputs of solar radiation (z_1) and upstream faunal drift (z_2) and outputs of producer export (y_1) consumer export (y_2), and community respiration (y_3). Intermediate flows are primary production (g_1), recruitment of fauna (g_2), producer respiration (g_3), and consumer respiration (g_4). $F_{1,2}$ represents the assimilation of producers by consumers.



box problem decomposes to determining "program," the variable part of the system's organization (Klir, 1969). The determination of systems program involves the development of rules governing states and transitions between states that consistently account for the observed behavior. Behavior of the benthic assemblages observed at Kalama Springs has been simplified to a sequence of three stages (Table 9). The behavior characterizing these three stages can be translated to the conceptual structure considered appropriate for the lotic ecosystem (Table 10).

According to the conceptual model, steady states of producer and consumer biomasses will occur when:

$$g_1 = g_3 + f_{1,2} + y_1 \quad (1)$$

$$f_{1,2} + g_2 = g_4 + y_2 \quad (2)$$

$$g_1 + g_2 = y_1 + y_2 + y_3 \quad (3)$$

The accumulation of producer and consumer biomass in stage I indicates:

$$g_1 > g_3 + f_{1,2} + y_1 \quad (4)$$

$$f_{1,2} + g_2 > g_4 + y_2 \quad (5)$$

$$g_1 + g_2 > y_1 + y_2 + y_3 \quad (6)$$

During this stage, the accumulation of producer biomass occurred at a faster rate in the unshaded riffles than the shaded riffles; in nitrate-enriched, unshaded riffles than unenriched, unshaded riffles; and in July than December. Initial accumulation rates were faster in environments of greater potential for primary production (i. e., higher light intensity, longer daylength, and higher nitrate concentration) than in environments of less potential, and indicative of the differences in rates of primary production among riffles.

Differential rates of producer biomass accumulation on bare substrates are frequently observed in streams (Wetzel, 1975). The rate of algal accumulation has been considered to be indicative of primary production rates (Cooke, 1956; Grzenda and Brehmer, 1960; Waters, 1961 a; Kevern, et al., 1966). The rate of primary production will be proportional to the rate of producer biomass accumulation if producer outputs ($g_3 + f_{1,2} + y_1$) are a linear function of inputs (g_1).

Table 10. Trends of ecosystem development (+, -, and 0 indicate increase, decrease, and no change, respectively).

Ecosystem Attribute	Stage			
	I	II	III	IV
Total Organic Matter $x_1 + x_2$	+	-0	+	0
Producer Biomass x_1	+	-0	+	0
Consumer Biomass x_2	+	+0	0	0
Primary Production g_1	+	-0	+	0
Specific Production g_1/x_1	-	+0	-	0
Community Respiration y_3	+	-0	0	0
Maintenance Cost $y_3/(x_1+x_2)$	+	0	-	0
Producer Drift y_1	+	-0	+	0
Consumer Drift y_2	0	+0	-	0

However, a constant ratio of producer outputs to inputs - $(g_3 + f_{1,2} + y_1)/g_1$ - is not representative of the benthic system because infinite increases in producer biomass, a consequence of this relationship, are not observed and producer outputs have been observed to be linear functions of producer biomass (x_1), not producer input (Brock and Brock, 1967; McIntire, 1973). If the ratio of producer outputs to biomass - $(g_3 + f_{1,2} + y_1)/x_1$ - is constant, then the ratio of outputs to inputs - $(g_3 + f_{1,2} + y_1)/g_1$ - will increase with increasing producer biomass; because specific production (g_1/x_1) decreased with increasing biomass. Algal accumulation rates will only be indicative of primary production rates when the ratio of producer outputs to inputs is low.

The consequences of a lotic system program based on a constant ratio of outputs to biomass and decreasing specific production with increasing biomass are observed in the Fraleigh-Wiegert (1975) model of an autotrophic thermal spring in which:

$$\begin{aligned} \frac{d x_1}{dt} &= g_1 - g_3 - y_1 \\ g_1 &= b_1 x_1^{b_2} \quad ; \quad g_3 = b_3 x_1 \\ y_1 &= b_4 x_1 \quad ; \quad b = \text{parameters} \\ f_{1,2} &= 0, \text{ no consumers in the system} \end{aligned}$$

In this model, biomass in the benthic system approaches a steady state and the rate of approach is a function of resource (light and nutrient) availability. The steady state biomass decreased with a decrease of resources. In this type of system, producer biomass is reduced only by catastrophic removal of the algal mat (Brock and Brock, 1967; Collins, et al., 1976).

The decrease of producer biomass during the initial portion of stage II indicates:

$$g_1 < g_3 + f_{1,2} + y_1 \quad (7)$$

This devastation of the algal assemblage is inconsistent with a system's program in which $(g_3 + f_{1,2} + y_1)/x_1$ is constant and inconsistent with the Fraleigh-Wiegert periphyton model. These inconsistencies are resolved if $f_{1,2}$ is not equal to zero and not a linear function of producer biomass ($f_{1,2}$ is not linear, donor controlled). The increase in faunal biomass and export in stage II is consistent with the

contention that consumers were responsible for the rapid decrease in producer biomass.

The relatively constant biomasses of producers (low) and consumers (high) that characterize most of stage II indicate equilibrium conditions for the components of the benthic system (equations 1, 2, and 3). Differences in primary production among riffles attributable to light intensity and nitrate concentration do occur in this stage. Because the biomass of producers is similar among riffles, these differences are a function of acclimation (by physiological changes within species or species changes within the producer component) to the ambient environment. Primary production per unit of producer biomass is higher in the unshaded and nitrate-enriched riffles than in the shaded and unenriched riffles.

If similar producer biomasses exist among riffles, then producer export (as a linear function of producer biomass) is expected to be similar among riffles. Moreover, if consumer recruitment (g_2) is the same in all riffles, differences of producer production (g_1) are expected to be reflected in differences of community respiration and faunal export. In the experimental streams, faunal export and community respiration were greater in unshaded riffles than shaded riffles, and in periods of longer daylength than shorter daylength. The export of post-larval chironomid stages rather than the biomasses of algae or fauna were apparently indicative of differences in the rate of primary production among riffles in this stage. O'Brian and DeNoyelles (1974) noted in planktonic ecosystems that the difference in primary production was manifested in the biomass of herbivores, not in the biomass of algae. However, the difference in primary production attributable to nitrate enrichment was not observed as differences in these systems outputs. The expected, but not observed differences probably were not great enough to be detected by the sampling methods.

The reduction of producer biomass to low levels after an initial, rapid accumulation is consistent with observations of natural autotrophic ecosystems. Dickman (1973) described the accumulation of periphytic diatoms and their subsequent devastation by oligochaetes,

while Waters (1961 a) observed a "rapid increase to population saturation" followed by a sudden reduction in biomass after 30 days. The suppression of primary production and producer biomass in the Red Cedar River system was coincident with the maximum biological demand of the consumer species (Ball and Bahr, 1975). The inverse relationship between the abundances of Achnanthes and caddis fly larvae observed by Douglas (1958) also is consistent with this hypothesized suppression.

System behavior observed during stage II and in previous research can be summarized as follows: (1) the biomasses of producers and consumers quickly reach a steady state, (2) grazing pressure is high enough to maintain a relatively low producer biomass and rate of primary production, and (3) system inputs are reflected in community respiration and consumer export rates. The consequence of a system program with a relatively high $f_{1,2}/g_1$ is that producer biomass will be indicative of primary production rates. Castenholz (1961) suggests a "periphyton anomaly": i. e., periods of high primary production potential (high light intensity, long daylength, and abundant nutrients) are characterized by producer biomass no higher than that in periods of low potential. Although Castenholtz refers to marine periphyton this anomaly also applies to lotic periphyton (McIntire, 1973).

An example of a lotic system program consistent with stage I and II is the McIntire and Colby (1978) general lotic ecosystem model reduced to components compatible with the conceptual model of this research. In this model:

$$dx_1/dt = g_1 - g_3 - y_1 - f_{1,2}$$

$$dx_2/dt = f_{1,2} - g_4 - y_2$$

Producer respiration and export are linear functions of biomass and specific primary production decreased with increasing producer biomass. Consumer respiration is indirectly a function of $f_{1,2}$, and export (emergence) is a linear function of consumer biomass. Grazing pressure reduces the producer biomass that accumulates during the spring and is high enough to decrease the rate of primary production.

The increase in producer biomass that typifies stage III indicates that producer input exceeds outputs (equation 4). Differences in rates of primary production are manifested in greater rates of algal biomass accumulation and export in riffles of higher resource (i. e., light intensity and nitrate enrichment given high light intensity) than in riffles of low resource. The increase in producer biomass is accompanied by an increasing rate of producer export per unit biomass (y_1/x_1) and a decreasing specific production rate (g_1/x_1). The ratio of the other producer outputs to producer inputs - $(g_3 + f_{1,2})/g_1$ - must decrease for producer biomass to increase in stage III. The decrease in energy flow to the consumer is indicated by the relatively low rates of faunal drift in this stage. A predicted consequence of this behavior is a fourth stage in which new steady states of biomass are approached. Theoretically, producer and consumer biomass will be high and relatively constant during the fourth stage with little difference in faunal drift among environments of high and low resource. Indeed, this situation was found in the experimental streams before the sequence of observations in these experiments (Bisson, et al., 1975). In this fourth stage, differences among treatments are expected in the system outputs of community respiration and producer export. The successional sequence is then two successive periods of increasing benthic biomass to steady state.

The occurrence of behavior typifying stage III indicates that the systems program of lotic benthos is not representative if the parameters governing the transition between states are static. Natural systems have the capacity to reorganize flows (Odum, 1976) and thereby change parameters of the system program. A mechanism of the change in program could be the change in genetic information (i. e., taxonomic structure) during succession. The results from the experimental streams indicates that the parameter change occurred within a time period of four months. If freshets and the accompanying scour of organisms is representative of natural streams as suggested by Wetzel (1975), then an appropriate model must incorporate the capacity to change program when the interval between freshets is greater than three months.

The successional behavior of benthic assemblages in the Kalama Springs experimental streams is not a unique phenomenon. Szczepanski and Szczepanski (1966) and Dickman (1973) describe a similar developmental pattern of the benthic assemblages colonizing artificial substrates. Dickman's observations indicated that a period of rapid diatom accumulation is followed by a period of relatively low producer biomass. The low diatom biomasses coincided with high oligochaete densities and, subsequently, filamentous algae accumulated rapidly. Producer biomass achieved another steady state with an associated change in faunal taxonomic structure from oligochaetes to caddis fly larvae. A nonaquatic analogy of this behavior is Odum's (1960) observations of old field succession. He noted that "succession may involve a series of steady states, each associated with a major life form." The structural changes of ecosystems with time (Major, 1974) appear to involve changes in systems program according to the producer-consumer conceptualization. This change in systems program accompanies the alteration of taxonomic structure whether the transition is from diatoms to filamentous algae or forbs to trees.

Systems Implications

An interpretation of the stepwise behavior of aquatic and terrestrial systems is dependent on the observer's perspective of order in natural systems. Natural systems are perceived to have four properties (Laszlo, 1972): (1) wholeness and order, (2) the capacity of self-stabilization, (3) the capacity of self-organization, and (4) hierarchical organization. The first and fourth properties are foundations of general systems theory (Bertalanffy, 1968). Systems are conceptualized to exist as "wholes," possessing characteristics which are not possessed by the parts singly. These wholes (holons) are structured in a "hierarchy," a "level structure" or a "set of superimposed subsystems" (Overton, 1975, 1977). The component subsystems at one level are systems in their own right at a lower level. The hierarchy of natural systems is a structure in which systems function as wholes or parts depending on the level of interest. A given holon may be considered a subsystem, system, or suprasystem.

Properties two and three describe responses of a natural system to constraints imposed on the system by its environment (i. e., the suprasystem of the system excluding that system). Self-stabilization is an equilibrium-directed behavior in which the variables of a system co-interact to approach an equilibrium between the system and its environment. After a perturbation (an external forcing of the system), the system "stabilizes" around the steady state defined by the environment and the fixed internal forces (parameters) of the system. This property accounts for the invariance of the whole relative to the more variant fluctuations of its constituent parts. The system compensates for changing conditions in the environment through changes in the system's internal variables. Self-organization is the capacity of systems to reorganize fixed internal forces (parameters) in a constant environment. This property results in the nonequilibrium-directed behavior with excess free energy being utilized by the system to develop more negentropic states: steady states approached by cointeracting systems variables are only temporary (quasi-stationary). Natural systems reorganize parameters going toward increasingly more complex states. This property is the difference between machines (artificial) and natural systems (Laszlo, 1972). Machines are "dead," their preferred state is an equilibrium. Natural systems have an interplay of external constraints and internal modifications that result in a progressive development of the system. System models without the capacity for parameter change represent the natural system as a machine, not as a natural system.

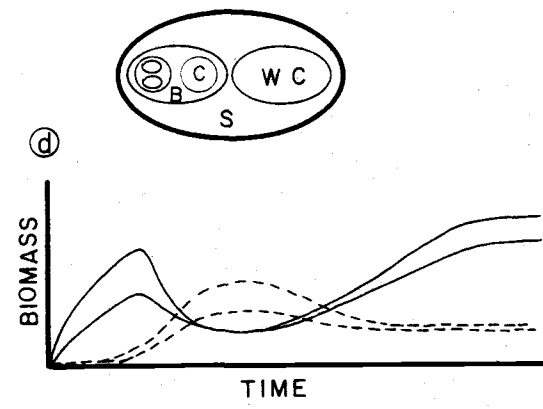
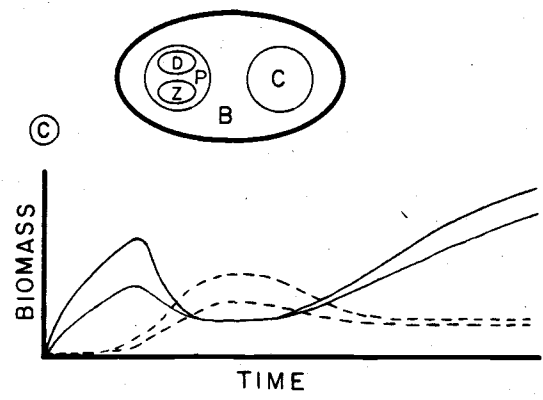
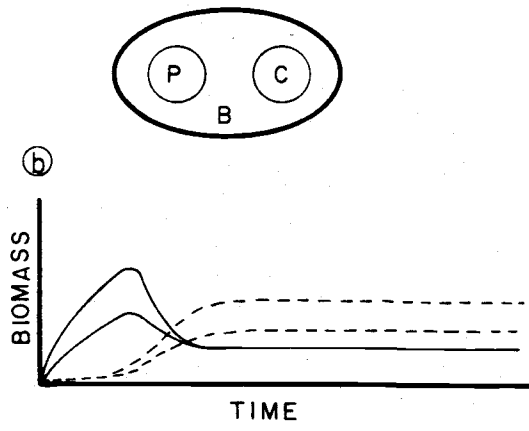
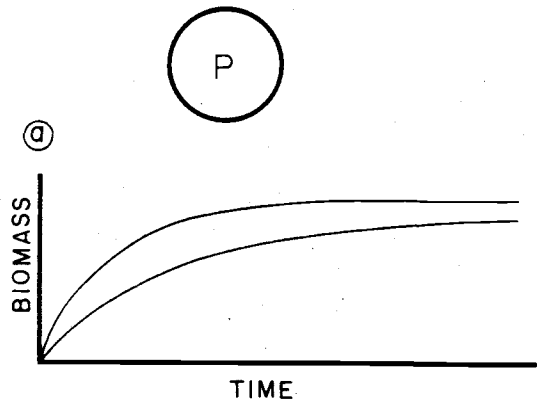
If favorable environments of enduring order exist, natural systems will then not only maintain their already attained level of organization, but intermittently evolve toward more highly organized states. Consequently systems within a suprasystem develop intermediate suprasystems with time in a constant environment and, thereby, the complexity of hierarchical organization will be increased. The newly evolved system stabilizes itself in the face of varying environmental forces and, subsequently, reorganize in relation to constant forces of the environment. The capacity for increasing complexity of the structural

hierarchy is infinite and is marked by alternating periods when equilibrium or nonequilibrium-directed behavior is predominant. This alteration of behavioral types results in a stepwise increase of biomass in the aquatic and terrestrial ecosystems. Succession is then perceived to be the evolution of hierarchical organization in these ecosystems in ecological time and climax is a period of time when rate of reorganization is slow. This conceptualization of ecosystem development is a modification of the system perspective of species evolution developed by Laszlo (1972) and Simon (1962).

Systems evolution of hierarchical organization is considered to be an appropriate explanation of the program changes observed in the experimental lotic system at Kalama Springs. Observations of benthic assemblages in these streams indicate alternate periods of reorganization and stabilization within the lotic system. The first stage is a period of internal reorganization for the producer system (i. e., periphyton). At this time, the environment of the producer system was physically constant with relatively small faunal populations. The one component model of periphyton by Fraleigh and Wiegert (1975) adequately represents this behavior (Figure 29 a). Parameters controlling the maximum possible biomass of algae relative to the type of substrate and the shear stress of the current are altered during this period of reorganization. The transition from the dominance of Achnanthes to a dominance of Diatoma represents a change from a system limited to the boundary layer of little turbulence around the substrate to a filamentous form that can extend beyond the boundary layer of the substrate into the water column. The corresponding alteration of system parameters results from a change in taxonomic composition that allows greater energy input to the periphyton system.

The development of the macrofaunal component in stage II represents the evolution of a benthic suprasystem with periphyton and faunal components (Figure 29 b). This structure is represented in the lotic ecosystem model of McIntire (1978) with periphyton and grazer components in the environment of the reciprocal system. The environment of these systems has biotic as well as physical and chemical components.

Figure 29. The hypothesized evolution of hierarchical structure in the lotic ecosystem: (a) reorganization of the producer system, (b) stabilization of the benthos system with producer and consumer subsystems, (c) reorganization of the benthos system with the differentiation of diatom and Zygnema components of the producer system, and (d) stabilization of the stream system with benthos and water column subsystems. Systems are identified by P (producer), C (consumer), B (benthos), D (diatom periphyton), Z (Zygnema periphyton), WC (water column), and S(stream). The behavior of benthic assemblages in environments of high and low potential for primary production is predicted according to each level of organization. The solid and dashed lines indicate producer and consumer biomass, respectively.



The subsequent reorganization of the benthic system in stage III results from another alternation of algal and faunal taxonomic structure. In this period, maintenance cost to the system as a whole and the internal energy flow from producer to consumer do not increase with increased energy input to the system (primary production). This change is observed in increasing producer biomass and is characteristic of many algal-herbivore interactions. In a review of the plant-animal relations in freshwater ecosystems, Porter (1977) notes that grazing pressure on an algal assemblage results in the increasing abundance of forms resistant to grazers. In this sense, grazers are a perturbing force on the producer system. The mechanisms for increased resistance to this perturbation may be changes in palatability, nutritive value, size, or some other morphological or physiological characteristic of algae. The transition from a diatom to a Zygnema-dominated algal assemblage is the transition from small, protein-rich taxa to a large, protein-poor form with a gelatinous sheath. McMahon, et al., (1974) observed a slower growth rate of fauna consuming protein-poor periphytic algae than protein-rich forms, even when the former assemblages had greater relative biomass. The larger gelatinous filaments of Zygnema may also have achieved a critical escape size from its predator (Paine, 1976). Adequate representation of this behavior in benthic assemblages requires two subsystems in the producer system to permit taxonomic accommodation to consumer pressure (Figure 29 c).

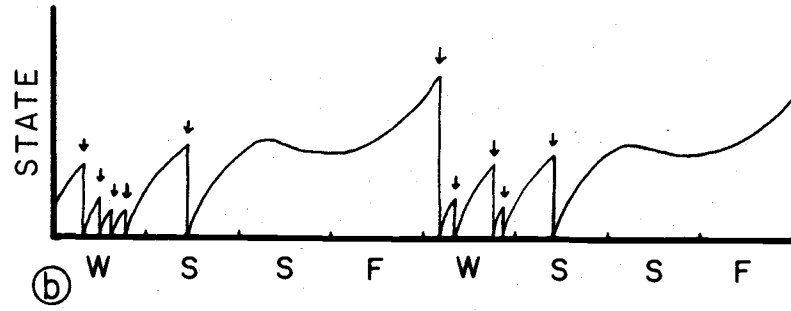
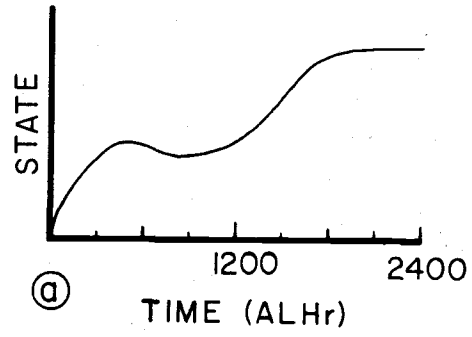
Reorganization of the benthic system results in the evolution of a suprasystem designated as the stream system (Figure 29 d). Components of this system are the water column and the benthos and, according to this organization, benthic biomass increases will be moderated by an increasing rate of export to the water column. Steady states will be approached within the stream system, but they may only be temporary. The growth of terrestrial aquatic plants in the experimental streams indicates that producers within the system have the capacity to reduce export losses and to evolve to a level of order beyond the stream system. Eventually, a march typical of the pre-experimental stream period at Kalama Springs is expected to develop.

The use of a hierarchical perspective of ecosystem structure and development offers insight into three aspects of lotic systems: seasonal occurrence of taxa, spatial heterogeneity, and perturbations. The seasonal pattern of algal taxa in non-thermal streams is characterized by low biomass of diatoms in winter, a spring "bloom" of diatoms, low algal biomasses in early summer, and filamentous algae in late summer and fall (Pearsall, 1923; Butcher, 1932; Blum, 1957; Whitton, 1975). In addition, chironomid-dominated fauna often develops in streams after the last freshet of the winter (Siegfried and Knight, 1977). If freshets are events that reset a stepwise behavior in natural stream analogous to the observed in the accumulation of organic matter in the experimental streams (Figure 30 a) and freshets in non-thermal streams occur during the winter season, then the behavior of the benthic assemblages in a hypothetical stream is given in Figure 30 b. The seasonal behavior predicted according to this is consistent with the seasonal behavior described above. In streams without freshets, the flora is expected to be dominated by filamentous algae. For example, Sherman and Phinney (1971) described the flora of a spring-fed river as largely filamentous and nonseasonal.

The distributions of benthic taxa are often spatially heterogeneous with two or more different assemblages randomly distributed on the substrate of a stream (Blum, 1960). If the effect of freshets is not uniform within the stream, patches of benthic assemblages of different successional age will be created. A continually changing array of insular patch types can then occur in the streambed. Presumably, the substrate of the benthic assemblage of any one patch will be a function of the time after the last freshet as well as the ambient physical and chemical environment of the stream. The behavior of the stream ecosystem will be the summation of behaviors of these temporally differentiated assemblages. Differences between streams of different chemical and physical environments therefore may be obscured by variation in the successional ages of assemblages within streams.

A third use of hierarchical perspective is in the analysis of systems' response to perturbations. With respect to the set of

Figure 30. The hypothesized stepwise increase of structural state in the experimental streams (a) and the predicted behavior of benthic assemblages in natural streams characterized by freshets in the winter season (b). The arrows indicate the occurrence of freshets.



superimposed systems that hierarchical organization represents, a given system in this hierarchy will exhibit one of three responses to environmental stress; sensitivity, insensitivity, or resistance (Laszlo, 1972). If a system is at a level of organization within the vertical range of systems decomposed by an environmental stress, the system is sensitive to the perturbation. After this decomposition, the range of sensitive systems will no longer exist in the ecosystem until an evolution of suprasystem occurs to recreate these levels of organization. Systems at levels of organization above the vertical range of sensitive systems, are insensitive to the perturbation. The disruption and recovery of systems at finer levels of spatio-temporal resolution will occur so rapidly, that the insensitive system will be "blind" to them (Patten, 1976). Systems at levels of organization below the vertical range of sensitive systems are resistant to the perturbation. The environmental stress does not decompose these systems, and from this resistant level of organization will evolve the higher level organization decomposed by the perturbation.

A perturbing force can be considered to be within and outside of an ecosystem, depending on the level of interest. A perturbation such as the simulated freshet at the Kalama Springs experimental streams is a devastating external force to the benthic system, yet regular freshets are characteristic of the lotic ecosystem (Margalef, 1963). The stream ecosystem is either sensitive, in the former case, or insensitive, in the latter case, to the same force depending on the level of interest. The sensitivity of physical and biological structures to the same environment stresses may be a means of unifying the analysis of lotic systems. The periphyton, benthos, stream levels of organization are parallel to the micro-, meso-, and macroform organization of sand structures in streams developed by American (Jackson, 1975) and Soviet (Popov, 1964) hydrologists on the basis of common sensitivity to environmental stress.

Perturbation and evolution of organization are counteracting forces in the hierarchy of natural systems. In a constant environment, organization becomes increasingly more complex, thermodynamically

improbable, and adapted to the reoccurring forces in the environment. Conversely, perturbations decompose sensitive levels of evolved structure to levels in which internal cohesiveness of the system is resistant to the disruptive force. In frequently perturbed natural systems, the evolution and reduction of hierarchical structure is commonly observed and largely stationary (reoccurring in a similiar fashion).

In the Kalama Springs streams, a transition from a diatom to a Zygnema dominated benthic assemblage occurred in all riffles. Riffles with environments of greater resource for primary production (higher light intensity, longer photoperiod, higher nitrate concentration) had greater algal biomass and export before the evolution of the benthic and stream systems than riffles of less resource. Differences in taxonomic structure attributable to differences in the physical and chemical environment were largely overshadowed by temporal fluctuations of algae and fauna. Similiar patterns of successional change associated with the benthic assemblages in natural streams is hypothesized. High light intensity and nitrate concentration may result in relatively high production of algal and faunal biomass in these streams. If freshets in natural streams occur at a frequency to prevent evolution of the stream system, streams of greater resource for primary production will produce greater amounts of algal and faunal biomass. If freshets occur at a magnitude that does not disrupt the benthic system, the difference in productive resources will be observed in faunal drift.

The observations in the experimental streams emphasize the problem of interpretation of events in a lotic ecosystem. The organization of the autotrophic system is dynamic, and the system organization changes in a short period of time. The effect of high light intensity or nitrate concentration may be observed as algal biomass and/or export, as faunal biomass and/or export, or not at all. The problem is that the lotic system has interactive components, not all of which occur at the same spatio-temporal frequency. Use of the hierarchical perspective is one means to interpret this ecosystem. Determination of hierarchical organization within this ecosystem, or any ecosystem, may be useful prerequisite to subsequent anaylses.

BIBLIOGRAPHY

- Allen, T. F. H. and J. F. Koonce. 1973. Multivariate approaches to algal stratagems and tactics in systems analysis of phytoplankton. *Ecol.* 54: 1234-1245.
- Ball, R. C. and T. G. Bahr. 1975. Intensive survey: Red Cedar River, Michigan. p. 431-460. IN: B. A. Whitton (ed.) *River Ecology*. Blackwell Scientific Publications. Oxford.
- von Bertalanffy, L. 1968. *General Systems Theory*. George Braziller, Inc. New York. 295 pp.
- Bisson, P. A., R. B. Herrmann, and R. N. Thut. 1975. Trout production in fertilizer nitrogen enriched experimental streams - interim report No. 3. Weyerhaeuser Company, Longview, Washington. 62 pp.
- Blum, J. L. 1954. Two winter diatom communities of Michigan streams. *Pap. Mich. Acad. Sci., Arts, Lett.* 39: 3-7.
- _____. 1956. The ecology of river algae. *Bot. Rev.* 22: 291-341.
- _____. 1957. An ecological study of the algae of the Saline River, Michigan. *Hydrobiol.* 9: 361-402.
- _____. 1960. Algal populations in flowing waters. p. 24-41. IN: C. A. Tryon, Jr. and R. T. Hartman (eds.) *The Ecology of Algae*. University of Pittsburg Press. Pittsburgh.
- Brock, T. D. 1967. Relationship between standing crop and primary productivity along a hot spring thermal gradient. *Ecol.* 48: 566-571.
- _____ and M. L. Brock. 1967. Recovery of a hot spring community from a catastrophe. *J. Phycol.* 5: 75-77.
- Brown, H. B. 1908. Algal periodicity in certain ponds and streams. *Bull. Torrey Bot. Club* 35: 223-248.
- Brown, T. E. and F. T. Richardson. 1968. The effects of growth environment of the physiology of algae: light intensity. *J. Phycol.* 4: 38-54.
- Budde, H. 1930. Die Algenflora der Ruhr. *Arch. Hydrobiol.* 21: 559-648.
- Butcher, R. W. 1932. Studies in the ecology of rivers. II. The microflora of rivers with special reference to the algae on the river-bed. *Ann. Bot.* 46: 318-361.
- _____. 1946. Studies in the ecology of rivers. VI. Algal growth in certain highly calcareous streams. *J. Ecol.* 33: 268-283.
- _____. 1947. Studies in the ecology of rivers. VII. The algae of organically enriched water. *J. Ecol.* 35: 186-191.
- _____. 1949. Problems of distribution of sessile algae in running water. *Verh. Int. Ver. Theoret. Ang. Lim.* 10: 98-103.

- Castenholz, R. W. 1961. The effect of grazing on marine littoral diatom populations. *Ecol.* 42: 783-794.
- Clements, F. E. 1916. Plant succession: an analysis of the development of vegetation. Carnegie Inst. Wash. Publ. 242 pp.
- Collins, N. C., R. Mitchell, and R. G. Wiegert. 1976. Functional analysis of a thermal spring ecosystem with an evaluation of the role of consumers. *Ecol.* 57: 1221-1232.
- Cooke, G. D. 1967. The pattern of autotrophic succession in laboratory microcosms. *Bioscience* 1967: 717-721.
- Cooke, W. B. 1956. Colonization of artificial bare areas by microorganisms. *Bot. Rev.* 22: 613-638.
- Cooley, W. W. and P. R. Lohnes. 1971. Multivariate Data Analysis. John Wiley and Sons, Inc. Canada. 365 pp.
- Cummins, K. W. 1974. Structure and function of the stream ecosystem. *Bioscience* 24: 631-641.
- Dickman, M. 1973. Changes in periphytic algae following bicarbonate additions to a small stream. *J. Fish. Res. Bd. Can.* 30: 1882-1884.
- Douglas, B. 1958. The ecology of the attached diatoms and other algae in a stony stream. *J. Ecol.* 46: 295-322.
- Duffer, W. R. and T. C. Dorris. 1966. Primary production in a southern Great Plains stream. *Limnol. Oceanogr.* 11: 143-151.
- Eddy, S. 1925. Fresh water algal succession. *Trans. Am. Microsc. Soc.* 44: 138-147.
- _____. 1934. A study of fresh-water plankton communities. Ill. Biol. Monogr. 12: 1-93.
- Eichenberger, E. and K. Wuhrmann. 1975. Growth and photosynthesis during the formation of a benthic algal community. *Verh. Int. Ver. Limnol.* 19: 2035-2042.
- Fjedingstad, E. 1964. Pollution of streams estimated by benthic phytomicro-organisms. *Int. Rev. Ges. Hydrobiol.* 49: 63-131.
- Fraleigh, P. C. and R. G. Wiegert. 1975. A model explaining successional change in standing crop of thermal blue-green algae. *Ecol.* 56: 656-664.
- Gasse, F. 1971. Organisation ultrastructurale des colonies de quelques Diatomees pennees araphidees, revelee par le microscope electronique a balayage. *C. R. Acad. Sci. Paris* 272: 3169-3171.
- Grzenda, A. R. and M. L. Brehmer. 1960. A quantitative method for the collection and measurement of stream periphyton. *Limnol. Oceanogr.* 5: 190-194.
- Hansmann, E. W., C. B. Lane, and J. D. Hall. 1971. A direct method for measuring benthic primary production in streams. *Limnol. Oceanogr.* 16: 822-836.

- Hustedt, F. 1937. Systematische und Okologische Untersuchungen über die Diatomeenflora von Java, Bali, und Samatra. Arch. Hydrobiol., Supplement- Band 15: 131-177.
- Hynes, H. B. N. 1970. The Ecology of Running Waters. Liverpool University Press. England. 555 pp.
- Jackson, R. G., II. 1975. Hierarchical attributes and a unifying model of bed forms composed of cohesionless material and produced by shearing flow. Geol. Soc. Am. Bull. 86: 1523-1533.
- Jones, J. G. 1975. Heterotrophic micro-organisms and their activity. p. 141-154. IN: B. A. Whitton (ed.) River Ecology. Blackwell Scientific Publications. Oxford.
- Kevern, N. R., J. L. Wilhm, and G. M. Van Dyne. 1966. Use of artificial substrata to estimate the productivity of periphyton. Limnol. Oceanogr. 11: 499-502.
- Klir, G. J. 1969. An Approach to General Systems Theory. Van Nostrand Reinhold Company. New York. 323 pp.
- Kobayasi, H. 1961. Productivity in sessile algal community of a Japanese mountain river. Bot. Mag. Tokyo 74: 331-341.
- Kofoed, C. A. 1903. The plankton of the Illinois River, 1894-1899. Bull. Ill. State Lab. Nat. Hist. 6: 95-629.
- Kolbe, R. W. 1927. Zur Okologie, Morphologie, and Systemtik der Brackwasser-Diatomeen. Pflanzenforschung (Jena) 7: 1-146.
- Kolkwitz, R. 1964. Zur Okologie der Saprobien. Rund. Deuts. Bot. Ger. 1964: 10-64.
- Kuhn, T. S. 1970. The Structure of Scientific Revolutions. University of Chicago Press. Chicago. 210 pp.
- Lackey, J. B. 1938. Flora and fauna of acid mine waters. Public Health Reports, Washington 53: 1399-1507.
- Laszlo, E. 1972. Introduction to Systems Philosophy. Harper and Row, Publishers. New York. 328 pp.
- Likens, G. E., F. H. Bormann, N. M. Johnson, and R. S. Pierce. 1967. The calcium, magnesium, potassium, and sodium budgets for a small forested ecosystem. Ecol. 48: 722-785.
- Lindeman, R. L. 1942. The trophic dynamic aspect of ecology. Ecol. 23: 399-418.
- Major, J. 1974. Kinds and rates of changes in vegetation and chronofunctions. p. 27-53. IN: R. Knapp (ed.) Handbook of Vegetation Science. VIII. Vegetation Dynamics. Dr. W. Junk Publishers. The Hague.
- Margalef, R. 1960. Ideas for a synthetic approach to the ecology of running waters. Int. Rev. Hydrobiol. 45: 133-153.

- Margalef, R. 1963. On certain unifying principles in ecology. *Am. Nat.* 97: 357-374.
- _____. 1968. *Perspectives in Ecological Theory*. University of Chicago Press. 111 pp.
- McConnell, W. J. and W. F. Sigler. 1959. Chlorophyll and productivity in a mountain river. *Limnol. Oceanogr.* 4: 335-351.
- McIntire, C. D. 1966. Some factors affecting respiration of periphyton communities in lotic environments. *Ecol.* 47: 918-930.
- _____. 1968. Structural characteristics of benthic algal communities in laboratory streams. *Ecol.* 49: 520-537.
- _____. 1973. Periphyton dynamics in laboratory streams: a simulation model and its implications. *Ecol. Monogr.* 43: 399-420.
- _____. 1975. Periphyton assemblages in laboratory streams. p. 403-430 IN: B. A. Whitton (ed.) *River Ecology*. Blackwell Scientific Publications. Oxford.
- _____ and J. A. Colby. 1978. A hierarchical model of lotic Ecosystems. *Ecol. Monogr.* (in press).
- _____, R. L. Garrison, H. K. Phinney, and C. E. Warren. 1964. Primary production in laboratory streams. *Limnol. Oceanogr.* 9: 92-102.
- _____ and W. S. Overton. 1971. Distributional patterns in assemblages of attached diatoms from Yaquina Estuary, Oregon. *Ecol.* 52: 728-777.
- McMahon, R. F., R. D. Hunter, and W. D. Russell-Hunter. 1974. Variation in aufwuchs in six freshwater habitats in terms of carbon biomass and of carbon:nitrogen ratio. *Hydrobiol.* 45: 391-404.
- Minckley, W. L. 1963. The ecology of a spring stream, Doe Run, Meade County, Kentucky. *Wild. Monogr.* 11: 1-124.
- Niessen, H. 1956. Okologische Untersuchungen uber die Diatomeen und Desmidiaceen des Murnauer Moores. *Arch. Hydrobiol.* 51: 281-375.
- O'Brian, W. J. and F. DeNoyelles. 1974. Relationship between nutrient concentration, phytoplankton density, and zooplankton density in nutrient enriched experimental ponds. *Hydrobiol.* 44: 105-121.
- Odum, E. P. 1960. Organic production and turnover in old field succession. *Ecol.* 41: 43-39.
- _____. 1969. The strategy of ecosystem development. *Science* 164: 262-270.
- Odum, H. T. 1957. Trophic structure and productivity of Silver Springs, Florida. *Ecol. Monogr.* 27: 55-112.
- _____ and C. M. Hoskin. 1957. Metabolism of a laboratory stream microcosms. *Inst. Mar. Sci.* IV:116-133.

- Odum, H. T. and E. C. Odum. 1976. Energy Basis for Man and Nature. McGraw-Hill Book Company. New York. 296 pp.
- Olson, F. C. 1950. Quantitative estimates of filamentous algae. Trans. Am. Microsc. Soc. 69: 272-279.
- Overton, W. S. 1975. The ecosystem modeling approach in the Coniferous Forest Biome. p. 117-138. IN: B. C. Patten (ed.) Systems Analysis and Simulation in Ecology. Academic Press. New York
- _____. 1977. A strategy of model construction. p. 50-73. IN: C. A. S. Hall and J. W. Day, Jr. (eds.) Ecosystem Modeling in Theory and Practice: An Introduction with Case Histories. John Wiley and Sons, Publishers. New York.
- Paine, R. T. 1966. Food web complexity and species diversity. Am. Nat. 100: 65-75.
- _____. 1976. Size-limited predation: an observational and experimental approach with the Mytilus-Pisaster interaction. Ecol. 57: 858-873.
- Patrick, R., J. Cairns, and S. S. Roback. 1967. An ecosystematic study of the fauna and flora of the Savannah River. Proc. Acad. Nat. Sci. Philadelphia. 118: 109-407.
- Patten, B. C. 1975. Ecosystem linearization: an evolutionary design problem. Am. Nat. 109: 529-539.
- Parsons, T. R. and M. Takahashi. 1973. Biological Oceanographic Processes. Pergamon Press. Oxford. 332 pp.
- Pearsall, W. H. 1923. A theory of diatom periodicity. J. Ecol. 11: 165-183.
- Picken, L. E. R. 1936. Mechanical factors in the distribution of a blue-green alga, Rivularia haematites. New. Phytol. 34: 211-228.
- Popov, I. V. 1964. Hydromorphological principles of the theory of channel processes and their use in hydrotechnical planning. Soviet. Hydrol. 1964: 188-195.
- Porter, K. G. 1977. The plant-animal interface in freshwater ecosystems. Am. Scientist. 65: 159-170.
- Sherman, B. J. and H. K. Phinney. 1971. Benthic algal communities of the Metolius River. J. Phycol. 7: 269-273.
- Siegfreid, C. A. and A. W. Knight. 1977. The effects of washout in a Sierra Foothill stream. Am. Midl. Nat. 98:200-207.
- Simon, H. A. 1962. The architecture of complexity. Proc. Am. Phil. Soc. 106: 63-76.
- Strickland, J. D. H. and T. R. Parsons. 1972. A Practical Handbook of Seawater Analysis. Bull. Fish.Res. Bd. Canada. No. 167. 310 pp.

- Szczepanski, A. and W. Szczepanski. 1966. Primary production and its dependence on the quantity of periphyton. *Bull L'Acad. Polonaise Sci. Cl. II*, 14: 45-50.
- Teal, J. M. 1957. Community metabolism in a temperate cold spring. *Ecol. Monogr.* 27: 283-302.
- Thut, R. N. and R. B. Hermann. 1969. Studies of the Weyerhaeuser experimental streams - interim report No. 2. Weyerhaeuser Company, Longview, Washinton. 86 pp.
- Vollenweider, R. A. (ed.) 1969. A Manual on Methods for Measuring Primary Production in Aquatic Environments, I B P Handbook No. 12. Blackwell Scientific Publications. Oxford. 213 pp.
- Warren, C. E. and G. E. Davis. 1971. Laboratory stream research: objectives, possibilities, and constraints. *Ann. Rev. Ecol. Syst.* 2: 111-144.
- Waters, T. F. 1961 a. Notes on the chlorophyll method of estimating the photosynthetic capacity of stream periphyton. *Limnol. Oceanogr.* 6: 486-488.
- _____. 1961 b. Standing crop and drift of stream bottom organisms. *Ecol.* 42: 532-537.
- Webster, J. R., J. B. Waide, and B. C. Patten. 1975. Nutrient recycling and the stability of ecosystems. p. 1-27. IN: F. G. Howell, J. B. Gentry, and M. H. Smith (eds.) *Mineral Cycling in Southeastern Ecosystems*. ERDA Symposium Series (Conf-740513). Washington.
- Wetzel, R. G. 1975. Primary production. p. 230-247. IN: B. A. Whitton (ed.) *River Ecology*. Blackwell Scientific Publications. Oxford.
- White, C. and W. S. Overton. 1974. Users manual for the FLEX2 and FLEX3 model processors. Bull. 15, Forest Research Laboratory. Oregon State University, Corvallis, Oregon.
- Whitford, L. A. 1956. The communities of algae in the springs and spring streams of Florida. *Ecol.* 37: 433-442.
- _____. and G. J. Schumacker. 1964. Effect of current on respiration and mineral uptake in Spirogyra and Oedogonium. *Ecol.* 45: 168-170.
- Whitton, B. A. 1975. Algae. p. 81-105. IN: B. A. Whitton (ed.) *River Ecology*. Blackwell Scientific Publications. Oxford.
- Wilhm, J. F. 1975. Biological indicators of pollution. p. 375-402. IN: B. A. Whitton (ed.) *River Ecology*. Blackwell Scientific Publications. Oxford.
- Wood, E. D., F. A. J. Armstrong, and F. A. Richards. 1967. Determination of nitrate in sea water by cadmium-copper reduction to nitrate. *J. Mar. Biol. Assn. U. K.* 47: 23.

Wright, J. C. and I. K. Mills. 1967. Productivity studies on the Madison River, Yellowstone National Park. *Limnol. Oceanogr.* 12: 568-577.